

Sexual selection predicts advancement of avian spring migration in response to climate change

Claire N. Spottiswoode^{1,4,*}, Anders P. Tøttrup² and Timothy Coppack³

¹Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

²Center for Macroecology, Institute of Biology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark

³Institute of Avian Research, Vogelwarte Helgoland, An der Vogelwarte 21, 26386 Wilhelmshaven, Germany

⁴DST/NRF Centre of Excellence at the Percy FitzPatrick Institute, University of Cape Town, Rondebosch 7701, South Africa

Global warming has led to earlier spring arrival of migratory birds, but the extent of this advancement varies greatly among species, and it remains uncertain to what degree these changes are phenotypically plastic responses or microevolutionary adaptations to changing environmental conditions. We suggest that sexual selection could help to understand this variation, since early spring arrival of males is favoured by female choice. Climate change could weaken the strength of natural selection opposing sexual selection for early migration, which would predict greatest advancement in species with stronger female choice. We test this hypothesis comparatively by investigating the degree of long-term change in spring passage at two ringing stations in northern Europe in relation to a synthetic estimate of the strength of female choice, composed of degree of extra-pair paternity, relative testes size and degree of sexually dichromatic plumage colouration. We found that species with a stronger index of sexual selection have indeed advanced their date of spring passage to a greater extent. This relationship was stronger for the changes in the median passage date of the whole population than for changes in the timing of first-arriving individuals, suggesting that selection has not only acted on protandrous males. These results suggest that sexual selection may have an impact on the responses of organisms to climate change, and knowledge of a species' mating system might help to inform attempts at predicting these.

Keywords: adaptation; bird migration; climate change; extra-pair paternity; phenology; protandry

1. INTRODUCTION

Long-term changes in the timing of seasonal activities are being observed in many animal and plant taxa, including widespread shifts in the phenology of migration and the onset of reproduction (reviewed by Walther *et al.* 2002; Root *et al.* 2003). In birds, this has been documented both in analyses of long-term, multi-species datasets of timing of spring arrival (reviewed by Lehikoinen *et al.* 2004) and of egg laying (Crick & Sparks 1999), as well as in intensive studies of single species or genera (e.g. Sheldon *et al.* 2003; Both *et al.* 2004). However, species appear to have responded to climate change to different degrees (Walther *et al.* 2002). For example, one recent analysis showed that over a 22-year period, changes in median passage date through Denmark of migrant warblers with comparable ecologies and non-breeding grounds varied from an earlier migration by 7 days in blackcaps *Sylvia atricapilla*, to a later migration by 2 days in wood warblers *Phylloscopus sibilatrix* (Tøttrup *et al.* 2006). Similar or greater variation has been revealed by other interspecific studies cited earlier; yet we lack general explanations for this variation. Furthermore, it is still uncertain to what degree these changes are phenotypically plastic responses or

microevolutionary adaptations to changing environmental conditions (Pulido & Berthold 2004). This remains a critical question in attempting to predict whether species and populations will be able to adapt ongoing human-caused environmental changes.

The changes in migration date have hitherto been investigated largely with respect to changes in climatic variables, migration distance and selection on breeding date in relation to environmental productivity (e.g. Coppack & Both 2002; Hüppop & Hüppop 2003). However, other forces may also affect the evolution of migration date in birds. As well as being shaped by stabilizing selection on breeding date, early spring arrival of males may be under directional selection by female choice. Earliest-arriving individuals are typically males (Møller 1994; Morbey & Ydenberg 2001; Møller 2004; Rubolini *et al.* 2004), and the considerable costs incurred during migration generate individual variation in arrival time, potentially providing a reliable cue of phenotypic quality for females. This is because early arrival is associated with occupation of superior territories and improved recovery of condition by the time of female arrival (Møller 1994; Kokko 1999; Ninni *et al.* 2004). Consistent with this idea, correlational studies at the population level suggest that earlier-arriving males often display more attractive sexual signals, such as song (Arvidsson & Neergaard 1991; Hoi-Leitner *et al.* 1993; Lampe & Epsmark 1994; Nyström 1997) and plumage

* Author for correspondence (cns26@cam.ac.uk).

The electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2006.3688> or via <http://www.journals.royalsoc.ac.uk>.

characters (Slagsvold & Lifjeld 1988; Ninni *et al.* 2004), and have a higher probability of obtaining extra-pair fertilizations (Langefors *et al.* 1998; Møller *et al.* 2003) or of breeding polygynously (Hasselquist 1998). For arrival time honestly to reflect individual quality, the marginal costs of early arrival must be greater for low-quality individuals than high-quality individuals (Kokko 1999), and this is supported by two studies of barn swallows *Hirundo rustica* (Møller 1994; Ninni *et al.* 2004).

