Seasonal colour change by moult or by the abrasion of feather tips: a comparative study

JÁCINT TÖKÖLYI[1]*, VERONIKA BÓKONY[2] and ZOLTÁN BARTA[1]

[1]*Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen, Egyetem tér 1, H-4010 Debrecen, Hungary*
[2]*Department of Limnology, University of Pannonia, Pf. 158, H-8210 Vezprém, Hungary*

Many birds undergo seasonal changes in plumage coloration by prebreeding moult, abrasion of cryptic feather tips, or both. Seasonal dichromatism is thought to result from optimizing coloration to the conflicting demands of different life-cycle periods, sexual selection for conspicuousness being substantial during the mating season, whereas selection for camouflage and for social signals may act in all seasons. Furthermore, energetic and time demands may constrain the extent of moult, thereby limiting colour change. We investigated the relative importance of several factors in shaping this variation in a songbird clade using phylogenetic comparative methods. We found that prebreeding moult relates most strongly to breeding onset and winter diet, demonstrating that both time and food availability constrain feather replacement. Feather abrasion was best predicted by winter flocking behaviour, and secondarily by open habitats, implying that exposure to predators and the simultaneous need for social signalling may favour the expression of partially obscured ornaments in the non-breeding season. The combined occurrence of prebreeding moult and feather abrasion was associated with the polygynous mating system, suggesting that species under strong sexual selection may employ both strategies of colour change to ensure the full expression of breeding coloration. © 2008 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2008, **94**, 711–721.

ADDITIONAL KEYWORDS: moult constraints – plumage coloration – predation risk – sexual selection – social signalling.

INTRODUCTION

Bird species show a striking diversity in the extent to which their coloration varies seasonally. For example, great tits (*Parus major*) remain in their colourful plumage throughout the year, with only faint fading to their yellow breast (Figuerola & Senar, 2005), whereas white-tailed ptarmigan (*Lagopus leucurus*) change gradually from a fully white to a finely patterned grey-brown appearance between winter and summer (Poole, 2005). Seasonal dichromatism may arise by at least two different means: (1) the partial or complete replacement of feathers during a second, prebreeding moult, or (2) the abrasion of differently coloured, usually dull feather tips, exposing the underlying, usually bright feather parts. Prebreeding

moult is common in many avian taxa ranging from waterfowl through shorebirds to passerines, whereas colour change by feather abrasion appears to be a characteristic of songbirds (Møller & Erritzøe, 1992; Figuerola & Senar, 2005). In some songbird families the two strategies occur concurrently, and closely related species often differ in the strategies adopted (Perrins, 1998; Poole, 2005). The reasons for this interesting interspecific variability are, however, scantly studied (Hamilton & Barth, 1962; Froehlich, Rohwer & Stutchbury, 2004).

The coloration of a bird's plumage is supposed to simultaneously fulfill several roles during the bird's life, often being under the influence of opposing selection pressures. For instance, plumage colour might serve as camouflage against predators, and at the same time as advertisement towards female and male conspecifics (Andersson, 1994). The relative

*Corresponding author. E-mail: jtokolyi@vocs.unideb.hu

importance of these roles, however, is assumed to change over the annual cycle of birds: display is usually important mainly during the breeding season, whereas defense against predators may be crucial all year round. A possible adaptation to this temporal variation in costs and benefits of plumage coloration can be the shift between breeding and non-breeding plumages. However, such shifts may not be achievable without any constraint, as moult (one of the major devices behind plumage change) is costly in terms of energy, time, compromised thermoregulation, and compromised flight ability (e.g. Murphy & King, 1991; Swaddle & Witter, 1997; Sanz *et al.*, 2004). The relative significance of these costs and benefits in shaping the interspecific variation in the extent and type of seasonal colour change are poorly understood.

In this study we investigate the environmental and life-history correlates of both means of seasonal dichromatism in a diverse set of songbird species, the finches and their allies, in which both the prebreeding moult and the abrasion of dull feather tips is common (Perrins, 1998; Poole, 2005). We use phylogenetic comparative methods to examine whether the covariation between seasonal colour-change strategies and various environmental and life-history factors fit the frameworks set by four main hypotheses.

First, the need to present sexually attractive plumages in the breeding season may select for seasonal colour change by either strategy. On the one hand, if the expression of feather ornaments is highest in freshly moulted feathers, as plumage coloration may gradually deteriorate after moult (McGraw & Hill, 2004; Figuerola & Senar, 2005; Delhey *et al.*, 2006), then it should be advantageous to moult just before the breeding season. On the other hand, feathers may be structurally adapted to uncover colourful ornaments by the abrasion of dull feather tips (Willoughby, Murphy & Gorton, 2002). As the benefits of bright, colourful plumage are expected to increase with the intensity of sexual selection, we expect prebreeding moult and/or abrasion to be more common in species with more intense sexual selection, i.e. with higher frequency of polygyny or stronger sperm competition, than in species with less intense sexual selection.

Second, predation may select for cryptic winter plumage, and thus seasonal colour change may be more common in species that are more exposed to predators. As the rate of predation on adults of small passerines is greater in open habitats than in closed habitats (Götmark & Post, 1996; Møller, Nielsen & Garamszegi, 2006), we predict more prevalent prebreeding moult and/or abrasion among species living in open habitats than in species occupying closed habitats.

Third, Hamilton & Barth (1962) suggested that dull non-breeding plumages reduce the levels of aggression between flock members in gregarious species. Accordingly, they demonstrated the frequent occurrence of seasonal dichromatism in species forming nomadic winter flocks in two taxa with prebreeding moult (Hamilton & Barth, 1962). However, more recent research showed that colourful ornaments may be adaptive in flocking species by serving as status signals (Rohwer, 1975; Senar, 1999). The ability to signal differences in dominance or aggressiveness is beneficial, as participants may assess the expected outcome of fights, and may thus avoid the costs of physical interaction (Rohwer, 1975). Furthermore, coverable badges may be used as status signals that are exposed only when birds are highly motivated to fight for resources (Hansen & Rohwer, 1986). Colour badges that are partially covered by cryptic feather tips may function in such a manner in certain species (Veiga, 1996). Thus, the hypothesis based on social signalling predicts that seasonal colour change, especially by abrasion, should be more common in species with, rather than without, nonbreeding flocking behaviour.

