



Large-scale geographic variation in iridescent structural ornaments of a long-distance migratory bird

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Iridescent colours produced during moult likely play an important role in pair formation in birds. We sought to quantify geographic variation in such colouration in a duck species, Eurasian teal *Anas crecca*, in winter (when mating occurs) to evaluate whether this variation reflects birds' breeding origins or differential individual migration strategies in both males and females. We combined information on feather production region and individual attributes (body size, sex and age) of Eurasian teal from 82 wintering sites in France. Feather production region (moult site or natal origin) was inferred using feather deuterium values (δD_f). We performed spectral measurements to evaluate speculum colour and brightness contrasts for 1052 teal collected over four years. Colouration differed strongly among wintering regions, with birds wintering in eastern France exhibiting higher colour contrast than those wintering in the west. Body size and colouration were positively related. There were no differences in cohort-specific δD_f values between separate wintering regions in France, indicating that within a winter quarter teal originated from areas across the entire breeding range. Overall, patterns of spatial variation in feather colouration were related most closely to body size which was consistent with predictions of a differential migration hypothesis, with larger and more colour-contrasting birds wintering closer to their breeding grounds. Because moult speed is also known to affect colour production, early breeders or individuals that skipped reproduction may have invested more or earlier in their feather quality to gain potential advantages in monopolizing future mates.

Colour traits are often involved in sexual communication (Anderson 1994), especially in birds (Hill and McGraw 2006) where individual condition at the time of moult can alter the expression of plumage colouration (Keyser and Hill 1999, McGraw et al. 2002, Hill 2006). Tissue colours are involved in many functions including camouflage, thermoregulation, territoriality or mating (Endler and Greenwood 1988, Kraaijeveld et al. 2007), and can signal information about individual health and quality (Lozano 1994, Peters et al. 2004).

In migratory birds, annual life-cycle periods (breeding, moulting, migrating, wintering) are inextricably linked. Understanding migratory connectivity as a factor potentially contributing to geographic structure of colour patterns has seldom been investigated (Alatalo et al. 1986, Roulin 2003, Norris et al. 2004, 2007, 2009). For instance, Norris et al. (2004, 2007, 2009) demonstrated the importance of moulting grounds on carotenoid and melanin-dependent feather colouration in American redstart *Setophaga ruticilla* and

female barn swallow *Hirundo rustica*, respectively. For many migratory bird species, moulting and mating locations are decoupled both in space and time. Because of difficulties associated with tracking migrants across seasons and sites, identifying linkages between specific habitats and colouration is challenging (Norris et al. 2007). In the American redstart, breeding latitude, as inferred from feather deuterium (δD_f) values, rather than body condition was associated with feather colour variation (Norris et al. 2007). The ability to acquire more colourful plumage and sexual ornaments on moulting areas may hence have carry-over effects (Norris 2005) to the following season by affecting plumage colouration and ornaments (Saino et al. 2004) and, hence, the likelihood of securing a mate. A common feature of these studies is that colouration was based on pigments that are deposited into growing feathers (i.e. carotenoids acquired during foraging for American redstart; melanin synthesized in barn swallow). However, in many bird species, feather microstructure can influence colour production

(Hill and McGraw 2006). Such structural colours are produced by interference arrays of melanin granules and/or air vacuoles suspended in feather keratin (Shawkey et al. 2007). Structural colours also play a major role in bird signalling (Amundsen and Pärn 2006) and were reportedly condition-dependent in many bird species (Keyser and Hill 1999, Doucet 2002, McGraw et al. 2002, Loyau et al. 2007, Legagneux et al. 2010). Compared to pigment colouration (especially carotenoid-based colouration), important additional genetic effects (Johnsen et al. 2003) that determine the microstructure of the feathers are involved in structural colouration. Variation in iridescent structural ornaments could also be linked to moulting areas (e.g. if differences in geographic origin are associated with genetic differences or different environmental resources), a possibility that has not yet been evaluated. Such geographic variation associated with moulting location may later be altered by individual migration strategies. If strong connectivity exists between moulting and wintering grounds, geographic genetic structure can arise (Clegg et al. 2003). This may have serious repercussions for individual fitness since feather colouration could affect mating success the following breeding season (Hill and McGraw 2006).