At the species level, if early arrival honestly reflects male quality and this is subject to sexual selection by female choice, then species with longer and hence presumably costlier migrations should experience stronger sexual selection. In support of this prediction, several traits considered to be generally associated with more intense female choice have been shown to be correlated with migratory behaviour. Migration distance is associated with elevated levels of extra-pair paternity (EPP; Spottiswoode & Møller 2004) and degree of sexually dichromatic plumage colouration (Fitzpatrick 1994; Spottiswoode & Møller 2004), and both the occurrence (Read & Weary 1992) and distance (Mountjoy & Leger 2001) of migration are positively associated with song complexity. Given that males may benefit from early arrival through increased mating success, they generally arrive on the breeding grounds earlier than females ('mate opportunity hypothesis', Morbey & Ydenberg 2001), and it might further be expected that males arrive relatively more in advance of females in species subject to more intense sexual selection. A greater degree of protandry is indeed observed in species that are more sexually dimorphic with respect to both body size (Kissner *et al.* 2003) and plumage dichromatism (Rubolini *et al.* 2004), and which show higher levels of EPP (Coppack *et al.* 2006). Thus, interspecific studies showing a general association between migration behaviour and indices of the intensity of sexual selection are consistent with intraspecific evidence that early male migration is a sexually selected trait.

Sexually selected traits reflect a balance between the typically opposing forces of sexual and natural selection, whereby the survival disadvantage they confer eventually prevents their development to ever-greater extremes (Darwin 1871). Thus, migrants may arrive at a date that is earlier than the naturally selected optimum with respect to climate or food availability (e.g. Brown & Brown 2000), but which is nonetheless favoured by benefits conferred through sexual selection. As global climate change renders spring environmental conditions more benign at northern latitudes, natural selection opposing ever-earlier migration should have relaxed. There is evidence from the population level that such a process has taken place, since the degree of protandry of a barn swallow population has significantly increased over the last three decades, as warmer springs make early arrival less costly for males (Møller 2004). Similarly, at the species level, one would expect species experiencing the strongest selection for early arrival to have most rapidly shifted their migration dates as natural selection against early migration weakens. If female choice is primarily responsible for early spring arrival of males, species experiencing the most intense sexual selection should have advanced their average spring migration dates to the greatest extent as conditions ameliorate earlier.

We test this prediction using a comparative approach to relate rates of change in timing of migration to a synthetic measure of three indices of the strength of sperm competition and selection by female choice: (i) molecular estimates of rates of EPP, (ii) testes mass relative to body mass and (iii) visual scores of sexual dichromatism. EPP reflects variance in male mating success (Møller & Ninni 1998), and has been shown to affect the strength of sexual selection intraspecifically (Sheldon & Ellegren 1999). Relative testes size and sexual dichromatism are both known to be interspecifically positively correlated with rates of EPP (Møller & Birkhead 1994; Møller & Briskie 1995; Owens & Hartley 1998) as well as with each other (Dunn *et al.* 2001), and are predictors of other sexually selected phenomena, such as sexual size dimorphism and social mating system (Dunn *et al.* 2001; Pitcher *et al.* 2005).

We predict that species with greater indices of intensity of sexual selection (i.e. higher EPP, larger relative testes mass and greater sexual dichromatism) will have advanced their migration dates to a greater degree. We estimate rates of change in timing of migration from two long-term datasets from Christiansø and Heligoland bird observatories in northern Europe.

2. MATERIAL AND METHODS

(a) *Migration data*

Phenological data were drawn from two long-term ringing schemes in northern Europe where spring migrants breeding in Nordic countries have been captured using standardized trapping protocols. These were the islands of: (i) Christiansø (55°19' N, 15°11' E), in the Baltic Sea 18 km northeast of Bornholm, Denmark and (ii) Heligoland (54°12' N, 07°56' E), in the North Sea about 50 km from the German mainland (see also Hüppop & Hüppop 2003; Tøttrup *et al.* 2006, respectively, for detailed descriptions of capture methods). Both sites have a negligible proportion of terrestrial-breeding birds. Ringing recoveries from both sites indicate that their migrant populations breed principally in Sweden and Finland (Rabøl & Rahbek 2002; e.g. Zink 1973–1985; Zink & Bairlein 1995), and those from Heligoland also farther west in Norway (Zink & Bairlein 1995), implying that they form a part of the same overall population. Pooling data from the two sites hence appears biologically justifiable.

We reanalysed raw data from the two sites to calculate rates of change in passage date during the overlapping years in the two datasets (1976–1997). In keeping with recent studies of migration phenology (e.g. Vähätalo *et al.* 2004; Sparks *et al.* 2005; Tøttrup *et al.* 2006), we defined change as the slope of a linear regression of an annual value of Julian day against year. This provides an estimate of the average annual change in migration date, measured in days, in which negative slopes indicate earlier migration, and positive slopes later migration. Two different annual values of Julian day were used as dependent variables, reflecting change in different segments of the population: (i) the day on which 50% of the total annual passage had been captured, providing an estimate of the median passage date of the entire annual population, and (ii) the day on which 5% of the total annual passage had been captured, providing an estimate of the passage date of the earliest-arriving individuals in the population. We used this percentage rather than the day of the first individual of the season (e.g. Tryjanowski *et al.* 2002) because it is much less susceptible to stochastic and sampling effects (see also Sparks

et al. 2005; Tøttrup *et al.* 2006 for discussion). Owing to the predominance of protandry, this segment is likely to comprise largely males. Ideally, analyses would be conducted for each sex separately, but these cannot be distinguished on the basis of external morphology for the majority of the species in our dataset.

