

Melanin-based plumage coloration and flight displays in plovers and allies

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Plovers and their allies exhibit an impressive diversity of melanin-based plumage patterns ranging from non-melanized to completely melanized species. We use phylogenetic comparative methods to test whether melanization has evolved in relation to sexual selection for attracting mates, to selection for signalling territory defence, or to natural selection for camouflage. First, according to sexual-selection theory, melanized plumage has evolved to amplify the courtship displays of males. As predicted by this hypothesis, we found that males with aerial displays had more melanized plumage than males of ground-displaying species. In addition, sexual dimorphism in melanization was greater in species with display flights than in species with ground displays. Second, melanization may have evolved through social interactions to signal competitive ability in territory defence. We did not find evidence for this hypothesis, since breeding density was unrelated to the melanization of either sex. Finally, melanized plumage may camouflage the incubating parent. The latter hypothesis was not supported, since melanization was unrelated either to the darkness of nest substrate or the extent of vegetation cover. Taken together, our results are most consistent with the sexual-selection hypothesis, and suggest that melanized plumage has evolved to enhance the aerial displays of male plovers.

Keywords: sexual selection; display behaviour; melanin; plumage colour; shorebirds

1. INTRODUCTION

Melanin-based coloration is a common type of plumage ornamentation in birds (Andersson 1994; Savalli 1995). The adaptive significance of interspecific variability in melanin-based plumage coloration, however, is less well understood than that of other plumage traits (Jawor & Breitwisch 2003). For instance, sexual dimorphism both in carotenoid-based and structural coloration relates to sexual selection (Owens & Hartley 1998; Badyaev & Hill 2000), whereas the extent of white plumage was found to be associated with flocking behaviour (Brooke 1998; Beauchamp & Heeb 2001). However, previous studies of avian coloration concluded that sexual selection is unlikely to have a strong effect on melanin-based plumage dimorphism (Owens & Hartley 1998; Badyaev & Hill 2000), and no study has specifically addressed the evolution of melanin-based plumage colours using phylogenetic methods.

Plovers and their allies (Charadriida, plovers henceforward) are ideal species in which to study melanin-based coloration because they exhibit striking interspecific variability in the extent of their black plumage, ranging from fully black to completely white. Plovers develop black patches typically on their head and breast when they moult into nuptial plumage during migration to the breeding grounds (del Hoyo *et al.* 1996). This suggests that the function of melanin-based coloration is related to breeding. The aim of our study was to test three major hypotheses to explain the interspecific variation in melanin-based coloration of plovers.

First, the sexual-selection hypothesis predicts that melanin-based colours of males influence their ability to

compete for females, or mate choice by females. For example, females prefer males with more extensive black patches in golden plover (*Pluvialis apricaria*) and dotterel (*Eudromias morinellus*) (Edwards 1982; Owens *et al.* 1994). The sexual displays of males may be amplified by the breast bands (Graul 1973). For instance, avocets and thick-knees display on the ground, whereas others such as many lapwings and oystercatchers perform aerial displays (Jehl & Murray 1986; Figuerola 1999; Székely *et al.* 2000). As black plumage is particularly conspicuous against the sky (Walsberg 1982), we expect more extensive black plumage in males and greater melanin-based sexual dimorphism in species with display flights than in ground-displaying species.

Second, melanin-based colours may signal competitive ability of birds in territory defence. For example, male golden plovers appeared to use the amount of black on their underparts as a status signal during competition for territories (Edwards 1982). The black head and breast markings of turnstones (*Arenaria interpres*) were involved in the recognition of neighbours, facilitating territory defence against unfamiliar individuals (Whitfield 1986). Social interactions are more frequent at high breeding densities than at low densities (Hötter 2000), thus the territory defence hypothesis predicts that species nesting at high densities should be more melanized than species nesting at low densities.