Finally, the costs of moult may constrain the incidence or extent of colour change (Rohwer & Butcher, 1988). Previous comparative studies found that migratory status or migration distance is related to the timing and frequency of moults per year (Svensson & Hedenström, 1999; Figuerola & Jovani, 2001). These findings suggest that migration, or the factors associated with it, may also be important for explaining interspecific variation in prebreeding moult. Resident species, for example, might trade-off prebreeding moult for early breeding because of time constraints (Froehlich *et al.*, 2004). Winter diet was also shown to influence moult: the availability of protein-rich food (insects) appears to be crucial for the nutritional demands of feather replacement (Froehlich *et al.*, 2004). However, diet and migratory status may covary, as food availability during the winter is likely to depend on geographical latitude. Furthermore, migratory status may influence moult by reasons other than the aforementioned constraints of time and food, e.g. the need for high-quality feathers during long-distance migration may necessitate a premigratory moult. Therefore, the effects of nutritional and time constraints, and other migration-related costs, on prebreeding moult remain entangled. Here, we examine the relative roles of breeding onset, winter diet, and migration distance in shaping the interspecific variation of prebreeding moult. We predict that prebreeding moult is more common and/or more extensive in species that begin breeding later, rely on more insectivorous diets, and migrate longer distances, than in species with the opposite

characteristics. We also predict that the effect of winter diet on prebreeding moult depends on the latitude of the nonbreeding habitat, because the availability of plant material during winter probably increases towards southern latitudes, whereas insects are scarce in tropical wintering habitats in the dry season that often coincidences with the time of prebreeding moult (Froehlich *et al.*, 2004). Finally, we also tested whether migratory status is related to colour change by abrasion, as abrading feathers may decrease flight efficiency (Schreiber *et al.*, 2006), and thus abrading feather tips might be selected against in long-distance migrants.

MATERIAL AND METHODS

PREBREEDING MOULT AND FEATHER ABRASION

We collected data on the extent of prebreeding moult and the occurrence of abrading feather tips for European and North American species of the songbird clade of Fringillidae, Passeridae, and Motacillidae (Barker *et al.*, 2004) from Perrins (1998) and Poole (2005). We included species for which data were available on at least one of the two colour-change strategies (*N* = 150, Appendix S1).

We used two measures of prebreeding moult. First, we recorded whether a prebreeding moult occurred in a species, including species with partial prebreeding moults. Second, we scored the extent of the prebreeding moult on a 1–6 scale as follows: (1) no feathers; (2) head; (3) head and throat; (4) head, throat, and breast; (5) head, throat, breast, and some other feathers; and (6) all body feathers moulted. We scored only adult males because first-year birds and females often moult differently, and one can expect the effect of sexual selection to be strongest on males. Only moult that occurs in late winter and/or early spring was considered, in order to distinguish the true prebreeding moult from the delayed postbreeding moult that occurs in some species (Svensson & Hedenström, 1999).

The occurrence of feather abrasion was recorded for a species if plumage descriptions noted that coloration changes from autumn to spring through abrasion or wear. Care was taken to discriminate feather abrasion from fading, a third alternative way for colour to change, resulting from the degradation of feather pigments (Blanco *et al.*, 2005). Data were insufficient to score the extent of abrasion on the body.

Prebreeding moult and abrasion are not mutually exclusive, as several species in our dataset use both strategies of seasonal colour change (*N* = 26, 17.3% of our species). To explain the simultaneous occurrence of the two strategies, we scored species as 1 if they displayed both prebreeding moult and abrasion (the 'combined strategy'), and 0 if they displayed only one or no colour-change strategy.

Although Froehlich *et al.* (2004) reported that prebreeding moult was not associated with colour change in some species, this observation was based on human vision, which may miss some of the variation in coloration that is visible to birds (Cuthill, 2006). Similarly, they considered only sexually dichromatic species, but this categorization again was made by humans, and may not be relevant to birds (Eaton, 2005). Here, we did not attempt to judge the extent of seasonal or sexual dichromatism. Also, we did not score whether males were 'dull' or 'bright' in winter (as done by Froehlich *et al.*, 2004), because these terms strongly depend on the light environment, the background habitat, and the visual system of the receiver (Butcher & Rohwer, 1989; Endler, 1990; Cuthill, 2006). We applied a single criterion of human vision to both prebreeding moult and feather abrasion: we scored each as 'present' only when the given species appeared seasonally dichromatic to the human eye. However, our conclusions remained unchanged when we included a few additional species that have prebreeding moult, but no seasonal changes visible to humans (results not reported). Also note that because plumage colour may gradually deteriorate after moulting (McGraw & Hill, 2004; Figuerola & Senar, 2005; Delhey & Senar, 2006), the prebreeding moult that replaces faded feathers with fresh ones might change coloration, even if the moulted plumage pattern remains the same.

CORRELATES OF COLOUR CHANGE

All data were collected from Perrins (1998) and Poole (2005), if not stated otherwise. We used two well-established measures of the strength of sexual selection. First, the social mating system was scored as monogamous (with less than 5% of the males being polygynous), weakly polygynous (5–15% of males), or strongly polygynous (> 15% of males) (Pitcher, Dunn & Whittingham, 2005). Second, as a measure of sperm competition, we obtained data on testis size (corrected for body mass) from Pitcher *et al.* (2005). We scored winter habitat as open (e.g. desert and grassland) or closed (e.g. forest and woodland; McNaught & Owens 2002); winter flocking behaviour as solitary (territorial or living in pairs) or gregarious (living in flocks); and late winter diet as granivorous, insectivorous, or mixed (vegetable matter and insects in approximately equal proportion) based on descriptions in the references. The onset of breeding is given in units of 10-day intervals, where interval 1 is the first third of January and interval 22 is the first third of August. Species were then assigned to these categories based on the approximate start of the egg-

laying period, assessed from annual cycle diagrams. Using distribution maps, we classified species as residents if their summer and winter distributions overlapped completely, and otherwise they were classified as migrants. Following Svensson & Hedenström (1999), migration distances were estimated from the summer and winter distribution midpoint values of longitudes and latitudes, according to the formula described by Imboden & Imboden (1972).