We included all species for which adequate phenological data were available from one or both sites, as well as published data on indices of sexual selection (described later). Two species occurring at Heligoland (great tit *Parus major* and chaffinch *Fringilla coelebs*, see Hüppop & Hüppop 2003) had to be excluded as they showed extreme among-year variation in trapping totals, indicative of irregular eruptive migration. All comparative data are summarized in electronic supplementary material 1, and scatterplots showing the raw arrival data as a function of year are illustrated in electronic supplementary material 2. We pooled data for those species occurring at both sites ($N=5$), thus improving the accuracy of individual estimates and permitting an overall analysis maximizing the sample size of species. For these species, we calculated phenological slopes for each site separately, and then pooled them subsequently. We did not pool data before phenological analysis because within a season some species (especially those migrating in an easterly or northeasterly direction, e.g. blackbird *Turdus merula* and pied flycatcher *Ficedula hypoleuca*) consistently reach Heligoland before Christiansø, as a consequence of the islands' geographical positions. Hence, slopes calculated from pooled data would provide an accurate estimate of neither site, whereas pooling slopes after calculation is appropriate because the rate of change of days per year is independent of timing within a season. Since there was variation among species and sites in the degree of confidence, with which the slopes reflecting changes in passage time were calculated we sought to minimize the error introduced by poorer estimates by weighting the mean of the two slopes for each site by the inverse of their variance (i.e. the inverse of the square of the standard error of the slope). Thus, the pooled values place more emphasis on the slope estimated with greater statistical confidence.

(b) Indices of sexual selection

We used linear models to examine species-specific rates of change as a function of a synthetic estimate of the strength of sexual selection. The three different estimates this comprised were obtained as follows: (i) rates of EPP were drawn from a variety of published sources, largely those synthesized by Spottiswoode & Møller (2004), supplemented with subsequent studies, listed in electronic supplementary material 1, and were arcsine-squareroot transformed before analysis, (ii) relative testes masses were extracted from the electronic supplementary material of Pitcher *et al.* (2005), who obtained and analysed a relative measure of testes mass by taking the residuals of a regression of log testes mass on log body mass across 1010 bird species, and (iii) degree of sexual dichromatism was scored by an ornithologist ignorant of the hypothesis under test, using Owens & Bennett's (1994) standard method. This generates an aggregate score of sexual differences in plumage colouration across five body regions, on a scale of 0 (sexes identical) to 10 (maximum dichromatism). We derived the synthetic measure from these three independent estimates using principal components analysis. All three variables loaded positively (eigenvectors: EPP=0.714, testes mass=0.241 and dichromatism=0.657) on the first principal

component, which explained 50.1% of their variance (eigenvalue=1.50) and was hence used as the predictor variable in subsequent analyses.

(c) Comparative analyses

We performed cross-species analyses in two ways: (i) using species as independent data points, ignoring phylogenetic non-independence, and (ii) using phylogenetically independent contrasts generated by the CAIC v. 2.6.9 software (Purvis & Rambaut 1995). The tree and sources of phylogenetic information are given in electronic supplementary material 3. We report the results using branch lengths estimated using a gradual model of evolution (Grafen 1989), because the contrasts thus generated better conformed to the assumptions of the comparative procedure. Although for the analysis of median passage date there were minor violations of the statistical assumptions of the comparative procedure (Garland *et al.* 1992), any consequent heterogeneity of variance did not influence our results; there were no outliers with standardized residuals greater than three (Jones & Purvis 1997), and results were extremely similar if the analysis was repeated with the independent variable expressed in ranks. Linear regressions of independent contrasts were forced through the origin (Grafen 1989).

3. RESULTS

Most species migrating through Christiansø and Heligoland advanced their passage dates over the 22-year study period (negative slopes in electronic supplementary material 1). Species with a greater index of the strength of sexual selection advanced their median date of population passage more rapidly than did less strongly sexually selected species. This was the case irrespective of whether independent data points were taken to be species (figure 1a; $R^2=0.643$, slope \pm s.e. = -0.124 ± 0.036 , $F_{1,7}=12.59$, $p=0.009$) or phylogenetically independent contrasts (figure 1b; $R^2=0.790$, slope \pm s.e. = -0.157 ± 0.031 , $F_{1,7}=26.40$, $p=0.001$). All linear contrasts in the latter analysis fell below the x-axis (figure 1b), indicating that for every paired comparison the more strongly sexually selected species had advanced its arrival date to a greater extent than the less sexually selected species. When rates of change in passage date of the first 5% of the population's annual passage were examined, the negative trend was still apparent (figure 2) but smaller proportions of the variance were explained, and the pattern was not statistically significant, albeit marginally not so for independent contrasts (species: $R^2=0.341$, slope \pm s.e. = -0.248 ± 0.037 , $F_{1,7}=3.62$, $p=0.099$; phylogenetically independent contrasts: $R^2=0.436$, slope \pm s.e. = -0.087 ± 0.038 , $F_{1,7}=5.41$, $p=0.053$).