Third, melanin-based coloration may have evolved by natural selection to camouflage the incubating parent. Plovers nest on the ground and the incubating parents are exposed to visually searching predators. The camouflage hypothesis makes two predictions. First, plovers that nest on dark substrate should be more extensively melanized than species nesting on light substrate. Second, plovers that nest in closed habitats should have more melanized

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plumage than species nesting in open habitats, since melanized plumage camouflages the incubating parent in closed habitats by providing lower contrast with the environment (Bennett & Owens 2002).

Here, we use phylogenetic comparative methods to test the predictions of these three hypotheses. We focus on melanin-based plumage on the head and breast of plovers, because in most species the black plumage is concentrated on the frontal part of the body. The sexual-selection hypothesis predicts changes in male melanization across species and differences between male and female melanization (i.e. melanin dichromatism), thus we use both of these response variables. In tests of both territory defence and camouflage hypotheses we use male and female melanization as response variables, since both sexes defend territories and incubate the clutch in most plovers (Liker & Székely 1997; Reynolds & Székely 1997).

2. MATERIAL AND METHODS

(a) *Measuring melanization*

We measured the extent of melanization in the breeding plumage of plovers using colour plates of three reference books (Hayman *et al.* 1986; Marchant & Higgins 1993; del Hoyo *et al.* 1996). We digitized illustrations that showed the birds in lateral view. Then we measured the size of black plumage patches on the frontal body region (i.e. head, neck and breast as bordered by the lower edge of the wing and a vertical line drawn from the base of the leg; see electronic Appendix A available on The Royal Society's Publications Web site) using Scion Image software (Scion Corporation 2000). We restricted our measurements to the head and breast of plovers, since these areas appeared to be highly variable in melanization across species. Although melanin pigments produce a range of colours, we specifically measured black, which is produced by eumelanins (Jawor & Breitwisch 2003). If several black patches were found, we calculated the sum of the area of these patches. Melanization was expressed as the proportion of black area relative to the total area of the frontal body (see electronic Appendix B). For sexually monomorphic species, i.e. species in which the plumage was not illustrated separately for males and females, both sexes were given the same proportion of melanization. Non-iridescent black plumage usually does not reflect ultraviolet light (Bennett *et al.* 1994). To test the latter assumption we measured the reflectance of black breast badges of Kentish plover *Charadrius alexandrinus*, and found that these badges did not reflect ultraviolet light (T. Székely and I. C. Cuthill, unpublished data; methods as in Cuthill *et al.* 1999).

We tested the reliability of our measurements in several ways. First, we estimated the repeatability (Lessells & Boag 1987) by measuring melanization in 15 randomly selected species twice by one observer, and once by another observer. Repeatability was high both within an observer ($r = 0.999$, $F_{14,15} = 15\,553$, $p < 0.001$) and between the observers ($r = 0.967$, $F_{14,15} = 32.143$, $p < 0.001$). Second, melanization was measured for the same species using pictures from two different books, one figure each from Hayman *et al.* (1986) and del Hoyo *et al.* (1996). These two measures were highly correlated (Pearson's correlation, $r = 0.888$, $n = 15$ species, $p < 0.001$). Third, we photographed taxidermy mounted specimens of 11 species, and estimated the melanization on these photographs. These measures were highly correlated with the measurements that we took from colour plates ($r = 0.938$, $n = 11$ species, $p < 0.001$),

suggesting that book illustrations represent consistently and accurately the amount of melanized plumage. Fourth, we compared our measurements taken from lateral view with estimates of frontal view. We measured melanization from frontal view using pictures from Hayman *et al.* (1986) for those species for which the illustrations were available from both perspectives. The measurements were highly correlated between lateral and frontal views ($r = 0.948$, $n = 9$ species, $p < 0.001$). Finally, we measured the melanization from both the lateral and frontal view using photographs of taxidermy mounted birds, and these measurements were also highly correlated ($r = 0.825$, $n = 11$ species, $p = 0.002$).

Sexual dimorphism in melanization (dichromatism henceforward) was calculated as $\log(\text{male melanization} + 1) - \log(\text{female melanization} + 1)$.