Ducks (family Anatidae) show complex mating behaviours and brightest plumages (Black 2005), involving both pigments and feather microstructure. The quality of iridescent feathers produced during moult is thought to play an important role during the subsequent fall and winter (Omland 1996, Black 2005) when pair formation occurs, often months before the breeding season (Black 2005). Timing of reproduction is also important; nesting earlier in the breeding season generally results in higher reproductive success among Anatidae (Béty et al. 2003, Blums and Clark 2004, Blums et al. 2005). Thus, despite potential disadvantages of severe weather and resource competition, wintering at locations closer to breeding grounds could be beneficial.

Here, we evaluated winter geographic variation in structural colouration of the speculum and approximate moulting locations of Eurasian teal *Anas crecca* using reflectance spectrometry to measure colouration and stable isotopes (δD_f values, see Methods) to determine moulting and breeding origins of birds from different wintering areas. Deuterium in precipitation is transferred through food webs to higher-order consumers, including birds (Wassenaar and Hobson 2001). Because feathers are metabolically inert after growth, δD_f values sampled from feathers in a given wintering season indicate approximate geographic location of the previous moulting area (Hobson et al. 2004). Body size, sex and age were also assessed as potential putative correlates of variation in speculum colouration. Both colour and brightness contrasts reflected by the speculum were considered, taking duck colour visual sensitivity into account (Vorobyev and Osorio 1998).

We contrasted two non-mutually exclusive hypotheses to account for potential geographic variation in speculum colouration of wintering teal. Breeding origin could affect both feather colouration and wintering area, in which case δD_f levels should differ among wintering areas. Because lower δD_f values generally indicate higher latitudes, there should be a negative relationship between δD_f and colouration as shown in American redstarts

(Norris et al. 2004). Alternatively, differential migration strategies may modify the structure described above. The body size and dominance hypotheses (Cristol et al. 1999) indeed predict that larger individuals (or those in better condition, considered most dominant) from multiple origins should winter closer to their breeding grounds (that is, further north and east in the East Atlantic Flyway as considered here) than smaller (or poor-condition and subordinate) birds. Under this hypothesis, δD_f levels may not necessarily differ among wintering areas because birds would not be expected to segregate according to breeding origin. If body size is a reliable proxy for individual quality and if individual quality translates into feather colouration, then more colourful birds are expected to be larger and to winter closer to their breeding grounds.

Material and methods

Study sites and species

Teal is a long distance migrant species that breeds and moults in north-eastern Europe and winters in south-western countries (Cramp and Simmons 1977, Arzel et al. 2006). Adult female teal replace all wing feathers soon after breeding either close to or on their breeding grounds (Cramp and Simmons 1977), whereas juvenile teal grow wing feathers prior to fledging. By contrast, males leave females during incubation, and sometimes travel to distinct, distant moulting sites where they congregate (Scott and Rose 1996).

One feather from the wing colour patch (part of the speculum with feathers restricted to the distal side of the secondary remiges) was collected from shot individuals ($n = 1052$) at 82 locations in France (Fig. 1a) during four consecutive winters (2001–2005). Hunters were asked to send one entire wing to us in envelopes. Wings were stored in a dark and dry place until laboratory measurements. Shot teal could be leaner than teal trapped in protected areas (Guillemain et al. 2007). However, using Guillemain et al.'s data (2007), we found no significant differences in wing length between individuals captured in protected areas and shot birds recovered in the vicinity of protected natural reserves in any sex and age class (adult females: $t = 0.70$, $DF = 336$, $p = 0.49$; juvenile females: $t = 1.91$, $DF = 1657$, $p = 0.06$; juvenile males: $t = 1.26$, $DF = 1459$, $p = 0.21$; no adult males were sampled here for reasons given below), suggesting that our results involving body size, as indexed by wing length, were unlikely to be strongly biased. The 82 wing collection locations within France were visually clustered into five biogeographic regions: Atlantic, Channel, Brenne, Camargue and East (Fig. 1a). These regions are consistent with major teal concentrations in winter (Fouque et al. 2009). Birds were sexed and aged (adults vs juveniles) using plumage criteria (covert and scapular feathers, Baker 1993). For all birds, hunters were asked to provide body mass upon sending the duck wings (nearest 10 g with a top-loading scale). Flattened wing length was measured by three experienced technicians (nearest 1 mm with a ruler) and 79.2% of the wings representing all regions were measured by only one technician.

