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Life history predicts advancement of avian spring migration in response to climate change

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Abstract

An increasing number of studies demonstrate that plant and animal phenologies such as the timing of bird migration have been advancing over the globe, likely as a result of climate change. Even closely related species differ in their phenological responses, and the sources of this variation are poorly established. We used a large, standardized dataset of first arrival dates (FAD) of migratory birds to test the effects of phylogenetic relationships and various life-history and ecological traits on the degree to which different species adapt to climate change by earlier migration in spring. Using the phylogenetic comparative method, we found that the advancement of FAD was greater in species with more generalized diet, shorter migration distance, more broods per year, and less extensive prebreeding molt. In turn, we found little evidence that FAD trends were influenced by competition for mating (polygamy or extra-pair paternity) and breeding opportunities (cavity nests). Our findings were robust to several potentially confounding effects. These evolutionary correlations, coupled with the low levels of phylogenetic dependence we found, indicate that avian migration phenology adapts to climate change as a species-specific response. Our results suggest that the degree of this response is fundamentally shaped by constraints and selection pressures of the species' life history, and less so by the intensity of sexual selection.

Keywords: bird migration, climatic change, Hortobágy, phylogenetic comparative method

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Introduction

Phenological traits such as the start of flowering are known to be sensitive to climatic processes (Peñuelas & Filella, 2001; Parmesan & Yohe, 2003; Macmynowski & Root, 2007) with several phenophases currently advancing as a response to recent climate change (Bradley *et al*., 1999). For instance, changes in the timing of bird migration is predicted by plant and invertebrate phenologies (Sparks *et al*., 2005), i.e. there are tendencies to migrate earlier in response to earlier springs in the birds' breeding range (Strode, 2003; Crick, 2004; Lehikoinen *et al*., 2004).

Different species respond differently to the same climatic change experienced over the same region. Identifying the causes of these differences may not only expand our insight on the effects of global change but may also help to predict which species are especially vulnerable to those effects and thereby may aid conservational efforts. A recent study by Møller *et al*. (2008) showed that bird species that did not advance their spring migration dates had declining population sizes at the end of the 20th century, suggesting that climatic responsiveness may indeed have a crucial influence on the species' conservation status.

Up to now, several studies have identified a number of potential factors such as life history, behavioral traits, and environmental conditions that may explain at least some of the interspecific variation in climatic responses in several taxa (Beebee, 1995; Forchhammer *et al*., 1998; Winkler *et al*., 2002; Crick, 2004; Rubolini *et al*., 2005; Spottiswoode *et al*., 2006). For example, changes in avian migration phenology have been related to various factors ranging from sexually selected traits through feeding and nesting behaviors, moult and migratory strategies to the attributes of the physical environment. Theory also predicts that factors such as risk of

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mortality and competition for territories interact in complex ways in shaping the diversity of arrival trends in response to changes in food peak date (Jonzén *et al*., 2007). These findings demonstrate that different selection pressures and constraints of life history and ecology may influence the effect of global change on different species. However, most interspecific studies of migration phenology change were left with one or more of the following shortcomings: (i) they were conducted on a small sample or a relatively undiverse clade of species, (ii) they did not focus on the change of migration phenology, rather they investigated other aspects of migration such as its timing, distance, or sexual dimorphism (i.e. protandry) across species; (iii) they did not control for the phylogenetic relationships among species, which is a significant source of variation among species in arrival trends (Rubolini *et al*., 2007). Thus we are still in need for large-scale comparative studies to detect general patterns in the degree to which different species advance their migration phenology in response to climate change.

In the present study, we aimed to explore the predictors of avian migration phenology change by using a large, standardized dataset and taking phylogeny into account. To do so, we applied the phylogenetic comparative approach to investigate the advancement of the species' first spring arrival to Hortobágy, the most important stop-over site of the East-European flyway. This flyway (known as the Baltic–Hungarian flyway) connects Finland, Baltic States, Hungary, and North-Africa, and is one of the most prominent migratory flyways for several bird species (Prange, 1995; Ecsedi, 2004). Data from this part of the globe should extend our knowledge on the effects of climate change, as most previous studies of migration phenology were conducted on the Atlantic flyways (i.e. western Europe and North America).