4. DISCUSSION

In this study, we have presented a sexual selection hypothesis that attempts to explain variation in the responses of migratory birds to climate change, and have provided some empirical support for our predictions. By necessity, the sample size of our interspecific analysis is small, and we make no claim that other ecological factors may not be of equal or greater importance than sexual selection. However, these results provide some indication that sexual selection is a force deserving further investigation in studies of phenology and climate change.

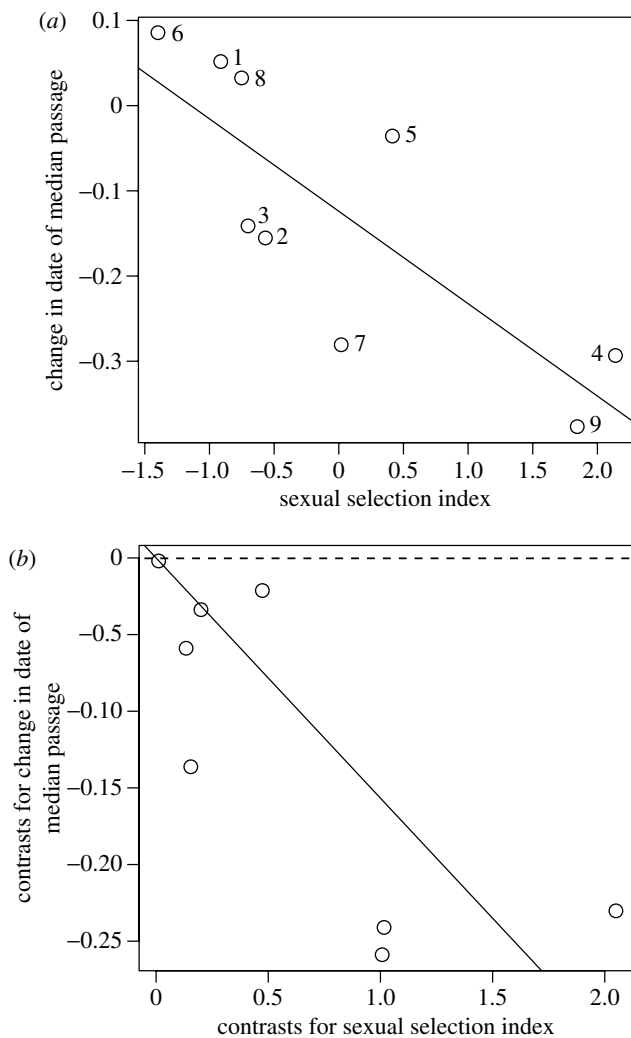


Figure 1. The annual change (measured in days per year) in the date at which 50% of the annual passage of migratory birds had been trapped on Christiansø and Heligoland in relation to their degree of sexual selection, with independent data points as (a) species and (b) phylogenetically independent contrasts. Data point labels on (a) refer to the following species: 1, *Acrocephalus palustris* (Christiansø only); 2, *Acrocephalus schoenobaenus* (Heligoland only); 3, *Acrocephalus scirpaceus*; 4, *Emberiza schoeniclus* (Christiansø only); 5, *Ficedula hypoleuca*; 6, *Phylloscopus sibilatrix* (Christiansø only); 7, *Phylloscopus trochilus*; 8, *Prunella modularis* and 9, *Turdus merula*. In (b), the x-axis is shown as a dotted line to assist interpretation of the contrasts.

Species with a greater estimate of the strength of sexual selection by female choice advanced their passage dates to a greater extent than species with weaker sexual selection, although this association was strong and statistically significant only for the median passage date of the annual population, whereas only a strong trend was apparent for the timing of the earliest-arriving 5% of the population, which should largely comprise males. This suggests that sexual selection may drive advancements in the population arrival date at least as much as that of protandrous males. Nonetheless, within a single species the degree of protandry has increased over the past 30 years (Møller 2004), and across species protandry is associated with indices of sexual selection (Rubolini *et al.* 2004; Coppack *et al.* 2006). Long-term changes in the degree of protandry might therefore be expected to be related to sexual selection across species, but unfortunately protandry is