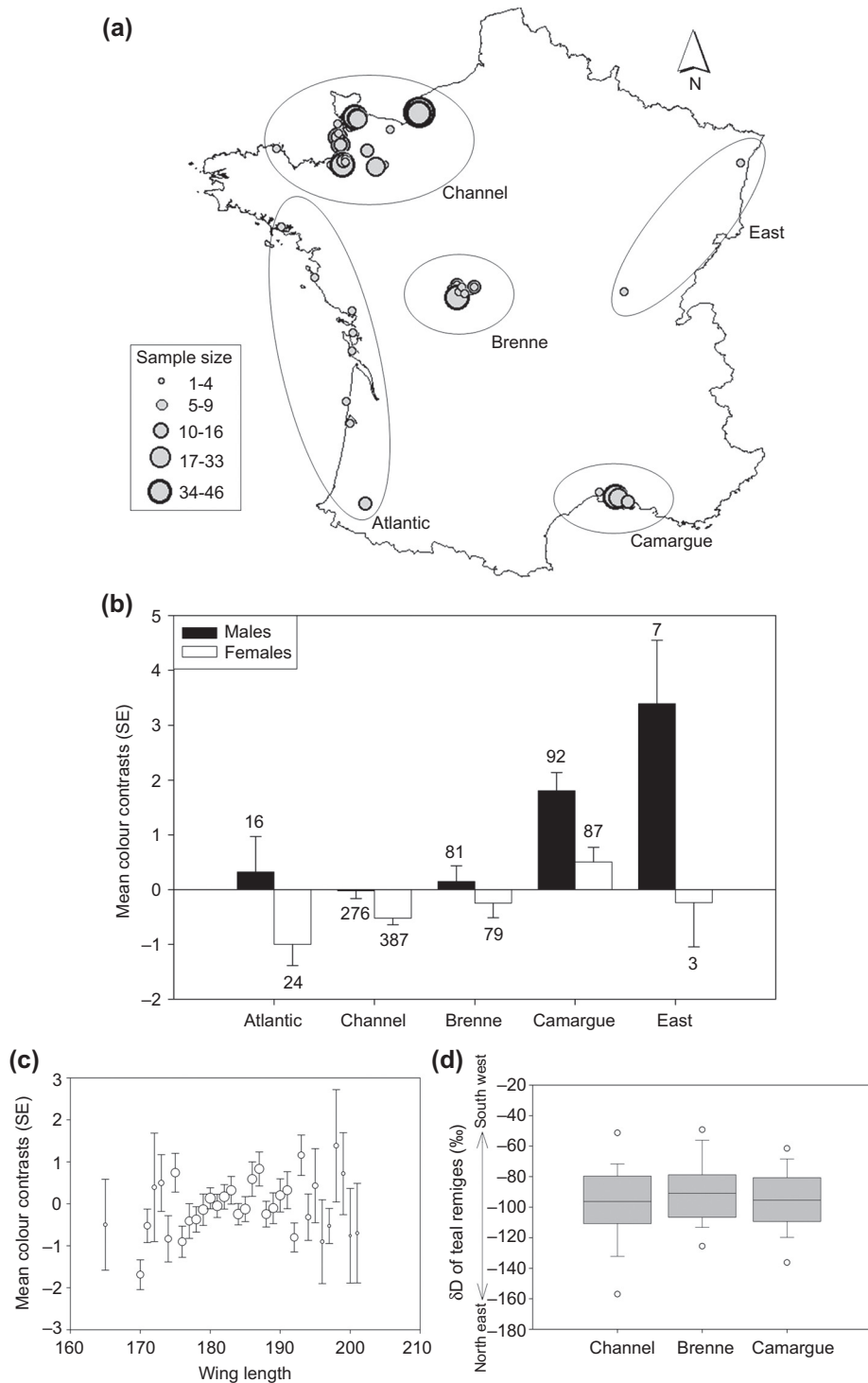


Figure 1. (a) Eurasian teal *Anas crecca* feathers sampled in France (wintering ground). Dot size is proportional to the number of individuals. Five regions are shown, from west to east: Atlantic, Channel, Brenne, Camargue, East. (b) Bar plot of the colour contrasts (residuals from a model with Date, Year, Wing length and Age) split by regions and sexes. Longitude and colour contrast are positively related in both sexes, but the relationship is more pronounced for males (see text and Table 1A). (c) Relationship between colour contrasts (residuals from a model with Date \times longitude, Sex \times longitude and the main effects, Year and Age) and wing length. (d) Boxplots (median, quantiles and SE) of the feather deuterium (δD_f) values for each of the wintering areas.