(b) *Display behaviour, breeding density and nest site*

We collected data on male sexual displays, breeding density, substrate colour and vegetation cover of nest sites using published sources (Hayman *et al.* 1986; Marchant & Higgins 1993; del Hoyo *et al.* 1996; Perrins 1998; Székely *et al.* 2000; see electronic Appendix B). Male sexual displays were scored by Székely *et al.* (2000) as (i) ground display; (ii) non-acrobatic aerial display; and (iii) acrobatic aerial display.

We followed this scoring for an additional set of species (see electronic Appendix B). The dotterel was excluded from the analyses of display behaviour because the displays are performed by females. We did not investigate the potential influence of mating system, since nearly all Charadriida are socially monogamous (see Székely *et al.* 2000).

Breeding density was scored as (i) solitary; (ii) solitary or in small, loose colonies (often described as semicolonial); (iii) typically loose colonies; (iv) large, loose or dense colonies; and (v) typically large and dense colonies.

We tested the reliability of the breeding density scores for a subset of species by comparing these scores with mean breeding densities (nests per hectare; data from Perrins 1998). These two measures of density were strongly correlated (Spearman's rank correlation, $r_s = 0.838$, $n = 15$ species, $p < 0.001$).

We extracted verbal descriptions of nest sites from the literature, and then these descriptions were randomized and scored blindly by three observers. Substrate colour of the nest site was scored as (i) uniform light substrate, such as sand; (ii) mainly light surface with some dark patches, such as dry mud; (iii) approximately equal proportion of light and dark patches, for instance shingle; (iv) mainly dark surface with some light patches, for instance tundra; and (v) uniform dark substrate, e.g. dark rocks.

Vegetation cover of the nest site was scored as (i) bare ground; (ii) very short and scarce vegetation; (iii) short grass cover; (iv) continuous grass cover with shrubs and some denser vegetation; and (v) covered nest sites such as forests and cavities.

Both substrate colour ($r = 0.714$, $F_{83,168} = 3.316$, $p < 0.001$) and vegetation cover ($r = 0.886$, $F_{82,166} = 6.506$, $p < 0.001$) were highly repeatable between the observers. We used the modal values of the three scores in the analyses (see electronic Appendix B).

(c) *Phylogenetic analyses*

We used a recent unpublished supertree of shorebirds in phylogenetic comparative analyses (G. Thomas and T. Székely, unpublished data). This supertree included 101 species of

plovers (parvorder Charadriiida excluding Laroidea; Monroe & Sibley 1993). Sample sizes were different between statistical analyses, since behavioural and ecological data were unavailable for some species.

We controlled for the phylogenetic relationships among species in two ways. First, we calculated phylogenetically independent contrasts (Felsenstein 1985) as implemented by the CAIC program v. 2.6 (Purvis & Rambaut 1995). Melanization was $\log(x + 1)$ transformed and male display, breeding density, substrate colour and vegetation cover were $\log(x)$ transformed before the calculation of phylogenetically independent contrasts. Unit branch lengths were used, since most branch lengths were not known. Melanin dichromatism was computed as contrasts in male melanization minus contrasts in female melanization. We tested the relationships between the contrasts in melanization (or dichromatism, dependent variable) and the contrasts in male display, breeding density, substrate colour and vegetation cover (independent variables) by least-square linear regressions forced through the origin (Harvey & Pagel 1991; Garland *et al.* 1992). Felsenstein's method assumes that the absolute values of the contrasts are independent of their standard deviations (Garland *et al.* 1992). This assumption was met by all variables. Another assumption of the method is that the evolution of continuous characters follows Brownian motion, thus the absolute values of the contrasts should be independent of the estimated nodal values for each trait. Although this assumption was not held in some analyses of melanization, Diaz-Uriarte & Garland (1996) concluded that independent contrasts are robust to violations of this assumption.

Second, we conducted matched-pair comparisons between closely related taxon pairs using Wilcoxon matched-pairs signed-ranks tests (Harvey & Pagel 1991; Székely *et al.* 2000; see electronic Appendix C for taxon pairs). When several species were available for a taxon pair, we calculated the mean of their melanization. The matched-pair method is restricted to the terminal nodes of the phylogeny, and thus it makes less stringent statistical assumptions than the independent contrasts method. Note that the results of our contrasts analyses are fully consistent with the results of matched-pair analyses. In addition, our conclusions remained unchanged when we used each species as an independent datum (results not shown).