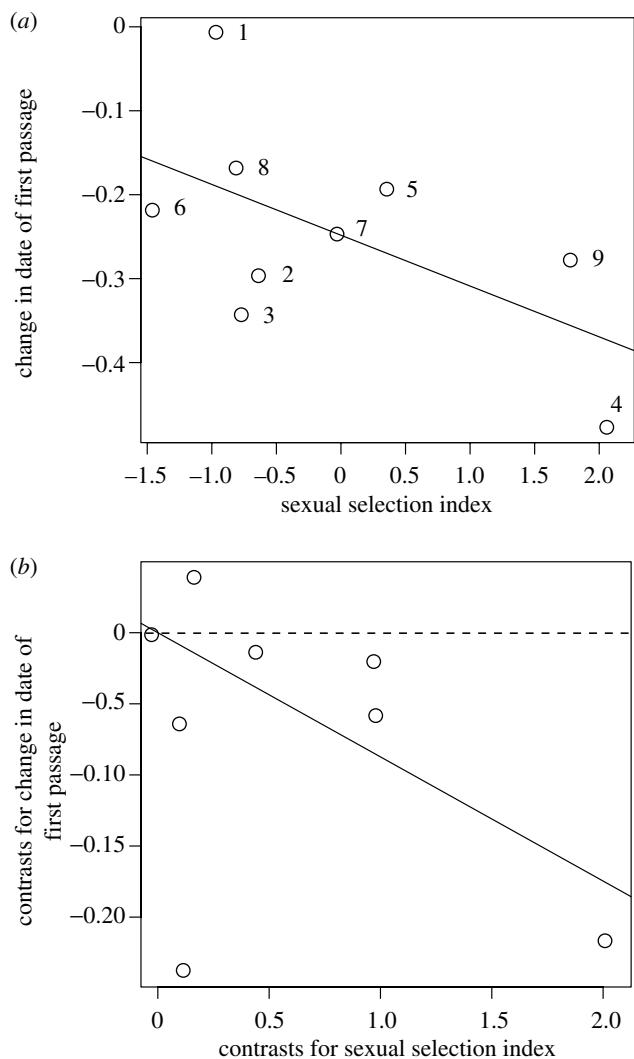


Figure 2. The annual change (measured in days per year) in the date at which 5% of the annual passage of migratory birds had been trapped on Christiansø and Heligoland in relation to their degree of sexual selection, with independent data points as (a) species and (b) phylogenetically independent contrasts. Data point labels are as for figure 1a. In (b), the x-axis is shown as a dotted line to assist interpretation of the contrasts.

difficult to calculate on a large scale, as most species cannot easily be sexed on morphological characters.

Some studies of migrant phenology have previously found a greater response to climate change in short- rather than long-distance migrants (e.g. on Christiansø, Tøttrup *et al.* 2006), as expected if they are exposed to different environmental conditions en route. If species with longer migrations experience more intense sexual selection (see §1), then for purely geographical reasons an association with sexual selection might result. Although multivariate analyses incorporating migration distance were precluded by our small sample size, consideration of only sub-Saharan African migrants (see electronic supplementary material 1) resulted in similarly negative trends (results not shown), suggesting that this is unlikely to have confounded our findings. Moreover, a confounding effect of migration distance would predict an association in a contrasting direction to that of our hypothesis.

It remains unclear whether phenological changes reported by recent studies are predominantly microevolutionary or purely phenotypically plastic (reviewed by

Pulido & Berthold 2004), although these are not mutually exclusive. For example, additive genetic variation in timing of migration has been demonstrated in quantitative genetic studies of autumn migration in blackcaps (Pulido *et al.* 2001), and of spring migration in barn swallows (Møller 2001), whereas a study of pied flycatchers has shown a lack of change in arrival date in spite of strong selection for it (Both & Visser 2001). Responses in the breeding date of collared flycatchers *Ficedula albicollis* to the North Atlantic Oscillation (NAO) have been shown to be plausibly explained by phenotypic plasticity alone (Przybylo *et al.* 2000). Our hypothesis is independent of these inconsistencies, however, since sexual selection on traits exhibiting environment-dependent phenotypic plasticity is not uncommon (e.g. Garant *et al.* 2004; Saino *et al.* 2004). Degree of change in arrival date could therefore have a sexually selected component (e.g. on a reaction norm) even in the absence of any genetic change in phenology, so long as arrival time remains a condition-dependent trait that provides honest information about male quality.