PHYLOGENETIC ANALYSES

To investigate the relationships between colour-change strategies and potential explanatory variables, we employed two comparative approaches. First, for binary dependent variables (occurrence of prebreeding moult, abrasion, or combined strategy), we used Pagel's (1994) discrete variable method to test whether the evolution of two categorical variables was correlated. This method is based on Markov chain models, and uses likelihood ratio tests to compare the fit of two alternative models: one assuming independent evolution of the two variables (e.g. habitat and abrasion), and another assuming that the rate of change in one variable depends on the state of the other variable (Maddison & Maddison, 2006). Statistical significance was estimated by running Monte Carlo tests using simulated data, with P-values based on 5000 simulation replicates. As this method cannot handle variables with more than two categories, we converted testis size into a dichotomous variable by assigning 0 to species with smaller than expected (negative) residual testis size, and 1 to species with greater than expected (positive) residual testis size. Breeding onset was converted to 0 when < 13 (the median interval, i.e. the first third of May) and to 1 when ≥ 13. Variables with three categories (mating system and diet) were dichotomized in two different ways, by merging the middle category with either the first or the last category.

Second, we used the extent of prebreeding moult as a continuous dependent variable in phylogenetic generalized least squares (PGLS) models (Pagel, 1997, 1999). This approach controls for the non-independence among species by incorporating a matrix of the covariances among species, based on their phylogenetic relationships (Martins & Hansen, 1997; Pagel, 1997, 1999), and also estimates the importance of phylogenetic corrections in the analyses (Freckleton, Harvey & Pagel, 2002). In all analyses, we set the degree of phylogenetic dependence (λ) to the most appropriate degree evaluated for each model by likelihood ratio statistics. Note however that our conclusions remained unchanged when we repeated the analyses by setting λ to 0, which means species-level analyses with no phylogenetic control, and by

setting λ to 1, which is principally equivalent to the method of independent contrasts (Felsenstein, 1985; Martins & Hansen, 1997). Mating system, flocking behaviour, habitat, and diet entered the models as fixed factors, whereas testis size, breeding onset, and migration distance were included as covariates.

To investigate the relative importance of predictor variables in explaining the occurrence and extent of colour-change strategies, we applied two kinds of multivariate analyses. First, for each dependent variable we built full models, including all possible predictors that were tested in bivariate analyses, and then we obtained the final models using stepwise backward elimination of nonsignificant effects, removing the predictor with the largest P-value in each step (Grafen & Hails, 2002). Second, we also evaluated our results using a different analytical approach, the information-theoretic model-comparison (Burnham & Anderson, 2002). Here, the initial models for each dependent variable included only those predictors that had a significant effect in the previous bivariate analyses, or, in the case of the combined strategy, those selected by the multivariate analyses of either prebreeding moult or abrasion. Note that including all predictors was not possible because the number of candidate models would have been too large, even exceeding the sample size. We then compared all possible submodels using the second-order Akaike's information criterion, corrected for small sample size (AIC_c). We evaluated the candidate models by their relative Akaike weights (ω_i), and the predictors by the sums of their Akaike weights across all models that contain the given predictor (Σ). In this approach, inference is based not on a single final model, but on an entire set of plausible models, and thereby it can estimate the importance of predictors with greater robustness and precision.

For the extent of prebreeding moult, we used PGLS models for the multivariate analyses. As the PGLS approach cannot handle binary variables as dependents, for the abrasion and combined strategy we performed the multivariate analyses, using generalized linear models with binomial error and logit link function (Dalgaard, 2002), without controlling for phylogeny. We expect that the results of the latter analyses are not seriously biased by the phylogenetic relatedness of the species, because the estimated value of λ was relatively small in most PGLS models (i.e. not significantly different from zero in all multivariate analyses, and in 74% of bivariate models, thereby indicating a low overall degree of phylogenetic dependence in our data. Note that we obtained similar results for the combined strategy when we repeated the multimodel comparison controlling for phylogeny in PGLS models, with the extent of prebreeding moult as a dependent variable, and including

Table 1. Bivariate relationships of the occurrence of a prebreeding moult, feather abrasion, and their combined strategy with ecological and life-history variables, in Pagel's maximum likelihood estimations controlled for phylogeny

	Prebreeding moult			Feather abrasion			Combined strategy		
	χ^2	P	N	χ^2	P	N	χ^2	P	N
Mating system*	11.62	0.022	129	4.48	0.421	131	12.26	0.004	119
Mating system†	9.36	0.033	129	7.96	0.030	131	10.74	0.003	119
Testis size	1.66	0.681	106	1.88	0.584	105	1.56	0.570	96
Habitat	0.19	0.089	123	8.06	0.026	129	3.70	0.194	115
Flocking behaviour	3.80	0.616	127	13.38	0.012	132	3.26	0.507	118
Migratory status	17.56	< 0.001	134	7.68	0.101	140	4.32	0.273	124
Breeding onset	17.94	0.001	127				6.06	0.177	117
Diet‡	5.39	0.058	89				1.66	0.273	85
Diet§	6.57	0.182	89				1.50	0.591	85

P-values are based on 5000 simulations. Mating system and winter diet were split into dichotomous dummy variables.
*Monogamy vs. weak or strong polygyny.
†Monogamy or weak polygyny vs. strong polygyny.
‡Granivory vs. mixed diet or insectivory.
§Granivory or mixed diet vs. insectivory.

abrasion into each candidate model as a fixed factor (results not shown).

We compiled a composite tree to represent phylogenetic relationships among species, using recent molecular data (Appendix S2). We set the branch lengths to be proportional to the number of nodes, i.e. gradual branch lengths, according to Nee's method (Maddison & Maddison, 2006). Pagel's analyses were conducted using the Mesquite software (Maddison & Maddison, 2006). For all other analyses we used the R statistical computing environment (R Development Core Team, 2003), with additional unpublished functions written by R. Freckleton (University of Sheffield) for the PGLS procedure. Sample sizes differ across tests because data are incomplete for some species. All statistical tests are two-tailed with a 95% confidence level. As the phylogenetic methods applied here do not allow the graphical presentation of phylogenetically corrected data, we present figures based on raw species data.