Body size correlates with many life-history and ecological traits (Harvey & Pagel 1991; Reynolds & Székely 1997), thus it may confound the relationships between melanization, breeding behaviour and ecology. We tested the effect of body size on melanization using phylogenetically independent contrasts, and found that body size, as measured by wing length (data from Hayman *et al.* 1986) was not related to melanization either in males ($r = 0.090$, $F_{1,90} = 0.743$, $p = 0.391$) or in females ($r = 0.113$, $F_{1,92} = 1.196$, $p = 0.277$). Body mass and tarsus length were also unrelated to melanization (results not given). All statistical tests are two-tailed.

3. RESULTS

(a) Sexual selection

Melanization was more extensive in males (0.152 median; 0.035–0.390 lower and upper quartile, respectively) than in females (0.107; 0.011–0.356; Wilcoxon matched-pairs signed-ranks test, $z = 3.939$, $n = 101$ species, $p < 0.0005$). Evolutionary increases in male melanization corresponded to changes toward aerial displays (table 1; figure 1a). The relationship between male melan-

ization and display behaviour remained statistically significant when we excluded species using acrobatic displays, and thus restricted the analysis to species exhibiting ground displays and non-acrobatic aerial displays (table 1). However, the relationship was no longer significant when ground-displaying species were excluded (table 1). The latter results suggest that the key difference in regard to melanization is between aerial- versus ground-displaying species. These results were consistent with the results of matched-pair comparisons, since males were more melanized in aerial species than in ground-displaying taxa ($z = 2.395$, $n = 10$ taxon pairs, $p = 0.017$; figure 2a).

Analyses of melanin dichromatism provided similar results to that of male melanization, since evolutionary increases in melanin dichromatism were correlated with changes toward aerial displays (table 1; figure 1b). The relationship between dichromatism and display behaviour also remained statistically significant when we excluded acrobatic species (table 1), whereas it was no longer significant when ground-displaying species were excluded (table 1). Consistently with these results, aerial-displaying species were more dichromatic than ground-displaying ones in matched-pair analysis ($z = 1.992$, $n = 10$ taxon pairs, $p = 0.046$; figure 2b).

(b) Territorial defence

Breeding density was unrelated to the melanization of both sexes using phylogenetically independent contrasts (males: $r = 0.161$, $F_{1,71} = 1.884$, $p = 0.174$; females: $r = 0.177$, $F_{1,71} = 2.286$, $p = 0.135$). These results were consistent with the matched-pair analyses (males: $z = -0.322$, $n = 21$, $p = 0.748$; females: $z = -0.241$, $n = 21$, $p = 0.809$).

The territory defence hypothesis also predicts that melanin dichromatism should be greater in species with male-only nest defence than in species with biparental nest defence. We did not find support for this prediction either, since species with male-only defence (0.000 median; 0.000–0.037 lower and upper quartile, respectively) did not differ in melanin dichromatism from species with biparental defence (0.000; 0.000–0.019; Wilcoxon matched-pairs signed-ranks test, $z = 0.000$, $n = 6$ species pairs, $p = 1.000$).

(c) Camouflage

We did not find any evidence that melanization relates to the characteristics of the nest site. First, substrate colour was not associated with melanization using phylogenetically independent contrasts (males: $r = 0.007$, $F_{1,93} = 0.005$, $p = 0.944$; females: $r = 0.056$, $F_{1,93} = 0.295$, $p = 0.588$). Second, vegetation cover was unrelated to melanization using independent contrasts (males: $r = 0.048$, $F_{1,93} = 0.218$, $p = 0.641$; females: $r = 0.032$, $F_{1,93} = 0.096$, $p = 0.758$). These results were fully consistent with that of matched-pair comparisons, since melanization was not different between closely related taxa with different substrate colour (males: $z = 0.710$, $n = 34$, $p = 0.478$; females: $z = 1.018$, $n = 34$, $p = 0.309$) and vegetation cover (males: $z = 0.920$, $n = 34$, $p = 0.357$; females: $z = 0.767$, $n = 34$, $p = 0.443$).