However, might climate change have any effect on the mechanisms ensuring the condition dependence of early arrival? The expression of condition-dependent secondary sexual plumage characters is influenced by large-scale climatic variation on the African wintering grounds in barn swallows (Saino *et al.* 2004). In collared flycatchers, a condition-dependent, sexually selected plumage character responded to NAO index in a phenotypically plastic manner, whereas a sexually selected but condition-independent plumage character did not (Garant *et al.* 2004). In both species, the condition-dependent plumage character is grown on the African wintering quarters. Similarly, in the sexually selected, condition-dependent character considered here, arrival date and costs are determined by conditions on the wintering quarters and while on migration (see Ninni *et al.* 2004 for an empirical example). It therefore seems reasonable to question whether condition dependence of arrival time will be preserved in the face of climate change. There is a clear link between changing climatic conditions and average timing of migration, but might the variance in arrival time also be affected? At the individual level, for condition dependence to be maintained, the physiological mechanisms ensuring that early arrival remains more costly for low-quality than high-quality individuals (Kokko 1999) must undergo a simultaneous temporal shift. Given that not all communities are expected to respond to climate change at the same rate (Walther *et al.* 2002; Root *et al.* 2003), selection acting in two regions and at two different times could generate a maladaptive outcome (e.g. Both *et al.* 2006). Weakened natural selection on the breeding grounds may permit early arrival, but have condition-determining mechanisms on migration changed at the same rate? If not, the arrival date could be susceptible to the mismatches between selective conditions before and during spring migration and those on the breeding grounds, conceivably leading to an eventual breakdown in the stability of the condition-dependent signal. This may be more probable in long-distance migrants where differences in climatic trends between breeding and non-breeding grounds are expected to be the greatest.

If the pattern suggested by our comparative results is general, then there may be other implications raised by

what is known of the ecological and genetic factors promoting sexual selection. Species able to adapt more quickly to climate change may have shared ecological attributes, and comparative studies of life history traits in relation to phenological responses may be informative. Rapid responses to changing environmental conditions might also be associated with relatively high genome-wide levels of genetic variation that also permit the maintenance of strong sexual selection (Petrie & Lipsitch 1994; Petrie *et al.* 1998).

This study has shown an association between the degree of overall phenological change and the strength of sexual selection across a small sample of Palearctic-breeding migratory passerine birds. This suggests that sexual selection might play a significant role in the way organisms respond to climate change, and hence that knowledge of a species' mating system may be of some practical predictive value in forecasting such responses. It remains unanswered whether this association indeed reflects a causal relationship, and whether it can be generalized to other taxa and to migration systems on other continents.

We are grateful to Christiansø Research Station and Vogelwarte Helgoland, as well as to the numerous voluntary co-workers at these observatories. We wish to thank J. M. Lausten, P. Lyngs and J. Rabøl for ensuring the high quality of the Christiansø data, and K. Hüppop and O. Hüppop for their commitment in making the backlog of Helgoland data accessible. The Danish National and Nature Agency and The National Environmental Research Institute, Department of Coastal Zone Ecology financed the collection of the Christiansø data. We also thank N. B. Davies, L. Zs. Garamszegi, I. P. F. Owens, S. Quader, A. P. Møller and three anonymous referees for their very helpful comments and discussion. R. M. G. Raman kindly performed the scoring of sexual dichromatism. C.N.S. was supported by St John's and Sidney Sussex Colleges, Cambridge. A.P.T. is supported by Danish National Science Foundation grant J. no. 21-03-0221.

REFERENCES

- Arvidsson, B. L. & Neergaard, R. 1991 Mate choice in the willow warbler—a field experiment. *Behav. Ecol. Sociobiol.* **29**, 225–229. (doi:10.1007/BF00166406)
- Both, C. & Visser, M. E. 2001 Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature* **411**, 296–298. (doi:10.1038/35077063)
- Both, C. *et al.* 2004 Large-scale geographical variation confirms that climate change causes birds to lay earlier. *Proc. R. Soc. B* **271**, 1657–1662. (doi:10.1098/rspb.2004.2770)
- Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. 2006 Climate change and population declines in a long-distance migratory bird. *Nature* **441**, 81–83. (doi:10.1038/nature04539)
- Brown, C. R. & Brown, M. B. 2000 Weather-mediated natural selection on arrival time in cliff swallows (*Petrochelidon pyrrhonota*). *Behav. Ecol. Sociobiol.* **47**, 339–345. (doi:10.1007/s002650050674)
- Coppack, T. & Both, C. 2002 Predicting life-cycle adaptation of migratory birds to global climate change. *Ardea* **90**, 369–378.
- Coppack, T., Tøttrup, A. P. & Spottiswoode, C. 2006 Degree of protandry reflects level of extrapair paternity in migratory songbirds. *J. Ornithol.* **147**, 260–265. (doi:10.1007/s10336-006-0067-3)