Specifically, we investigated the phylogenetic relationships between the advancement of spring migration and various species-characteristics by testing the following predictions outlined by previous studies:

(1) *Life-history constraints*. Main features of the species' life history are expected to influence the pay-offs of advanced arrival to the breeding grounds. First, short-distance migrants have been suggested to respond more strongly to climate change than long-distance migrants (e.g. Lehikoinen *et al*., 2004; Rubolini *et al*., 2007; Thorup *et al*., 2007). Second, passerines that have delayed post-breeding molt (i.e. replace flight feathers at wintering grounds) also have delayed spring migration (Rubolini *et al*., 2005), suggesting that the costs of molting may hinder the advancement of migration phenology in response to climate change. Third, annual brood number has been proposed to affect migration phenology change, as species producing more broods per season may profit more by an extended breeding period (Jenni & Kéry, 2003). Accordingly, an analysis of mean/median migration dates found greater advancements of spring passage dates in species laying more broods (Møller *et al*., 2008). Finally, species with longer life span and greater generation time may be less responsive to climatic effects (Sandvik & Erikstad, 2008) and thus may take longer to adapt to climate change.

(2) *Ecological constraints*. Some studies showed that species with different diets and different habitats may differ in the degree to which they advanced their spring arrivals (Loxton *et al*., 1998; Loxton & Sparks, 1999; Butler, 2003), and diet flexibility may affect climatic responsiveness (Sandvik & Erikstad, 2008). Furthermore, cavity-nesting species migrate earlier than species using more abundant nest sites, presumably as a result of intense competition for nesting cavities (Rubolini *et al*., 2005), thus the type of nesting is expected to influence selection for early spring arrival. In line with these predictions, theory implies that arrival advancement in response to a shift in food peak date should generally get stronger when the resource distribution over the breeding season is narrower and the competition for territories is less intense (Jonzén *et al*., 2007).

(3) *Sexual selection constraints*. Several studies indicated that the intensity of mating competition may influence the intensity of selection for early spring arrival in birds. Migration distance is associated with elevated levels of extra-pair paternity (EPP) (Spottiswoode & Møller, 2004) and plumage dichromatism (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 in passerines. Species with greater sexual dimorphism in body size migrate earlier in spring (Rubolini *et al*., 2005). Using a small sample of western European passerines, Spottiswoode *et al*. (2006) showed that species with a stronger index of sexual selection indeed advanced their date of spring passage to a greater extent.

To test these predictions, we investigated the temporal trends in the species' first arrival dates (FAD), a measure that has been used successfully in several studies of phenological change (reviewed by Lehikoinen *et al*., 2004; Rubolini *et al*., 2007). Although sampling effort and population size may influence the date that the first bird is observed (Miller-Rushing *et al*., 2008), various measures of migration phenology are positively correlated, and FAD trends are consistent within species irrespective of the degree of standardization in data collection (Rubolini *et al*., 2007). Nevertheless, to minimize the risk of bias in our FAD data, sampling effort was constant over our study and we controlled for

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population size trends in our analyses, as detailed below.

Materials and methods

Spring arrival dates

Data on the timing of spring migration were collected in the Hortobágy National Park (HNP), the largest unbroken alkaline grassland in Europe, consisting of steppe areas interspersed with saline marshes. Hortobágy is located in Eastern Hungary, where the effects of global change on plant phenology have already been detected (Walkovszky, 1998; Kovács-Láng *et al*., 2002). Twenty-seven hectares of the HNP is protected by the Ramsar Convention because of its importance as a breeding and stopover site for waterbirds, with 341 species recorded (Ecsedi, 2004).

Our database was compiled from the field records of G. K., collected between 1969 and 2007 during his regular field trips in the south-western part of the HNP as a member of the Ranger Service of the HNP. During the study period 42 720 h were spent on the field (mean $\pm$ SD = 219.1 $\pm$ 27.7 h month^{-1}) and a total of 15 4000 km covered (789.7 $\pm$ 107.7 km month^{-1}), following standardized census routes between 1 January and 31 May in each year. Because all data were collected by the same person following the same protocol, we consider the sampling effort adequately standardized and constant over the years.

We focused on bird species that are migratory in Central Europe and breed in the Western Palearctic (one species, the Curlew Sandpiper *Calidris ferruginea* is Arctic-breeding). We included only species meeting the following criteria: (1) no gap longer than 3 years between years with sightings, (2) a time span of at least 10 years with no gap longer than 3 years, and (3) the total number of years without sightings is less than one-third of the years within the continuous time span with sightings (Macmynowski *et al*., 2007). In total, 117 species met these criteria (Appendix S1), including 44 passerines and 73 nonpasserines (mainly waterbirds and shorebirds).

For each species, we calculated the degree of advancement of spring arrival (FAD trends henceforth; see Appendix S1) as the slope of a linear regression between the FAD (expressed as Julian days) and years (Spottiswoode *et al*., 2006; Rubolini *et al*., 2007). Negative slopes indicate an advancement of spring arrival during the study period, more negative values indicate a greater degree of advancement.