The number of black patches on the head and breast may be a better indicator of crypsis than the total area of black. To test this proposition, we investigated whether

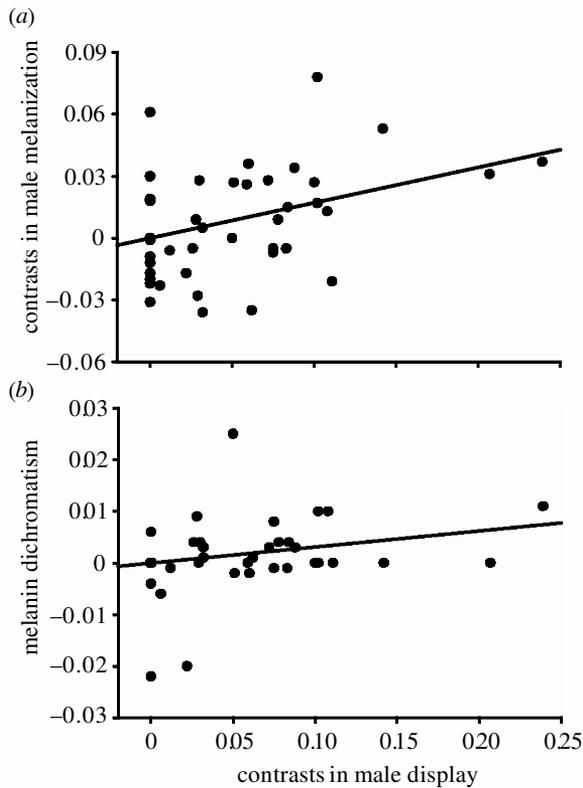


Figure 1. Relationships between phylogenetically independent contrasts in display behaviour of male plovers and (a) contrasts in male melanization ($r = 0.483$, $F_{1,43} = 13.107$, $p = 0.001$), (b) melanin dichromatism, i.e. contrasts in male melanization minus contrasts in female melanization ($r = 0.331$, $F_{1,43} = 5.282$, $p = 0.027$). Regression lines are forced through the origin.

the number of patches is related to the characteristics of the nest site using phylogenetically independent contrasts. These analyses confirmed that the number of black patches was unrelated to substrate colour and vegetation cover both in males and females (results not shown).

(d) *Multivariate analyses*

Finally, we investigated the effects of sexual selection, territorial defence and camouflage using stepwise multiple regression analyses of phylogenetically independent contrasts (table 2). The initial models included male display, breeding density, substrate colour and vegetation cover as explanatory variables. The final models confirmed that display behaviour of males explained a significant proportion of variation in both male melanization and melanin dichromatism (table 2), whereas breeding density, substrate colour and vegetation cover all remained non-significant (table 2).

4. DISCUSSION

Our analyses provided three key results. First, we found that interspecific differences in both male plumage melanization and melanin dichromatism were related to differences in display behaviour. Agility in male displays relates to mating success in shorebirds (Grønstøl 1996; Blomqvist *et al.* 1997), thus display behaviour appears to be a sexually selected trait. Second, the relationship between melanization and display was specifically owing to differences