- Crick, H. Q. P. & Sparks, T. H. 1999 Climate change related to egg-laying trends. *Nature* **399**, 423–424. (doi:10.1038/20839)
- Darwin, C. 1871 *The descent of man and selection in relation to sex*. London, UK: John Murray.
- Dunn, P. O., Whittingham, L. A. & Pitcher, T. E. 2001 Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* **55**, 161–175. (doi:10.1554/0014-3820(2001)055[0161:MSSCAT]2.0.CO;2)
- Fitzpatrick, S. 1994 Colourful migratory birds: evidence for a mechanism other than parasite resistance for the maintenance of 'good genes' sexual selection. *Proc. R. Soc. B* **257**, 155–160.
- Garant, D., Sheldon, B. C. & Gustafsson, L. 2004 Climatic and temporal effects on the expression of secondary sexual characters: genetic and environmental components. *Evolution* **58**, 634–644. (doi:10.1554/03-356)
- Garland, T. J., Harvey, P. H. & Ives, A. R. 1992 Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Syst. Biol.* **41**, 18–32. (doi:10.2307/2992503)
- Grafen, A. 1989 The phylogenetic regression. *Phil. Trans. R. Soc. B* **326**, 119–157.
- Hasselquist, D. 1998 Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. *Ecology* **79**, 2376–2390. (doi:10.2307/176829)
- Hoi-Leitner, M., Nechtelberger, H. & Dittami, J. 1993 The relationship between individual differences in male song frequency and parental care in blackcaps. *Behaviour* **126**, 1–12.
- Hüppop, O. & Hüppop, K. 2003 North Atlantic Oscillation and timing of spring migration in birds. *Proc. R. Soc. B* **270**, 233–240. (doi:10.1098/rspb.2002.2236)
- Jones, K. E. & Purvis, A. 1997 An optimum body size for mammals? Comparative evidence from bats. *Funct. Ecol.* **11**, 751–756. (doi:10.1046/j.1365-2435.1997.00149.x)
- Kissner, K. J., Weatherhead, P. J. & Francis, C. M. 2003 Sexual size dimorphism and timing of spring migration in birds. *J. Evol. Biol.* **16**, 154–162. (doi:10.1046/j.1420-9101.2003.00479.x)
- Kokko, H. 1999 Competition for early arrival in migratory birds. *J. Anim. Ecol.* **68**, 940–950. (doi:10.1046/j.1365-2656.1999.00343.x)
- Lampe, H. M. & Epsmark, Y. O. 1994 Song structure reflects male quality in pied flycatchers, *Ficedula hypoleuca*. *Anim. Behav.* **47**, 869–876. (doi:10.1006/anbe.1994.1118)
- Langefors, Å., Hasselquist, D. & von Schantz, T. 1998 Extra-pair fertilizations in the sedge warbler. *J. Avian Biol.* **29**, 134–144.
- Lehikoinen, E., Sparks, T. H. & Zalakevicius, M. 2004 Arrival and departure dates. *Adv. Ecol. Res.* **35**, 1–31.
- Morbey, Y. E. & Ydenberg, R. C. 2001 Protandrous arrival timing to breeding areas: a review. *Ecol. Lett.* **4**, 663–673. (doi:10.1046/j.1461-0248.2001.00265.x)
- Mountjoy, D. J. & Leger, D. W. 2001 Vireo song repertoires and migratory distance: three sexual selection hypotheses fail to explain the correlation. *Behav. Ecol.* **12**, 98–102.
- Møller, A. P. 1994 Phenotype-dependent arrival time and its consequences in a migratory bird. *Behav. Ecol. Sociobiol.* **35**, 115–122. (doi:10.1007/s002650050077)
- Møller, A. P. 2001 Heritability of arrival date in a migratory bird. *Proc. R. Soc. B* **268**, 203–206. (doi:10.1098/rspb.2000.1351)
- Møller, A. P. 2004 Protandry, sexual selection and climate change. *Global Change Biol.* **10**, 2028–2035. (doi:10.1111/j.1365-2486.2004.00874.x)
- Møller, A. P. & Birkhead, T. R. 1994 The evolution of plumage brightness in birds is related to extrapair paternity. *Evolution* **48**, 1089–1100. (doi:10.2307/2410369)
- Møller, A. P. & Briskie, J. V. 1995 Extra-pair paternity, sperm competition and the evolution of testis size in birds. *Behav. Ecol. Sociobiol.* **36**, 357–365. (doi:10.1007/s002650050158)
- Møller, A. P. & Ninni, P. 1998 Sperm competition and sexual selection: a meta-analysis of paternity studies of birds. *Behav. Ecol. Sociobiol.* **43**, 345–358. (doi:10.1007/s002650050501)
- Møller, A. P., Brohede, J., Cuervo, J. J., de Lope, F. & Primmer, C. 2003 Extrapair paternity in relation to sexual ornamentation, arrival date, and condition in a migratory bird. *Behav. Ecol.* **14**, 707–712. (doi:10.1093/beheco/arg051)
- Ninni, P., de Lope, F., Saino, N., Haussy, C. & Møller, A. P. 2004 Antioxidants and condition-dependence of arrival date in a migratory bird. *Oikos* **105**, 55–64. (doi:10.1111/j.0030-1299.2004.12516.x)
- Nyström, K. G. K. 1997 Food density, song rate, and body condition in territory-establishing willow warblers (*Phylloscopus trochilus*). *Can. J. Zool.* **75**, 47–58.
- Owens, I. P. F. & Bennett, P. M. 1994 Mortality costs of parental care and sexual dimorphism in birds. *Proc. R. Soc. B* **257**, 1–8.
- Owens, I. P. F. & Hartley, I. R. 1998 Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proc. R. Soc. B* **265**, 397–407. (doi:10.1098/rspb.1998.0308)
- Petrie, M. & Lipsitch, M. 1994 Avian polygyny is most likely in populations with high variability in heritable male fitness. *Proc. R. Soc. B* **256**, 275–280.
- Petrie, M., Doums, C. & Møller, A. P. 1998 The degree of extra-pair paternity increases with genetic variability. *Proc. Natl Acad. Sci. USA* **95**, 9390–9395. (doi:10.1073/pnas.95.16.9390)
- Pitcher, T. E., Dunn, P. O. & Whittingham, L. A. 2005 Sperm competition and the evolution of testes size in birds. *J. Evol. Biol.* **18**, 557–567.
- Przybylo, R., Sheldon, B. C. & Merilä, J. 2000 Climatic effects on breeding and morphology: evidence for phenotypic plasticity. *J. Anim. Ecol.* **69**, 395–403. (doi:10.1046/j.1365-2656.2000.00401.x)
- Pulido, F. & Berthold, P. 2004 Microevolutionary responses to climatic change. *Adv. Ecol. Res.* **35**, 151–183.
- Pulido, F., Berthold, P., Mohr, G. & Querner, U. 2001 Heritability of the timing of autumn migration in a natural bird population. *Proc. R. Soc. B* **268**, 953–959. (doi:10.1098/rspb.2001.1602)
- Purvis, A. & Rambaut, A. 1995 Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comput. Appl. Biosci.* **11**, 247–251.
- Rabøl, J. & Rahbek, C. 2002 Population trends in the Baltic passerine migrants, elucidated by a combination of ringing data and point- and summer-count indices. *Dansk Ornitologisk Forenings Tidsskrift* **96**, 15–38.
- Read, A. F. & Weary, D. M. 1992 The evolution of bird song: comparative analyses. *Phil. Trans. R. Soc. B* **338**, 165–187.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. 2003 Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60. (doi:10.1038/nature01333)
- Rubolini, D., Spina, F. & Saino, N. 2004 Protandry and sexual dimorphism in trans-Saharan migratory birds. *Behav. Ecol.* **15**, 592–601. (doi:10.1093/beheco/arh048)
- Saino, N., Szép, T., Ambrosini, R., Romano, M. & Møller, A. P. 2004 Ecological conditions during winter affect sexual selection and breeding in a migratory bird. *Proc. R. Soc. B* **271**, 681–686. (doi:10.1098/rspb.2003.2656)