Predictors of FAD trends

We collected data on the species' life history from Snow & Perrins (1998) if not stated otherwise. Populations migrating through Hungary are well represented by the data compiled in this book since the Baltic-Hungarian flyway is one of the main migratory routes of the species we considered (Snow & Perrins, 1998). We categorized the species as long or short distance migrants, i.e. species spending the winter in tropical Africa or north of the Sahara (Snow & Perrins, 1998; Jonzén *et al*., 2006). We also estimated migration distances similarly to Svensson & Hedenström (1999) from the summer and winter distribution midpoint values of longitudes and latitudes according to the formula described by Imboden & Imboden (1972). The timing of postbreeding molt was categorized as occurring either at the summer quarters or in the wintering area. We recorded whether prebreeding molt occurred in the species, and we scored its extent 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 molted (Tökölyi *et al*., 2008). Annual fecundity was measured as the average number of broods subsequently raised per season (henceforth brood number). We also collected data on the typical age at maturity and the maximum life span recorded (both in years). Diet complexity was scored by recording whether the species' diet included plant materials, insects, other invertebrates, fish, amphibians, reptiles, birds, and mammals, and we counted the number of different food types (range: 1–7). We categorized breeding habitat as woodland, grassland, and wetland. Nest type was categorized as cavity for species that use preexistent cavities that they cannot excavate themselves, and as open for all other species (Rubolini *et al*., 2005).

We gathered several kinds of data on the strength of sexual selection. Mating system was categorized as monogamous, or polygamous if polygyny and/or polyandry occurred in the species. We also expressed the degree of polygamy by the percentage of polygynous males and/or polyandrous females. The strength of sperm competition was measured by two variables: the percentage of extra-pair offspring (EPP rate; taken mainly from the standardized dataset of Griffith *et al*., 2002) and the relative testis size (i.e. the residuals of testes mass regressed on body mass; testis masses were taken from the revised dataset of Calhim & Birkhead, 2007). Sexual dimorphism in body size was expressed as the residuals of male body mass regressed on female body mass. Sexual dimorphism in plumage coloration (i.e. dichromatism) was scored on a 0–10 scale as the sum of scores from five body regions (head, breast-belly, back, wing, tail), where each body region was scored separately as 0 – no difference in color, intensity, or pattern between the sexes, 1 – difference between the sexes only in shade or intensity of color, 2 – difference in

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color (hue) or pattern between the sexes (Owens & Bennett, 1994; Owens & Hartley, 1998; Dunn *et al*., 2001). For passerines, song repertoire was categorized as complex (i.e. species with > 100 song types) or simple, and syllable repertoire size was measured as the mean number of different syllable types within song (taken from Read & Weary, 1992, and Garamszegi & Møller, 2004). Because all these variables are highly intercorrelated, we obtained comprehensive indices for the strength of sexual selection by principal component analysis. First, following Spottiswoode *et al*. (2006), we combined EPP rate, residual testes mass, and dichromatism into a single principal component, explaining 41.7% of total variance (available for $n = 26$ species only). Second, to increase sample size, we combined those data that were available for most species, i.e. the degree of polygamy, body mass dimorphism, and dichromatism, into another principal component, explaining 41.3% of total variance ($n = 115$).

Before analyses, EPP rate and maximum life span were $\log_{10}$-transformed to improve their fit to normal distribution. All data on the species' life history, ecology, and sexual selection are presented in Appendix S2. Summaries of the principal components are given in Appendix S3.

Phylogenetic analyses

To represent phylogenetic relationships among species, we compiled a composite tree using mostly molecular data (Appendix S4). We set branch lengths proportional to the number of nodes, i.e. gradual branch lengths, according to Nee's method (Maddison & Maddison, 2005). To investigate the relationships between FAD trends and life-history traits, we used Phylogenetic Generalized Least Squares (PGLS) models (Pagel, 1997, 1999). This approach controls for the nonindependence among species by incorporating a variance–covariance matrix that represents their phylogenetic relationships (Martins & Hansen, 1997; Pagel, 1997, 1999). In all analyses we set the phylogenetic dependence to the most appropriate degree (λ) evaluated for each model by likelihood ratio statistics (Freckleton *et al*., 2002). First we conducted bivariate analyses to identify the life-history predictors of FAD trends. Then we used the latter results to formulate candidate multivariate models of predictors that appeared significant in the bivariate analyses (note that including all predictors was not possible because the number of candidate models would have been too large). We investigated the relative importance of these predictors by information-theoretic model-comparison (Burnham & Anderson, 2002) in which inference is based on an entire set of plausible models. We evaluated the candidate models by the second-order Akaike's information criterion corrected for small sample size ($\mathrm{AIC_c}$). As no single model was clearly superior compared with the others in the model set, we performed model averaging and calculated model-averaged coefficients θ (i.e. weighted by the relative Akaike weights ω_i of the models) and their unconditional standard errors $\mathrm{SE_u}$ (Burnham & Anderson, 2002). We also evaluated the relative importance (Σ) of predictors by the sums of their Akaike weights across all models that contain the given predictor.