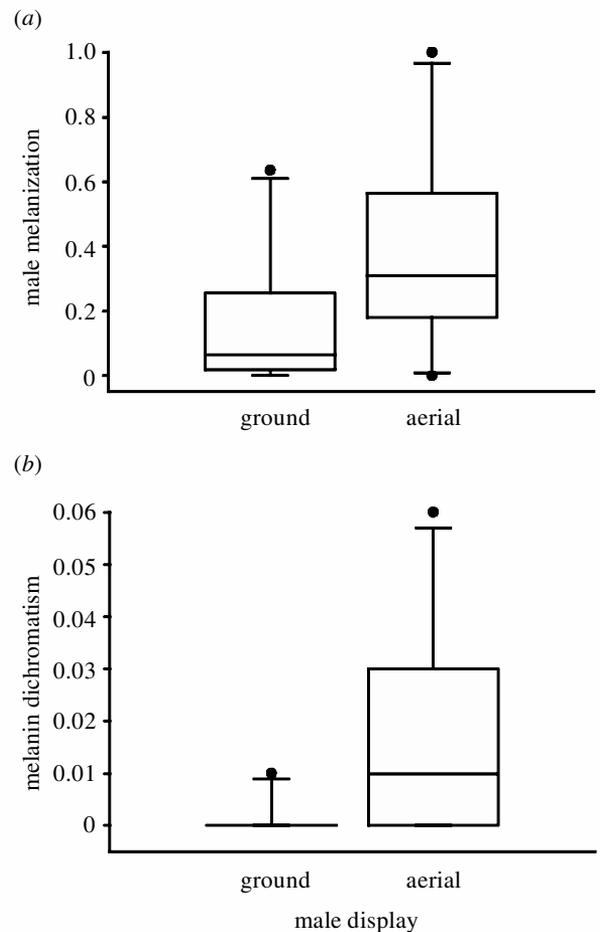


Figure 2. Matched-pairs comparisons of (a) male melanization and (b) melanin dichromatism between ground-displaying and aerial-displaying plovers (Wilcoxon matched-pairs signed-ranks tests, male melanization: $z = 2.395$, $n = 10$ taxon pairs, $p = 0.017$; melanin dichromatism: $z = 1.992$, $n = 10$ taxon pairs, $p = 0.046$). Box plots show the medians (horizontal bars), 25th and 75th percentiles (top and bottom of boxes, respectively), 10th and 90th percentiles (top and bottom whiskers, respectively) and outliers (dots).

between aerial- and ground-displaying species. Third, we did not detect any relationship between proxies of territory defence or camouflage, and plumage melanization. To our knowledge, this is the first avian study that demonstrates a relationship between interspecific variation in melanin-based coloration in males, dichromatism and sexual selection as manifested by display behaviour.

Our results are consistent with the sexual-selection hypothesis, and suggest that the frontal melanization of male plovers has evolved to enhance aerial displays. When plovers display in the air, the sky provides a contrasting background that makes the displaying bird conspicuous (Walsberg 1982). Recently, the interspecific variation in light environments has been shown to influence plumage colour (Marchetti 1993; Endler & Thery 1996; McNaught & Owens 2002), suggesting that plumage coloration is often adapted to provide maximum contrast against the background of the displays. Species displaying in closed habitats tend to exhibit longer-wavelength colours such as orange and red (McNaught & Owens 2002) or more numerous bright patches than species breeding in open habitats (Marchetti 1993). Thus, plovers with

Table 1. Melanization of males and melanin dichromatism in relation to male displays in plovers. (Least-square linear regressions of independent contrasts were forced through the origin.)

male display	male melanization			melanin dichromatism		
	<i>r</i>	<i>F</i>	<i>p</i>	<i>r</i>	<i>F</i>	<i>p</i>
all species ^a	0.483	13.107	0.001	0.331	5.282	0.027
acrobatic species excluded ^b	0.383	5.672	0.023	0.336	4.19	0.049
ground-displaying species excluded ^c	0.211	1.170	0.290	0.098	0.243	0.626

^a d.f. = 1, 43.

^b d.f. = 1, 33.

^c d.f. = 1, 25.

Table 2. Multivariate analyses of melanization of males and melanin dichromatism in plovers. (Stepwise multiple regressions of independent contrasts were forced through the origin.)

final model	male melanization ^a		melanin dichromatism ^b	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
male display	0.411	0.009	0.361	0.024
variables excluded from the final model				
breeding density	-0.163	0.330	-0.066	0.695
substrate colour	-0.133	0.426	-0.061	0.717
vegetation cover	-0.160	0.338	0.028	0.866

^a Final model $F_{1,37} = 7.510$.