RESULTS

PREBREEDING MOULT

A prebreeding moult was more common in polygynous than in monogamous species (Table 1). Neither the occurrence nor the extent of prebreeding moult was related to testis size, habitat, or flocking behaviour (Tables 1, 2). Prebreeding moult occurred more frequently in migratory than in resident species (Table 1), and species that migrate longer distances showed more extensive prebreeding moults (Table 2). Species with more extensive prebreeding moults had

Table 2. Bivariate relationships of the extent of the prebreeding moult with ecological and life-history variables, in phylogenetic generalized least squares (PGLS) models

	λ	F (df)	P
Mating system	0.21	1.67 (2,128)	0.193
Testis size	0.26	0.86 (1,105)	0.357
Habitat	0.11	0.78 (1,122)	0.378
Flocking behaviour	0.15	0.41 (1,125)	0.524
Migration distance	< 0.001	28.26 (1,129)	< 0.001
Breeding onset	0.07	20.78 (1,126)	< 0.001
Diet	< 0.001	6.11 (2,88)	0.003

The degree of phylogenetic dependence (λ) was set to the most appropriate value in each model, evaluated by likelihood ratio statistics.

a later breeding onset (Fig. 1; Table 2) and a more insectivorous diet (Fig. 2A; Table 2). The effect of breeding onset on moult extent remained significant when we controlled for breeding latitude and migration distance (breeding onset, $F_{1,122} = 26.35$, $P < 0.001$; breeding latitude, $F_{1,122} = 0.07$, $P = 0.794$; migration, $F_{1,122} = 8.71$, $P = 0.004$). Winter latitude was significantly related both to the extent of prebreeding moult ($F_{1,129} = 22.74$, $P < 0.001$, $\lambda = 0.11$) and to winter diet ($F_{2,95} = 24.23$, $P < 0.001$, $\lambda = 0.01$). The interaction of diet and winter latitude had a significant effect on the extent of prebreeding moult ($F_{3,87} = 7.98, P < 0.001$, $\lambda < 0.001$): towards more southern latitudes, granivorous species moulted more, whereas species with mixed diets moulted less extensively (Fig. 2B). After
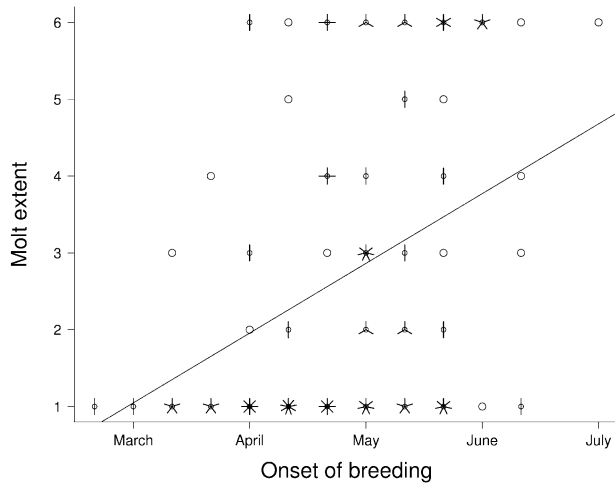
Figure 1. Species breeding later have a more extensive prebreeding moult. The number of spikes indicates the number of overlapping data points (species).

controlling for migration distance, the extent of the prebreeding moult was still significantly related to both breeding onset (migration, $F_{1,120} = 8.14$, $P = 0.005$; breeding onset, $F_{1,120} = 26.42$, $P < 0.001$) and the interaction of diet and winter latitude (migration, $F_{1,83} = 23.62$, $P < 0.001$; diet*latitude, $F_{3,83} = 3.42$, $P = 0.021$). In the stepwise model selection, the final model contained breeding onset ($F_{1,79} = 11.58$, $P = 0.001$), the interaction of diet and winter latitude ($F_{3,79} = 8.12$, $P < 0.001$), and mating system ($F_{2,79} = 4.76$, $P = 0.011$). The best model in the AIC$_c$-based model comparison was identical to the final model of the stepwise procedure (Table 3). Based on multimodel inference, breeding onset ($\Sigma = 0.83$), diet*latitude ($\Sigma = 0.83$), and mating system ($\Sigma = 0.81$) appeared similarly important in explaining the extent of the prebreeding moult, whereas migration distance had a smaller impact ($\Sigma = 0.58$).

FEATHER ABRASION

Colour change by feather abrasion was associated with strongly polygynous mating systems (Table 1), flocking behaviour (Fig. 3A; Table 1), and open habitats (Fig. 3B; Table 1), whereas it was unrelated to testis size and migratory status (Table 1). In the stepwise model selection, the final model contained flocking behaviour only ($\chi^2_1 = 11.75$, $P = 0.001$, $N = 132$). The result of the AIC$_c$-based model comparison was fully consistent with the latter result: the best model contained flocking behaviour only, and the first three best models consistently included flocking behaviour (Table 4). Habitat ($\Sigma = 0.47$) was more important in explaining the occurrence of abrasion
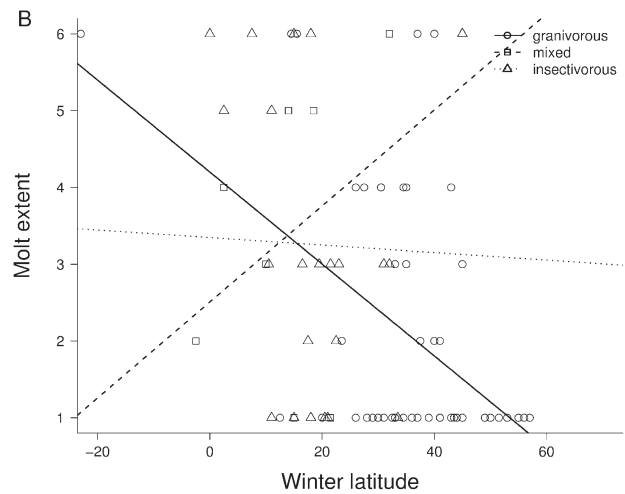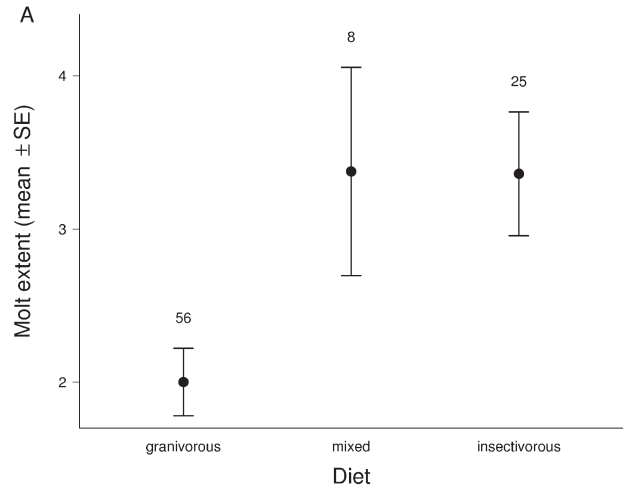