Eurasian teal wings were collected in compliance with European legal requirements (European Convention ETS no. 123). Working with dead ducks harvested legally by hunters exempted any approval by a committee for animal protection. All hunters, technicians and

researchers that participated in data collection received training (provided by the Museum National d'Histoire Naturelle and the Office National de la Chasse et de la Faune Sauvage) in duck capture, identification and measurement techniques.

Colour measurements and spectral analysis

Speculum reflectance was measured with a portable spectrometer (see details in Legagneux et al. 2010). Reflectance spectra were taken at 90° incidence relative to a 99% reflectance standard (300–700 nm Spectralon) and to dark current (black velvet background). We used the physiological visual model of Vorobyev and Osorio (1998) with malarial visual sensitivities measured by Jane and Bowmaker (1988). Colour and brightness contrasts were computed against a standard black background (wing flash-marks are surrounded by black patches onto the same or adjacent secondary remiges) with diffuse daylight CIE D65 as ambient light irradiance. All computations were conducted with Avicol software (Gomez 2006).

Stable isotope analysis

Potential exists to discriminate birds from broad regions of western Europe and east into northern Russia, due to strong gradients in growing season precipitation and hence feather isotopes (Hobson et al. 2004). Some assignment error using isotopes occur and statistical approaches have been designed to reduce uncertainty when mapping animal origins (Wunder and Norris 2008). However, our aim was to investigate if birds from different wintering areas originated from distinct, but broad-scale moulting grounds, rather than attempt to estimate specific bird origins. Stable isotope analysis was performed on a randomly-selected sample, stratified by age and sex cohort (excluding adult males that may moult in areas that differ from their birth place or breeding grounds) so that the colour contrast distribution of the subsample ($n = 126$: 14 per age/sex/region classes) matched that of the entire sample. Three regions were sub-sampled for this analysis because larger sample sizes were available: Channel (total $n = 663$), Brenne (total $n = 160$) and the Camargue (total $n = 179$). Feathers were cleaned of surface oils using a 2:1 chloroform:methanol solution, then dried in a fume hood. Stable-isotope assays were performed at National Hydrology Research Center, Environment Canada, Saskatoon. Stable hydrogen isotopes of feathers were measured using comparative equilibration method as described by Wassenar and Hobson (1998). Stable-hydrogen isotope ratios ($^2\text{H}/^1\text{H} = R$) are expressed in δ notation (‰) where $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ and R_{standard} is the hydrogen isotope ratio of Vienna Standard Mean Ocean Water. For a detailed description of sample preparation, analytical and within-sample measurement errors, keratin standards and analyses see (Clark et al. 2006). The δD_f values derived from teal sampled on the wintering grounds (September–January) were used to infer feather growth region during the previous June–August (Hobson et al. 2004).

Data analysis

General linear models (GLM) were used on the full dataset to evaluate whether colour or brightness contrasts were related to wintering latitude (X) and longitude (Y). Year, date (in days since 1 August), body size, body mass, sex and age classes were also included in the models; these

variables were previously tested on the same dataset (Legagneux et al. 2010) and only additive effects were found. We started with a model (named Base in the tables) that included Year + Date + Age + Sex + Wing length and Year + Date + Sex for the colour and brightness contrasts, respectively (Legagneux et al. 2010). We then evaluated models with interactions between latitude or longitude and the other variables. On the reduced dataset ($n = 126$) which incorporated δD_f measurements, the objective was to assess the relationship between colouration and isotopic signatures. The subsample was structured according to region, sex and age (see above). We applied the same covariates listed above except that X and Y were replaced with three REGIONS (Channel, Brenne and Camargue) in the GLMs. Note that results were qualitatively unchanged when region was replaced with longitude or latitude (X and Y, analyses not shown). Because the core range of the breeding/moulting locations may be of higher quality for breeding birds, we also included a non-linear (quadratic) effect of inferred moult location (δD_f^2). Competing models were ranked using Akaike's information criterion (AIC_c) (Burnham and Anderson 2002) and plausible models were considered to be those within two AIC_c units of the best-approximating model (i.e. with the lowest AIC_c value). When two or more models presented equal fit (i.e. $\Delta AIC_c < 2$), we model-averaged the estimates of parameters and associated unconditional standard errors. All means and slopes (β) are presented with SE. Statistical analyses were performed in R 2.11 using AICcmodavg package.