We tested the robustness of our results by investigating several possible confounding effects. First, the starting year from which we had data on arrival dates varied among species between 1969 and 1988 (1969–1977 for the 95% of species; see Appendix S1). Second, FAD data may strongly depend on population size, e.g. population increases may lead to the detection of increasingly earlier arrivals (Tryjanowski & Sparks, 2001), so we collected data on population size trends from long-term studies in the HNP from Ecsedi (2004). Third, we included data on body mass (averaged for males and females) as it is strongly correlated with several life-history traits and thereby it might mask some effects of global change. Fourth, out of our 117 species 99 breed in or near the study area (i.e. in Hungary) while the remaining 18 migrate further. Since arrivals to the breeding grounds and to stopover sites might be under different selection pressures and constraints (at least partially), species breeding in Hungary and those that do not may differ in the advancement of their arrivals to Hortobágy. Finally, errors in estimating the degree of phylogenetic dependence might occur, in which case the low λ values in our analyses might have increased type I error rates. To control for these possible confounding factors, we repeated our bivariate analyses by (1) including the starting year of observations, the trends in Hortobágy population sizes, or body mass into the models, and also testing the interactions between these confounders and the respective predictors; (2) restricting the analyses to species breeding in Hungary; (3) setting λ either to 0.5 or to 1, the latter being basically equivalent to the independent contrasts method (Felsenstein, 1985; Martins & Hansen, 1997).

For all analyses we used the R statistical computing environment (R Development Core Team, 2003). We report mean ± SE values and two-tailed statistical tests with a 5% significance level. Sample sizes differ across tests because data are incomplete for some species.

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Results

The mean slope of FAD trends was -0.34 ± 0.05 days yr^{-1} (range: -2.57; 0.70). Slopes were negative for 93 species, out of which 45 was statistically significant,

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whereas 24 species had positive slopes, out of which only two were significant (Appendix S1). The degree of phylogenetic dependence (λ) was low overall, not differing significantly from zero in any PGLS model.

Short-distance migrants advanced their FAD to a greater extent than long-distance migrants (Table 1; Fig. 1a), and FAD trends were positively related to migration distances (Table 1; Fig. 1b). Species molting primaries at summer quarters advanced their FAD more than species that molt their flight feathers on wintering grounds (Table 1; Fig. 1c; note that the interaction with migration could not be tested because all short-distance migrants in our dataset molt their primaries in summer quarters). Species without prebreeding molt advanced their FAD more than species with a prebreeding molt (Table 1; Fig. 1d), and FAD trends were positively related to the extent of prebreeding molt (Table 1). These relationships were similar for short- and long-distance migrants (occurrence of prebreeding molt × migration strategy: $P = 0.222$, extent of prebreeding molt × migration strategy: $P = 0.211$). Species that produce more broods annually, and those with more complex diets, advanced their FAD to a greater extent than less fecund and more specialist species, respectively (Table 1; Fig. 1e,f). These relationships were again similar for short- and long-distance migrants (brood number × migration strategy: $P = 0.789$, diet × migration strategy: $P = 0.415$). FAD trends were not different between woodland, grassland, and wetland species (Table 1), and there was no interaction between habitat and migration strategy ($P = 0.155$), or between habitat and diet ($P = 0.443$). FAD trends were unrelated either

Table 1 Bivariate phylogenetic relationships of FAD trends with life-history traits