Figure 2. The prebreeding moult is more extensive in species with more insectivorous diets (A), and increases with the latitude of wintering grounds, whereas granivorous species moult less extensively towards greater (i.e. more northern) latitudes (B). Numbers above the error bars denote the corresponding sample sizes.

than was the mating system ($\Sigma = 0.29$), and both had a smaller impact than did flocking behaviour ($\Sigma = 0.79$).

THE COMBINED STRATEGY

The combined occurrence of prebreeding moult and abrasion was more common in the more polygynous species (Fig. 4; Table 1), whereas it was unrelated to all other predictors (Table 1). These results were qualitatively unchanged when we excluded species with no colour-change strategy from the analyses (results not shown). In the stepwise model selection, the final model contained mating system only ($\chi^2_2 = 9.85$, $P = 0.007$, $N = 120$). The result of the AIC$_c$-

Table 3. Comparison of multivariate phylogenetic generalized least squares (PGLS) models for the extent of the prebreeding moult

Predictors	k	AIC_c	Δ_i	ω_i
Breeding onset, diet*latitude, mating system	7	317.39	0.00	0.33
Breeding onset, diet*latitude, mating system, migration distance	8	317.66	0.27	0.29
Breeding onset, diet*latitude	5	320.30	2.92	0.08
Diet*latitude, mating system, migration distance	7	320.38	2.99	0.07
Breeding onset, mating system, migration distance	5	320.99	3.61	0.06
Mating system, migration distance	4	321.21	3.83	0.05
Breeding onset, diet*latitude, migration distance	6	321.76	4.37	0.04
Breeding onset, migration distance	3	321.89	4.51	0.04
Migration distance	2	322.56	5.18	0.03
Diet*latitude, migration distance	5	324.36	6.97	0.01
Diet*latitude, mating system	6	325.67	8.29	0.01
Diet*latitude	4	327.51	10.12	< 0.01
Breeding onset	2	328.53	11.14	< 0.01
Breeding onset, mating system	4	330.23	12.85	< 0.01
Mating system	3	338.34	20.95	< 0.01

Akaike's information criterion, corrected for small sample size (AIC_c), number of estimated parameters (k), AIC_c differences between the best model and each candidate model (Δ_i), and Akaike weights (ω_i) are given for each candidate model ($n = 82$ species). Models with $\Delta_I < 2$ are considered to have substantial support; ω_i is a relative estimate of the probability that a given model is actually the best model in the model set.

based model comparison was again fully consistent with the stepwise approach: the best model contained the mating system only, and the first four best models all consistently included mating system (Table 5). The sums of Akaike weights also supported the finding that the mating system was by far the most important predictor ($\Sigma = 0.94$) of the combined colour-change strategy, followed by the relatively small impacts of flocking behaviour ($\Sigma = 0.30$) and breeding
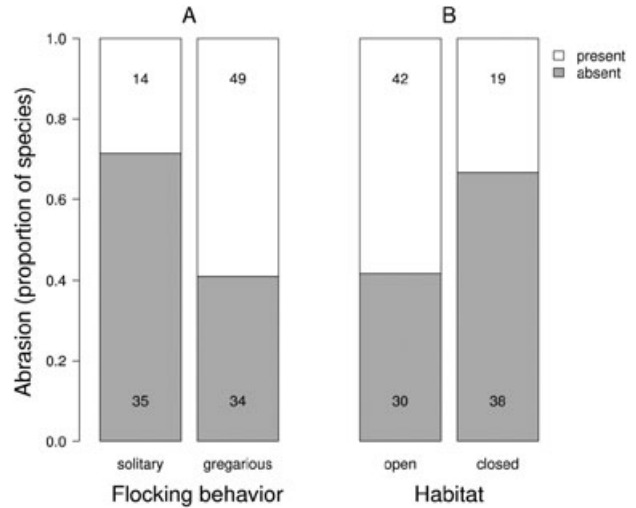

Figure 3. Feather abrasion is more common in species with winter-flocking behaviour (A) and open wintering habitats (B). Numbers on the bars denote sample sizes.

Table 4. Comparison of multivariate generalized linear models for the occurrence of feather abrasion ($N = 116$ species)

Predictors	k	AIC_c	Δ_i	ω_i
Flocking behaviour	2	156.62	0.00	0.35
Flocking behaviour, habitat	3	157.56	0.94	0.22
Flocking behaviour, mating system	4	158.29	1.67	0.15
Habitat	2	158.48	1.86	0.14
Flocking behaviour, mating system, habitat	5	159.89	3.27	0.07
Mating system, habitat	4	160.63	4.01	0.05
Mating system	3	162.22	5.60	0.02

See Table 3 for further explanation.

onset ($\Sigma = 0.25$), whereas diet*latitude was of minor importance ($\Sigma = 0.03$).

Bivariate analyses of the predictor variables revealed several interrelations among the predictors (Appendix S3). However, the variance inflation factor was < 2 in all of the multivariate models above, indicating that multicolinearity was not a problem in our analyses.