Results

Results of the model selection procedure indicated that year, date, sex, age and two continuous variables (longitude and wing length) as well as some interactions with longitude explained colour and brightness variation (Table 1). Colour contrast was positively related to longitude but not to latitude, with longitude also interacting with date and sex; individuals wintering in the east exhibited greater colour contrast than did western individuals (Fig. 1b, Table 1A). This gradient was more pronounced for males ($\beta = 4.4 \cdot 10^{-3} \pm 6.6 \cdot 10^{-4}$) than for females ($\beta = 2.5 \cdot 10^{-3} \pm 5.9 \cdot 10^{-4}$, Fig. 1b). The interaction between date and longitude revealed that colour contrast was related to longitude, but only during late winter. For instance, relationships were always positive but weaker in September and November ($\beta < 1.9 \cdot 10^{-3} \pm 1.3 \cdot 10^{-3}$ in September and November and $\beta > 3.3 \cdot 10^{-3} \pm 0.9 \cdot 10^{-3}$ in the other months). Yearlings were duller than adults (effect size = -0.54 ± 0.16). Wing length and colour contrast were positively related ($\beta = 6.7 \cdot 10^{-2} \pm 1.3 \cdot 10^{-2}$, Fig. 1c).

For brightness contrast, two competitive models were obtained (Table 1B), providing some indication of an interaction between date and longitude. Brightness contrast decreased with collection date ($\beta = -2.2 \cdot 10^{-3} \pm 5.3 \cdot 10^{-4}$) and differed by year and sex \times longitude (Table 1B). Brightness contrast decreased with longitude, an effect that was more pronounced in males than in females ($\beta = -3.4 \cdot 10^{-3} \pm 7.7 \cdot 10^{-4}$ and $\beta = -2.2 \cdot 10^{-3} \pm 5.3$

Table 1. Results of model selection from generalized linear models on colour (A) and brightness (B) contrasts of teal speculum (n = 1052). Year, Age and Sex were the explanatory cofactors and Date, Wing length (Wing), X (longitude) and Y (latitude) were the explanatory covariates. When an interaction (×) is indicated, the main effects were also incorporated in the model (though not shown here). The best-approximating models are shown in bold. Variables, number of estimated parameters (k), ΔAIC_c , Akaike weights (ω_i), deviance (Dev) and Log-likelihood (LL) are provided for the six most parsimonious candidate models. Base models (Base) incorporated additive effects of Year + Date + Age + Sex + Wing in (A) and Year + Date + Sex in (B) (see text for details).

Model	k	ΔAIC_c	ω_i	Dev	LL
Base + Sex × X + Date × X	13	0	0.69	6050.8	-2319.1
Base + Sex × X	12	3.51	0.12	6084.6	-2321.8
Base + Date × X	12	4.36	0.08	6089.8	-2322.2
Base + Age × X + Date × X	13	6.05	0.03	6087.6	-2322.1
Base + Wing × X + Date × X	12	6.37	0.02	6089.5	-2322.2
Base + X	11	6.86	0.01	6117.5	-2324.5
Base	10	63.96	0.00	6490.3	-2354.1

Model	k	ΔAIC_c	ω_i	Dev	LL
Base + Year × X + Date × X + Sex × X	15	0	0.49	4588.8	-2279.2
Base + Year × X + Sex × X	14	1.36	0.25	4590.1	-2280.9
Base + Year × X + Date × X	14	2.97	0.11	4591.7	-2281.7
Base + Year × X	13	3.62	0.08	4592.4	-2283.0
Base + Date × X + Sex × X	11	5.27	0.04	4594.0	-2285.9
Base + Date × X	10	8.48	0.01	4798.0	-2288.5
Base	8	58.48	0.00	5027.9	-2288.5