^b Final model $F_{1,37} = 5.549$.

ground displays may benefit from exhibiting small black stripes and patches on their light frontal plumage (e.g. many *Charadrius* plovers), whereas extensive black plumage appears to be advantageous for species with display flights (e.g. *Pluvialis* plovers, oystercatchers). Note that in two aerial-displaying species, golden plover and dotterel, melanization relates to mating success (Edwards 1982; Owens *et al.* 1994). An association between aerial displays and frontal melanization was also observed in bustards *Otididae*, although this relationship has not been corroborated by phylogenetic comparative analyses (Dale 1992). Thus, it appears that the relationship between aerial displays and increased frontal melanization may not only occur in shorebirds.

Székely *et al.* (2000) showed that the extent and direction of sexual size dimorphism are related to the evolution of male displays in shorebirds, so that sexual selection favours small males with acrobatic display flights. Here, we demonstrate that, in a similar set of species and the same type of display behaviour, sexual selection acts differently on another trait: melanin-based coloration. Unlike in the study of Székely *et al.* (2000) on sexual size dimorphism, in our study the key difference was between aerial- and ground-displaying taxa, and not between acrobatic and non-acrobatic species. Melanization increases the resistance of feathers to abrasion and increases the strength of feathers (Bonser 1995). Thus, species that display in the air may gain a twofold benefit from melanized feathers: first, increased conspicuousness against the light background, and second, enhanced resistance to fracture that may be particularly important in aerial displays.

We did not find evidence for the territorial defence hypothesis that higher breeding density selects for more melanized plumage. Furthermore, sexual dimorphism in territory defence was not associated with increased melanin dichromatism. Thus, selection for social signalling during territorial encounters does not seem to explain the interspecific variation in melanin-based coloration among plovers. This result is unexpected given that melanin-based ornaments appear to function as social signals of aggression and/or hormonal status in several birds (Jawor & Breitwisch 2003). Although there may be selection for black badges of status or individual markings in shorebirds (Edwards 1982; Whitfield 1986), this may not necessarily result in increased melanization at high breeding densities. In short-distance territorial signalling, conspicuousness may be less important than the individual variability of the signals, which could be maintained by small markings as well as by larger ones.

The predictions of the camouflage hypothesis were not supported by our analyses: neither substrate colour nor vegetation cover was associated with plumage melanization. However, we did not investigate the plumage patterns of the back and wings, which may also be important in camouflaging the incubating birds. The effect of substrate pattern was studied in *Charadrius* and closely related plovers by Graul (1973), who conjectured that black breast bands function as disruptive coloration in species nesting on discontinuous substrates such as dark and light substrate patches. The hypothesis of Graul (1973) remains to be tested, although we note that Graul's scores for discontinuous substrate correlate with our substrate

colour scores (Spearman's rank correlation, $r_s = -0.505$, $n = 29$ species, $p = 0.005$), and the number of black plumage patches was unrelated to substrate colour in our analyses. There are three important distinctions between the seminal study of Graul (1973) and ours. Graul (1973) was specifically concerned with breast bands, whereas we used the proportion of melanized plumage. Second, Graul (1973) scored species according to substrate discontinuity whereas our scores refer to substrate colour. Finally, the study of Graul (1973) did not control for phylogenetic relationships.

Bearing these caveats in mind, we note that our results are based on a larger set of species and a larger range of melanization than that of Graul (1973). Thus, we suggest that even if breast bands may serve disruptive functions in some *Charadrius* plovers, melanin-based coloration is unlikely to be strongly selected for camouflage in Charadriidae. The relatively open habitats occupied by plovers allow early detection of predators, thus plovers may rather escape from their nest early than stay and rely on crypsis. However, further tests of the hypothesis of Graul (1973) are still warranted by looking at the number and width of breast bands.

Taken together, we found that the extent of plumage melanization is related to display behaviour in plovers. We suggest that melanized plumage enhances sexual signals under specific ambient light conditions. We found no evidence that selection for territorial defence and cryptic plumage of incubating parents influence the melanin-based coloration in plovers and allies.

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