DISCUSSION

In this study we aimed to explore the environmental and life history covariates of the interspecific variation in the two main strategies of seasonal dichromatism. We obtained three key results. First, both the occurrence and the extent of the prebreeding moult was most strongly related to the onset of breeding and
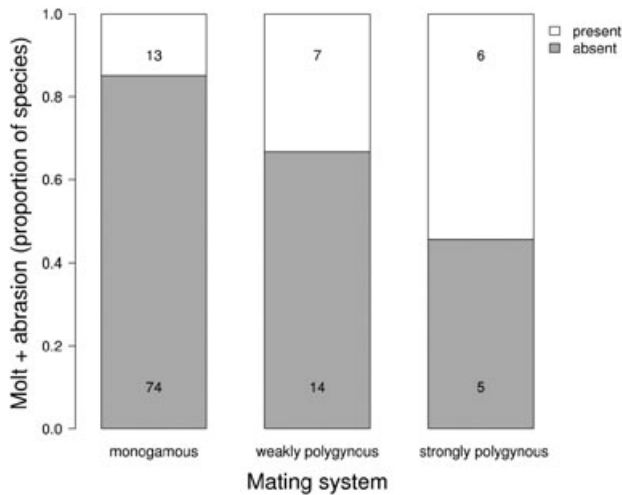
Figure 4. The combined colour-change strategy (i.e. both prebreeding moult and feather abrasion) is more common in species with a more polygynous social mating system. Numbers on the bars denote sample sizes.

Table 5. Comparison of multivariate generalized linear models for the combined occurrence of a prebreeding moult and feather abrasion ($N = 72$ species)

Predictors	k	AIC_c	Δ_i	ω_i
Mating system	3	75.81	0.00	0.50
Mating system, flocking behaviour	4	77.73	1.92	0.19
Breeding onset, mating system	4	78.06	2.24	0.16
Breeding onset, mating system, flocking behaviour	5	80.04	4.23	0.06
Flocking behaviour	2	81.59	5.78	0.03
Diet*latitude, mating system	6	82.71	6.90	0.02
Breeding onset	2	82.86	7.04	0.01
Breeding onset, flocking behaviour	3	83.77	7.95	0.01
Diet*latitude, mating system, flocking behaviour	7	84.55	8.73	0.01
Breeding onset, diet*latitude, mating system	7	85.17	9.35	0.00
Breeding onset, diet*latitude, mating system, flocking behaviour	8	87.08	11.27	0.00
Diet*latitude, flocking behaviour	5	87.15	11.34	0.00
Diet*latitude	4	87.17	11.36	0.00
Breeding onset, diet*latitude	5	89.45	13.64	0.00
Breeding onset, diet*latitude, flocking behaviour	6	89.53	13.72	0.00

See Table 3 for further explanation.

winter diet, that is, the factors that may constrain feather replacement because of time and energy costs. Second, colour change by abrading feather tips was best predicted by non-breeding flocking behaviour, indicating the role of selection for social signalling in determining the need and type of seasonal colour change. Finally, the combined occurrence of prebreeding moult and abrasion was more common in the more polygynous species, suggesting that species under strong sexual selection may use multiple strategies to acquire colourful breeding plumages. These results show that a complex set of selective forces and constraints, acting in different life-cycle periods, are necessary to explain the observed patterns of seasonal dichromatism among passerine birds, such as finches and sparrows.

Our results strongly support the theory that the costs of moulting may significantly constrain the evolution of the prebreeding moult. In line with the suggestions and findings of previous studies (Hamilton & Barth, 1962; Rohwer & Butcher, 1988; Froehlich *et al.*, 2004), we found that both the occurrence and the extent of the prebreeding moult is related to migration distance. The role of migration in shaping various moult strategies has been suggested by theoretical models and previous phylogenetic comparative studies alike (e.g. Holmgren & Hedenström, 1995; Svensson & Hedenström, 1999; Barta *et al.*, 2008), and this relationship is explained as an effect of natural selection that results in optimal timing of costly life-history events, such as breeding, migration, and moulting. Froehlich *et al.* (2004) proposed that the relation between migration and the prebreeding moult may reflect time constraints on resident species, which may be selected to begin breeding as early as possible, and hence have no time left to moult once more before breeding. Our results are consistent with this hypothesis, demonstrating that species with a later breeding onset moult more extensively in spring. Furthermore, we found that winter diet was a similarly important determinant of spring moult, suggesting that the nutritional demands of feather replacement may also be a significant constraint for the evolution of the prebreeding moult. The impact of different diet types varied with wintering latitude, implying that moulting is most constrained in granivorous northern winterers and omnivorous tropical winterers. This finding is different from the results of Froehlich *et al.* (2004), who found that the prebreeding moult was unrelated to diet in temperate winterers, although it was constrained in insectivorous Neotropical winterers by the scarce abundance of insects during moulting. However, their dataset was limited to species with complete (not partial) prebreeding moults, and included very few insectivorous species among temperate winterers. Based on a dataset with 67 tropical and 83 temperate

winterers, our results indicate that diet has an impact on the evolution of the prebreeding moult, even after accounting for the constraints of breeding onset and migration, challenging the previous assumption that partial prebreeding moults are unlikely to have significant energetic costs (Froehlich *et al.*, 2004). Finally, our study indicates that high levels of polygyny also select for a prebreeding moult. Thus, in addition to the nutritional and time constraints, the sexual-selection advantage conferred by freshly moulted breeding plumages also appear important in shaping the interspecific variation of the prebreeding moult.