10^{-4} , respectively). This is the inverse pattern of the colour contrast (brightness and colour contrasts were negatively related). Brightness was negatively related to longitude in all years, but the strength of this relationship varied among years ($\beta = -2.8 \cdot 10^{-2} \pm 7.6 \cdot 10^{-4}$, $\beta = -6.2 \cdot 10^{-3} \pm 1.8 \cdot 10^{-3}$, $\beta = -3.5 \cdot 10^{-3} \pm 6.8 \cdot 10^{-4}$, $\beta = -1.9 \cdot 10^{-3} \pm 5.1 \cdot 10^{-4}$ and $\beta = -2.7 \cdot 10^{-3} \pm 3.3 \cdot 10^{-3}$ in 2001, 2002, 2003, 2004 and 2005, respectively). Note that individuals from the eastern region (n = 10) were not outliers responsible for the effect of longitude: removing data for this region did not change model ranks (Supplementary material Appendix 1, Table A1).

On the reduced dataset involving δD_f measurements, region, date, sex and δD_f were retained in the most parsimonious models for colour variation (Table 2A, B). Colour contrast differed according to region (mean colour contrast = 12.3 ± 0.3 ; 13.2 ± 0.4 and 14.3 ± 0.4 for Channel, Brenne and Camargue, respectively, Table 2A) and decreased slightly with collection date ($\beta = -1.6 \cdot 10^{-2} \pm 1.9 \cdot 10^{-2}$). Colour contrast was weakly positively related to δD_f ($\beta = 2.1 \cdot 10^{-2} \pm 2.7 \cdot 10^{-2}$). Brightness contrast also differed according to region (mean brightness contrast = 20.8 ± 0.3 ; 21.2 ± 0.3 and 19.6 ± 0.4 for Channel, Brenne and Camargue respectively), date ($\beta = 1.1 \cdot 10^{-4} \pm 4.9 \cdot 10^{-3}$) and sex (effect size = 0.96 ± 0.40) but not according to δD_f (Table 2B). Moreover, δD_f only varied with date, sex (in interaction with date, Table 2C) and age, while δD_f was similar among wintering regions (Fig. 1d).

Table 2. Results of model selection from generalized linear models on colour (A) and brightness contrasts (B) of teal speculum on a reduced dataset (n = 126) that incorporate δD_f values. Year, Region (Channel, Brenne and Camargue), Age and Sex were the explanatory cofactors. Date, Wing length and δD_f were the explanatory covariates. We also included a non-linear (quadratic) effect of the putative moult location (δD_f^2). In (C) we used the same covariates to explain δD_f variation. Column headings and base models are defined in Table 1.

Model	k	ΔAIC_c	ω_i	Dev	LL
Region + Date + δD_f	6	0	0.23	684.4	-278.3
Region + Date	5	0.16	0.22	697.8	-279.5
Region + Date × δD_f^2	7	0.25	0.21	673.2	-277.3
Region + Date + δD_f^2	7	2.23	0.08	684.2	-278.3
Region + Date + Sex	6	2.35	0.07	697.7	-279.5
Region × δD_f + Date	8	2.88	0.06	675.1	-277.5
Null model	2	22.34	0.00	805.2	-292.8

Model	k	ΔAIC_c	ω_i	Dev	LL
Region + Date + Sex	6	0	0.46	512.9	-260.7
Region + Date + Sex + Year	9	1.36	0.23	490.2	-258.0
Region + Date + Sex + Year + Age	10	3.52	0.08	489.4	-257.9
Region + Date	5	3.65	0.07	538.1	-263.6
Region + Date + Year	8	4.88	0.04	514.3	-260.9
Region + Date + δD_f	6	5.69	0.03	537.4	-263.6
Null model	2	25.92	0.00	625.3	-278.0

Model	k	ΔAIC_c	ω_i	Dev	LL
Date × Sex + Age	6	0	0.43	61847.2	-553.04
Date × Sex	5	0.03	0.42	61851.1	-554.16
Region × Sex + Year × Sex + Age	8	3.57	0.07	61847.2	-552.56
Region + Date	5	4.88	0.04	65551.9	-556.59
Year + Date	6	5.09	0.03	63381.2	-555.59
Region × Date	7	8.75	0.01	65232.6	-556.29
Null model	2	31.39	0.00	70211.6	-573.05