- Sheldon, B. C. & Ellegren, H. 1999 Sexual selection resulting from extrapair paternity in collared flycatchers. *Anim. Behav.* **57**, 285–298. (doi:10.1006/anbe.1998.0968)
- Sheldon, B. C., Kruuk, L. E. B. & Merilä, J. 2003 Natural selection and inheritance of breeding time and clutch size in the collared flycatcher. *Evolution* **57**, 406–420. (doi:10.1554/0014-3820(2003)057[0406:NSAIOB]2.0.CO;2)
- Slagsvold, T. & Lifjeld, J. T. 1988 Plumage colour and sexual selection in the pied flycatcher *Ficedula hypoleuca*. *Anim. Behav.* **36**, 395–407.
- Sparks, T. H., Bairlein, F., Bojarinova, J. G., Hüppop, O., Lehikoinen, E. A., Rainio, K., Sokolov, L. V. & Walker, D. 2005 Examining the total arrival distribution of migratory birds. *Global Change Biol.* **11**, 22–30. (doi:10.1111/j.1365-2486.2004.00887.x)
- Spottiswoode, C. & Møller, A. P. 2004 Extra-pair paternity, migration and breeding synchrony in birds. *Behav. Ecol.* **15**, 41–57. (doi:10.1093/beheco/arg100)
- Töttrup, A. P., Thorup, K. & Rahbek, C. 2006 Patterns of change in timing of spring migration in North European songbird populations. *J. Avian Biol.* **37**, 84–92. (doi:10.1111/j.2006.0908-8857.03391.x)
- Tryjanowski, P., Kuzniak, S. & Sparks, T. 2002 Earlier arrival of some farmland migrants in western Poland. *Ibis* **144**, 62–68. (doi:10.1046/j.0019-1019.2001.00022.x)
- Vähätalo, A. V., Rainio, K., Lehikoinen, A. & Lehikoinen, E. 2004 Spring arrival of birds depends on the North Atlantic Oscillation. *J. Avian Biol.* **35**, 210–216. (doi:10.1111/j.0908-8857.2004.03199.x)
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395. (doi:10.1038/416389a)
- Zink, G. 1973–1985 *Der Zug europäischer Singvögel*. Möggingen, Germany: Vogelzug Verlag.
- Zink, G. & Bairlein, F. 1995 *Der Zug europäischer Singvögel. Ein Atlas der Wiederfunde beringter Vögel. 5. Lieferung*. Wiesbaden, Germany: Aula.