	F	df	P	η^2 (CI)	$b \pm$ SE
Migration strategy	9.93	1 116	0.002	0.079 (0.011–0.183)	Short: −0.52 ± 0.08 Long: −0.23 ± 0.05
Migration distance	14.89	1 116	<0.001	0.114 (0.028–0.226)	0.0001 ± 0.00002
Timing of postbreeding molt	4.82	1 116	0.030	0.040 (0–0.129)	Summer: −0.40 ± 0.06 Winter: −0.16 ± 0.06
Occurrence of prebreeding molt	4.98	1 113	0.028	0.042 (0–0.133)	Absent: −0.49 ± 0.12 Present: −0.29 ± 0.04
Extent of prebreeding molt	5.06	1 109	0.027	0.044 (0–0.139)	0.057 ± 0.025
Number of broods per year	5.03	1 115	0.027	0.042 (0–0.132)	−0.121 ± 0.054
Diet complexity	4.2	1 116	0.043	0.035 (0–0.121)	−0.077 ± 0.037
Habitat	1.3	2, 116	0.275	0.022 (0–0.087)	Woodland: −0.21 ± 0.08 Grassland: −0.39 ± 0.13 Wetland: −0.39 ± 0.06
Age at maturity	1.81	2 104	0.168	0.034 (0–0.113)	1st year: −0.35 ± 0.05 2nd year: −0.33 ± 0.14 3rd year: −0.80 ± 0.34
Maximum life span	0.89	1 82	0.348	0.011 (0–0.091)	−0.300 ± 0.318
Nest type	0.9	1 116	0.346	0.008 (0–0.067)	Open: −0.33 ± 0.05 Cavity: −0.52 ± 0.27
Mating system	1.61	1 116	0.207	0.014 (0–0.081)	Monogamy: −0.37 ± 0.05 Polygamy: −0.22 ± 0.10
Degree of polygamy	0.02	1 114	0.891	0.0002 (0–0.007)	0.0004 ± 0.003
EPP rate	0.13	1 30	0.723	0.004 (0–0.136)	−0.069 ± 0.194
Residual testis mass	1.16	1 59	0.287	0.019 (0–0.132)	−0.069 ± 0.065
Sexual dimorphism in body mass	1.41	1 116	0.238	0.012 (0–0.078)	−1.128 ± 0.951
Plumage dichromatism	0.09	1 116	0.761	0.001 (0–0.033)	−0.004 ± 0.012
Song repertoire	0.1	1 18	0.757	0.006 (0–0.175)	Simple: −0.41 ± 0.16 Complex: −0.34 ± 0.13
Syllable repertoire size	0.36	1 33	0.554	0.011 (0–0.156)	−0.104 ± 0.173
Sexual selection index 1 (EPP rate, testis mass, dichromatism)	1.07	1 25	0.312	0.041 (0–0.251)	−0.095 ± 0.092
Sexual selection index 2 (polygamy, dichromatism, mass dimorphism)	0.25	1 114	0.617	0.002 (0–0.049)	−0.024 ± 0.048

Effect size estimates (η^2) are given as the proportion of variance explained by each variable, along with their 95% confidence intervals (CI). For covariates, $b \pm$ SE shows slope estimates, whereas for factors it shows mean FAD trends for each factor level. FAD, first arrival dates; EPP, extra-pair paternity.

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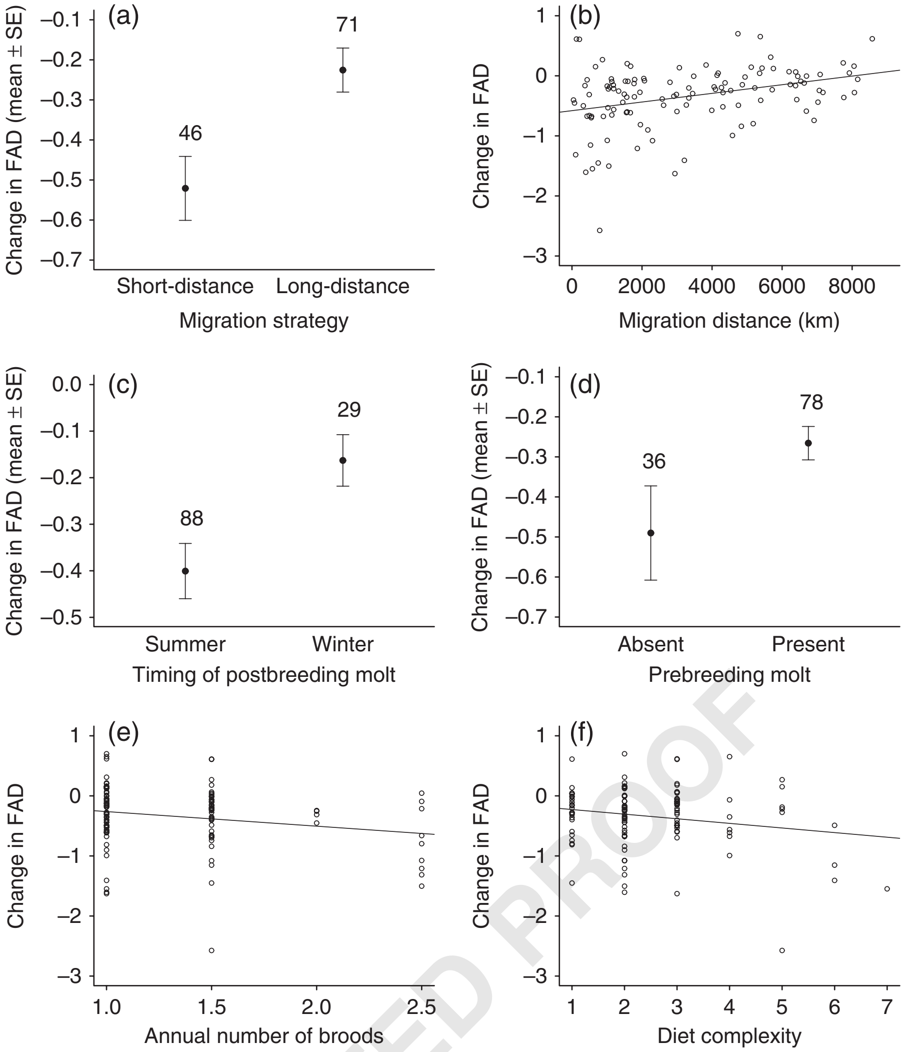