Seasonal colour change by the abrasion of feather tips is not a complete alternative to the prebreeding moult, as the interspecific variation in the occurrence of abrasion appears to have its determinants unrelated to the prebreeding moult. Most importantly, abrasion is more common in flocking species than in those living solitarily in the non-breeding season. Additionally, abrasion is more frequent in open habitats than in closed habitats. Although the latter effect was less strongly supported than the effect of flocking behaviour, the second best model for abrasion contained both habitat and flocking behaviour (Table 4). These two lines of evidence suggest that predation risk in open wintering grounds may select for a less conspicuous non-breeding plumage, but in a way that some ornaments hidden by cryptic feather tips may still be expressed in flocking species. Such 'coverable badges' or 'remnants of breeding coloration' may serve as status signals in winter flocks of birds, as has been shown for a number of finch and sparrow species (Hansen & Rohwer, 1986; Senar, 1999), or may facilitate early pairing (McGraw, 2004). Furthermore, birds may be able to control the degree of abrasion of their feathers by preening, thereby adjusting the expression of their colour badges to the signalling needs presented by their social environment (Møller & Erritzøe, 1992; Veiga, 1996; González *et al.*, 2001). As habitat type is related to many ecological characteristics of the species, including almost all other predictors used in our study (Appendix S3), it is admittedly a rather weak proxy for predation pressure on adult birds. Therefore, we call for great caution when interpreting our findings on habitat type. Until more direct measures of predation pressure become available for the nonbreeding seasons, our results suggest that the importance of winter predation in determining seasonal colour change ranges from medium (for feather abrasion) to low (for the prebreeding moult). This finding is in line with the recent conclusion of Møller *et al.* (2006) that the risk of predation may be a consequence, rather than the determinant, of sexually selected displays in songbirds. Finally, although sexual selection in polygynous species favoured seasonal colour change by abrasion, according to our results, the occurrence of abrasion appeared more strongly influenced by selection for optimal winter coloration, i.e. for social signalling and camouflage.

Since feather abrasion as a strategy of seasonal dichromatism had been virtually unstudied by comparative approaches, our study is the first one to investigate this phenomenon in a phylogenetic context. However, there is still much to explore in this field. The apparent lack of costs associated with abrasion begs the question of why not all birds achieve seasonal colour change by abrasion, instead of by the demanding process of moulting. One explanation may be that the full exposure of ornamented plumage might be difficult in less abrasive habitats (Froehlich *et al.*, 2004). Our finding that abrasion is less common in species occupying closed habitats might support this idea, if feather wear is better facilitated in open habitats by airborne particles, contact with substrates, or solar radiation (Miller, 1961; Burtt, 1986). To our knowledge, these possibilities are completely unexplored.

Finally, we have also found that a number of species employ both a prebreeding moult and abrasion to change their appearance seasonally. For instance, both lazuli bunting (*Passerina amoena*) and Lapland bunting (*Calcarius lapponicus*) males change from a rather dull nonbreeding plumage to a spectacular breeding aspect mostly by abrading buffy feather tips, but before breeding they also renew some of their head and chin feathers by moulting. Our results show that this combined strategy is strongly associated with the polygynous mating system, implying that species under intensive sexual selection exhibit both more extensive prebreeding moults and more frequent abrasion. Polygynous species may be strongly selected to express highly ornamented breeding plumage, and thus they may benefit from combining moulting and abrasion if this enables a more extensive or more reliable colour change. For example, because of the costs of moulting, a bird with a partial prebreeding moult may increase the area of colourful plumage by additionally abrading some feathers that cannot be moulted. Alternatively, if abrasion is not complete, e.g. if the habitat is less abrasive or the birds cannot preen certain plumage areas (e.g. on the head) to enhance abrasion, then it may pay males to moult some feathers before breeding to ensure the expression of breeding colours. In polygynous species, the sexual-selection advantage of such multiple efforts for seasonal colour change seems to override the impact of both the costs of moulting and the selective forces acting on winter plumage colour.

To summarize, we have provided phylogenetic comparative evidence that in a diverse clade of finches and sparrows, the two strategies of seasonal dichromatism evolve in response to partially different selec-

tion pressures, as reflected by various life-history traits. We found that both nutritional and time constraints are important determinants of the prebreeding moult, which may still be selected for in strongly polygynous species. Abrasion of dull feather tips, a previously neglected component of seasonal colour change, may optimize the degree of ornamentation for the different life-cycle periods, as both camouflage and social signalling seem to favour limited expression of colour badges during winter, whereas intensive sexual selection in polygynous species may promote full exposure of breeding coloration.

REFERENCES

Andersson M. 1994. *Sexual selection*. Princeton, NJ: Princeton University Press.

Barker FK, Cibois A, Schikler P, Feinstein J, Cracraft J. 2004. Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences of the USA* **101:** 11040–11045.

Barta Z, Houston AI, McNamara JM, Welham RK, Hedenström A, Weber TP, Feró O. 2008. Optimal moult strategies in migratory birds. *Philosophical Transactions of the Royal Society of London, Series B* **363:** 211–230 (doi: 10.1098/rstb.2007.2136).

Blanco G, Frías O, Garrido-Fernández J, Hornero-Méndez D. 2005. Environmental-induced acquisition of nuptial plumage expression: a role of denaturation of feather carotenoproteins? *Proceedings of the Royal Society of London, Series B* **272:** 1893–1900.

Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer Verlag.

Burtt EH Jr. 1986. An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood warblers. *Ornithological Monographs* **38:** 1–126.

Butcher GS, Rohwer S. 1989. The evolution of conspicuous and distinctive coloration for communication in birds. *Current Ornithology* **6:** 51–107.

Cuthill IC. 2006. Color perception. In: Hill GE, McGraw KJ, eds. *Bird coloration. II. Function and evolution*. Cambridge: Harvard University Press, 3–40.

Dalgaard P. 2002. *Introductory statistics with R*. New York: Springer Verlag.

Delhey K, Peters A, Johnsen A, Kempenaers B. 2006. Seasonal changes in blue tit crown color: do they signal individual quality? *Behavioral Ecology* **17:** 790–798.

Eaton MD. 2005. Human vision fails to distinguish widespread sexual dichromatism among sexually 'monochromatic' birds. *Proceedings of the National Academy of Sciences of the USA* **102:** 10942–10946.

Endler JA. 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society* **41:** 315–352.

Felsenstein J. 1985. Phylogenies and the comparative method. *The American Naturalist* **125:** 1–15.

Figuerola J, Jovani R. 2001. Ecological correlates in the evolution of moult strategies in Western Palearctic passerines. *Evolutionary Ecology* **15:** 183–192.

Figuerola J, Senar JC. 2005. Seasonal changes in carotenoid- and melanin-based plumage coloration in the Great Tit *Parus major*. *Ibis* **147:** 797–802.

Freckleton RP, Harvey PH, Pagel M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist* **160:** 712–726.