Discussion

To our knowledge, this is the first study to examine geographic variation in structural-based feather colouration in a long-distance migrant bird species. Speculum colouration in teal differed among wintering areas. However, this spatial organization in speculum colours was not related to different breeding or moulting origins of birds; rather, the δD_f values indicated considerable mixing of teal from diverse breeding regions (or from the same vast area, Guillemain et al. 2009) within the wintering areas. Our results nevertheless demonstrate a geographic structure of wing colouration in winter. Teal wintering further east had more brightly-coloured speculums than did individuals wintering further west, and wing colour contrast increased with body size. Guillemain et al. (2009) recently confirmed a pattern of differential migration in teal over a latitudinal gradient in Europe (Cristol et al. 1999), with relatively more males occurring further north. This result was not associated with different body masses between northern and southern wintering areas. However, because of the physical geography and wintering conditions of Europe (Gill 2007),

higher quality individuals (i.e. larger, more dominant birds) should actually winter further east or north-east rather than simply further north to be closer to the breeding grounds. Differential migration in Europe may thus occur in a different way than in North America where the gradient is mostly latitudinal (Cristol et al. 1999).

In contrast with our results, Norris et al. (2007) reported that American redstarts moulting farther north showed more orange-red feathers than southern birds that exhibited more yellowish feathers. Norris et al. (2004, 2007) argued that geographic variation in colour (carotenoid-based ornaments) was related to the availability of dietary carotenoids on the moulting grounds. Their results were obtained with a songbird, a typical income breeder that depends heavily on immediate food supply to ensure reproduction and growth (Meijer and Drent 1999), and possibly its energy needs during moult. Our results indicated that feather colours were associated with wintering locations and body size, but were not related to moulting location. Teal speculum colours are produced by feather structure, which differs from carotenoid-like pigments. Structural colours are thought to be influenced more by genotype or condition (Hill 2006) than by immediate dietary quality. Therefore, it is perhaps not surprising that feather micro-structure was more closely linked to a phenotypic trait such as body size than by the geographic area where the feathers were grown. Structural colours do not depend on a dietary pigment (such as carotenoid), so direct links between diet and colouration are less likely in the production of duck's speculum feathers. Geographic variation in a colour trait may not necessarily be related to moulting origin.

Timing of moulting could play a more prominent role here because early breeding is a key aspect of avian (especially waterfowl) reproductive success (Béty et al. 2003, Blums and Clark 2004, Blums et al. 2005, Elmberg et al. 2005). There is indeed growing evidence that moult speed (growth rate of moulting feathers) influences the expression of coloured (either structural or pigmented) ornaments (Serra et al. 2007, Griggio et al. 2009, Vágási et al. 2010, Maia and Macedo 2011). Griggio et al. (2009) experimentally manipulated moult speed in the blue tit *Cyanistes caeruleus* which resulted in a reduction of brightness and saturation of structural crown feathers that have grown more rapidly. For migratory birds, there is a trade-off between investment in reproduction and in moult (de La Hera et al. 2009). Early breeders or individuals that skipped reproduction may have invested more or earlier in moulting, migrating first and wintering closer to their breeding sites. In our study, geographic structure of speculum colouration was more pronounced in males than in females. Adult male teal are known to travel to distinct and sometimes distant sites where they congregate (Scott and Rose 1996) and moult earlier than females (and juveniles). Thus, adult males have a double advantage by: 1) migrating earlier and possibly selecting their wintering habitat according to their own phenotypic quality (including feather colouration); and, 2) having more time to moult than females and juveniles. Strong male-male competition may occur for access to suitable habitats located closer to future breeding areas, and influence the timing of reproduction. This suggests greater competition for wintering sites located closer to breeding grounds.

Assortative mating according to body condition (Heitmeyer 1995) may then explain the geographic variation of colouration found in both sexes, with more colourful females then halting migration earlier than less colourful ones. Further studies are needed to investigate geographic variation in male and female mate choice, especially in relation to coloured ornaments and conspecific density.

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