Fig. 1 The annual change (days per year) in the date at which the first individuals of migratory bird species had been observed in Hortobágy (FAD trends), in relation to life-history traits. Numbers above the error bars denote the corresponding sample sizes. FAD, first arrival dates.

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to the age at maturity or to the maximum life span of the species (Table 1). Although later-maturing species had more advanced FAD among short-distance but not in long-distance migrants (age at maturity × migration strategy: $P = 0.047$), this result should be treated with caution because we had only four short-distance migrants that mature after their first year. In contrast, the interaction between migration strategy and maximum life span was not significant ($P = 0.272$). Secondary cavity-nesting species did not differ in FAD trends from species that build their own nest sites (Table 1). Although cavity-nesting species had more advanced FAD among short-distance but not in long-distance migrants (nest type × migration strategy: $P = 0.004$), this result again might be an artefact since we had only two short-distance migrants that nest in cavities. FAD trends were not related to any measure of the strength of sexual selection (Table 1), and had no significant interactions with migration strategy (all $P > 0.232$). The only exception was that EPP rate was negatively related to FAD trends in short-distance migrants but positively in long-distance migrants (nest type × migration strategy: $P = 0.029$; Fig. 2).

To investigate the relative importance of migration and molt strategies, brood number, and diet complexity in explaining FAD trends, we evaluated all possible combinations of these predictors in multivariate analyses. The AIC$_c$-based model-comparison (Table 2) showed that out of the nine most supported models (i.e. $\Delta_i < 2$), diet was included in seven, migration strategy in six, brood number in five, prebreeding molt in four, and postbreeding molt in only one; although

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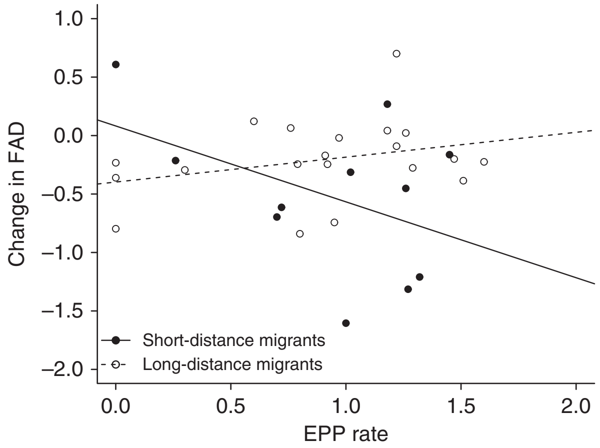

Fig. 2 The relationship between FAD trends and EPP rates [the % of extra-pair offspring; $\log_{10}(x + 1)$ transformed] in short- and long-distance migratory bird species. FAD, first arrival dates; EPP, extra-pair paternity.

model uncertainty was high ($\omega_{\max} = 0.12$). Model-averaging revealed that the most important predictors of FAD trends were diet complexity ($\Sigma = 0.65$; $\theta \pm \mathrm{SE_u} = -0.049 \pm 0.026$) and migration strategy ($\Sigma = 0.63$; $\theta \pm \mathrm{SE_u} = -0.135 \pm 0.067$), followed by the annual number of broods ($\Sigma = 0.52$; $\theta \pm \mathrm{SE_u} = -0.101 \pm 0.062$) and the occurrence of prebreeding molt ($\Sigma = 0.48$; $\theta \pm \mathrm{SE_u} = 0.086 \pm 0.055$), whereas the timing of postbreeding molt had smaller impact ($\Sigma = 0.27$; $\theta \pm \mathrm{SE_u} = 0.035 \pm 0.034$).