Froehlich DR, Rohwer S, Stutchbury BJ. 2004. Prebreeding molt constraints versus winter territoriality. Is conspicuous winter coloration maladaptive? In: Greenberg R, Marra PP, eds. *Birds of two worlds: the ecology and evolution of migration*. Baltimore, MD: Johns Hopkins University Press, 321–355.

González G, Sorci G, Smith LC, de Lope F. 2001. Testosterone and sexual signaling in male house sparrows (Passer domesticus). *Behavioral Ecology and Sociobiology* **50:** 557–562.

Grafen A, Hails R. 2002. *Modern statistics for the life sciences*. New York: Oxford University Press.

Götmark F, Post P. 1996. Prey selection by sparrowhawks, Accipiter nisus: relative predation risk for breeding passerine birds in relation to their size, ecology and behaviour. *Philosophical Transactions of the Royal Society of London Series B* **351:** 1559–1577.

Hamilton TH, Barth RH. 1962. The biological significance of seasonal change in male plumage appearance in some New World migratory species. *The American Naturalist* **96:** 129–144.

Hansen AJ, Rohwer S. 1986. Coverable badges and resource defence in birds. *Animal Behaviour* **34:** 69–76.

Holmgren N, Hedenström A. 1995. The scheduling of molt in migratory birds. *Evolutionary Ecology* **9:** 354–368.

Imboden C, Imboden D. 1972. Formel für Orthodrome und Loxodrome bei der Berechnung von Richtung und Distanz zwischen Beringungs- und Wiederfundort. *Die Vogelwarte* **26:** 336–346.

Maddison WP, Maddison DR. 2006. Mesquite: a modular system for evolutionary analysis. Version 1.12. Available at http://mesquiteproject.org.

Martins EP, Hansen TF. 1997. Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist* **149:** 646–667.

McGraw KJ. 2004. Winter plumage coloration in male american goldfinches: do reduced ornaments serve signaling functions in the non-breeding season? *Ethology* **110:** 707–715.

McGraw KJ, Hill GE. 2004. Plumage color as a dynamic trait: carotenoid pigmentation of male house finches (*Carpodacus mexicanus*) fades during the breeding season. *Canadian Journal of Zoology* **82:** 734–738.

McNaught MK, Owens IPF. 2002. Interspecific variation in plumage colour among birds: species recognition or light environment? *Journal of Evolutionary Biology* **15:** 505–514.

Miller AH. 1961. Molt cycles in equatorial Andean Sparrows. *Condor* **63:** 143–161.

Murphy ME, King JR. 1991. Protein intake and the dynamics of the postnuptial molt in White-crowned Sparrows, *Zonotrichia leucophrys gambelii*. *Canadian Journal of Zoology* **69:** 2225–2229.

Møller AP, Erritzøe J. 1992. Acquisition of breeding coloration depends on badge size in male house sparrows *Passer domesticus*. *Behavioral Ecology and Sociobiology* **31:** 271–277.

Møller AP, Nielsen JT, Garamszegi LZ. 2006. Song post exposure, song features, and predation risk. *Behavioral Ecology* **17:** 155–163.

Pagel M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London Series B* **255:** 37–45.

Pagel M. 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta* **26:** 331–348.

Pagel M. 1999. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. *Systematic Biology* **48:** 612–622.

Perrins CM, ed. 1998. *The complete birds of the Western Palearctic on CD-ROM, version 1*. Oxford: Oxford University Press.

Pitcher TE, Dunn PO, Whittingham LA. 2005. Sperm competition and the evolution of testes size in birds. *Journal of Evolutionary Biology* **18:** 557–567.

Poole A, ed. 2005. *The birds of North American online*. Ithaca: Cornell Laboratory of Ornithology. Available at http://bna.birds.cornell.edu/BNA/

R Development Core Team. 2003. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available at http://R-project.org/

Rohwer S. 1975. The social significance of avian winter plumage variability. *Evolution* **29:** 593–610.

Rohwer S, Butcher GS. 1988. Winter versus summer explanations of delayed plumage maturation in temperate passerine birds. *The American Naturalist* **131:** 556–572.

Sanz JJ, Moreno J, Merino S, Tomás G. 2004. A trade-off between two resource-demanding functions: post-nuptial moult and immunity during reproduction in male pied flycatchers. Journal of Animal Ecology **73:** 441–447.

Schreiber RW, Schreiber EA, Peele AM, Burtt EH Jr. 2006. Pattern of damage to albino great frigatebird flight feathers supports hypothesis of abrasion by airborne particles. *Condor* **108:** 736–741.

Senar JC. 1999. Plumage colouration as a signal of social status. In: Adams NJ, Slotow RH, eds. *Proceedings of the 22nd International Ornithological Congress*. Durban: Birdlife South Africa, 1669–1686.

Svensson E, Hedenström A. 1999. A phylogenetic analysis of the evolution of moult strategies in Western Palearctic warblers (Aves: Sylviidae). *Biological Journal of the Linnean Society* **67:** 263–276.

Swaddle JP, Witter MS. 1997. The effects of molt on the flight performance, body mass, and behavior of European starlings (*Sturnus vulgaris*): An experimental approach. *Canadian Journal of Zoology* **75:** 1135–1146.

Veiga JP. 1996. Permanent exposure versus facultative concealment of sexual traits: an experimental study in the house sparrow. *Behavioral Ecology and Sociobiology* **39:** 345–352.

Willoughby EJ, Murphy M, Gorton HL. 2002. Molt, abrasion, and color change in Lawrence's goldfinch. *Wilson Bulletin* **114:** 380–392.

SUPPLEMENTARY MATERIAL

The following material is available for this article online:

Appendix S1. Data used in the analyses.

Appendix S2. The composite phylogeny used in the study (a) and references (b).

Appendix S3. Bivariate relationships between the variables used as predictors for the occurrence and/or extent of the prebreeding moult and feather abrasion. For pairs of two categorical variables, Pagel's maximum likelihood estimations are given, with P-values based on 1000 simulations. For all other cases, phylogenetic generalized least squares (PGLS) models are reported.

This material is available as part of the online article from:
http://www.blackwell-synergy.com/doi/abs/10.1111/j.1095-8312.2008.01027.x
(This link will take you to the article abstract).

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.