In all the analyses including potential confounding variables, our results remained qualitatively similar (see Appendix S5). Although body mass was not related to FAD trends ($r = -0.15$, $P = 0.105$, $n = 117$), species for which the observations began earlier showed greater advancement of spring arrival dates ($r = 0.28$, $P = 0.002$, $n = 117$), and species with increasing populations in Hortobágy during the study period advanced their FAD to a greater extent than species with decreasing, stable or fluctuating populations ($F_{1,86} = 4.93$, $P = 0.009$). Despite these potential sources of bias, however, controlling for their effects did not change our conclusions in that we found migration and molt strategies, brood number and diet complexity consistently more likely to predict FAD trends than the rest of studied variables such as sexual selection indices (Appendix S5). Therefore our results are likely to be robust.

Discussion

Our study has provided three main results. First, the estimate of phylogenetic dependence was low in all models of FAD trends. Second, the degree to which birds advanced their spring arrival dates was significantly related to main life-history components such as migration, molt, reproduction, and foraging strategies.

Table 2 Comparison of multivariate PGLS models for FAD trends ($n = 113$ species)

Models	k	AIC$_c$	Δ_i	ω_i
Brood number + diet	3	163.11	0.00	0.12
Migration + molt2	3	163.35	0.24	0.10
Migration + diet + brood number	4	163.53	0.42	0.09
Migration + diet + molt2	4	163.81	0.70	0.08
Migration + diet	3	164.22	1.11	0.07
Migration	2	164.65	1.54	0.05
Brood number + diet + molt1	4	164.76	1.65	0.05
Brood number + diet + molt2	4	165.00	1.89	0.04
Migration + diet + brood number + molt2	5	165.10	1.99	0.04
Molt1 + molt2 + migration	4	165.81	2.71	0.03
Migration + brood number	3	165.82	2.72	0.03
Migration + brood number + molt2	4	165.89	2.79	0.03
Diet + molt2	3	166.20	3.10	0.02
Migration + diet + brood number + molt1	5	166.41	3.30	0.02
Brood number + diet + molt1 + molt2	5	166.52	3.41	0.02
Migration + diet + molt1 + molt2	5	166.77	3.66	0.02
Molt1 + molt2	3	166.85	3.74	0.02
Diet	2	166.94	3.84	0.02
Migration + molt1	3	167.17	4.07	0.02
Migration + diet + molt1	4	167.22	4.12	0.01
Molt1 + molt2 + diet	4	167.25	4.15	0.01
Brood number + molt1	3	167.52	4.41	0.01
Molt2	2	167.56	4.45	0.01
Molt1 + molt2 + brood number	4	167.82	4.72	0.01
Migration + diet + brood number + molt1 + molt2	6	167.99	4.88	0.01
Migration + brood number + molt1	4	168.04	4.94	0.01
Diet + molt1	3	168.16	5.05	0.01
Brood number	2	168.17	5.06	0.01
Migration + brood number + molt1 + molt2	5	168.20	5.10	0.01
Brood number + molt2	3	168.45	5.35	0.01
Molt1	2	168.83	5.73	0.01

AIC$_c$ values, 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. 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.

Predictors abbreviated as: migration: migration strategy (short/long distance), brood number: annual number of broods, diet: complexity of the diet, molt1: timing of postbreeding molt (summer/winter quarters), molt2: occurrence of prebreeding molt (present/absent).

FAD, first arrival dates; PGLS, Phylogenetic Generalized Least Squares.

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Third, FAD trends were unrelated to various proxies of sexual selection. We discuss each of these results in detail below.

Throughout our analyses we found that the degree of phylogenetic dependence did not differ significantly from zero. This means that the advancement of spring arrivals can be treated as a species-specific response that adapts readily to current conditions with little phylogenetic inertia. This finding is in accordance with Rubolini *et al*. (2007) who documented that the change in spring arrival dates was significantly repeatable among species. In this respect, FAD trends seem to be similar to many physiological and life-history traits that often exhibit low levels of phylogenetic dependence (Garamszegi *et al*., 2005; Bókony *et al*., 2008; Tökölyi *et al*., 2008). Thus, while phylogeny explains a significant proportion of variation across species (e.g. in FAD trends; Rubolini *et al*., 2007), this variation appears to be influenced more strongly by adaptation (e.g. to climate change) than by common descent.

One of the strongest predictors of FAD trends was migratory strategy: species that migrate shorter distances advanced their arrivals to a greater extent than long-distance migrants. This supports the conclusion of several recent studies in both Europe and North-America, using both the first and mean or median dates of arrivals (e.g. Lehikoinen *et al*., 2004; Macmynowski & Root, 2007; Rubolini *et al*., 2007; Thorup *et al*., 2007; Miller-Rushing *et al*., 2008; Møller *et al*., 2008; but see Jonzén *et al*., 2006). Long migration routes may constrain the degree to which arrivals can be advanced in response to climate change for several reasons (reviewed by Lehikoinen *et al*., 2004). On the one hand, migration of long-distance migratory bird species may be under stronger endogenous control. This would, however, imply a strong phylogenetic dependence, but we have found just the opposite. On the other hand, if short-distance migrants are exposed to warming climate all year round while southerly wintering species only in late spring (Lehikoinen *et al*., 2004), short-distance migrants may have more as well as better cues to match their phenology to.

Besides the effect of migration strategy, three other life-history components appeared important in explaining the change in spring migration phenology. First, species with more complex diets advanced their FADs to a greater extent than more specialist species. A wider variety of consumed food might allow generalist species to find appropriate food during migration and upon arrival on the breeding grounds, and thus they might be able to better respond to global change than more specialized foragers. This latter finding parallels theoretical expectations that a wider temporal distribution of food resources should enable stronger response to an advance in food peak date if both prebreeding mortality and competition for territories are relatively low (Jonzén *et al*., 2007), which might indeed be the case for the relatively large-bodied, nonhole nesting species in our sample. Second, the more broods a species produces annually, the more it has advanced its spring arrival. This corroborates the result of Møller *et al*. (2008) and suggests that species that have the chance to raise more broods in a season are under stronger selection for earlier arrival, which might accelerate their response to climate warming. Third, species without prebreeding molt and, to a lesser extent, those molting primaries at summer quarters, advanced their FADs more than species with a prebreeding molt and those that molt their flight feathers at their winter quarters. This implies that the costs associated with molting in late winter and especially in early spring might hinder the birds' response to climate change, i.e. species that have to renew their feathers before migration cannot arrive as early to the breeding grounds as species without this constraint. In sum, our results highlight the importance of the time and energetic constraints of the species' life history and ecology in their propensity to adapt to a warming climate.

On the other hand, we found no effect of habitat, generation time, and nest type on the advancement of spring arrivals. This suggests that these traits have minor impact on FAD trends in the species investigated here, but we do not claim that they may have no significance at all in general. First, our dataset is dominated by species with aquatic habitats (mostly waterbirds and shorebirds), whereas an American study investigating more habitat types found that grassland species advanced their spring arrival significantly more than other birds (Butler, 2003). Second, species in our dataset begin reproducing when 1–3 years old, thus they may have no time lag in their response to global warming. However, adaptation to climate change may be slower in species with longer generation time such as seabirds, whose climatic responsiveness tends to correlate positively with longevity (Sandvik & Erikstad, 2008). Third, due to the nature of our study site, we had very few data on secondary cavity-nesting species, thus our analyses may have lacked the power to detect any effect of nest site. Among our short-distance migrants, cavity-nesting species seemed to have advanced their FADs more than open-nesting species, which may support that strong competition for vacant cavities intensifies the selection for early spring arrival (Rubolini *et al*., 2005). However, due to our small sample size for short-distance cavity-nesters, this issue requires further testing, especially because theory predicts that stronger competition for nest sites should weaken the phenological response to a shift in food peak date in most cases (Jonzén *et al*., 2007).

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In contrast to previous findings of Spottiswoode *et al*. (2006), our results consistently failed to support the importance of sexual selection in the advancement of spring arrivals. Neither the various measures of social and genetic mating system, nor the expression or dimorphism of several sexually selected traits were related to FAD trends, even when we controlled for migration distance. The single exception was the interaction between EPP rate and migratory strategy, indicating that among our 11 short-distance migrants, the greater the rate of EPP, the greater the advancement in arrivals. Thus, strong selection by sperm competition might facilitate the advancement of spring arrivals at least in some species that are less constrained by migration distance. However, given the small sample size of both our latter result and the study of Spottiswoode *et al*. (2006; $n = 9$ species), the generality of sexual-selection effects on arrival trends remains uncertain. Notably, the relationship between the 'sexual selection index' and the change in arrival dates was significant only for the median passage date of the annual population, not for the first arrival dates (Spottiswoode *et al*., 2006) which we used in our study. Although median passage dates are potentially less biased by deviant individuals and observation errors than FADs, the earliest migrants may respond more strongly to climate change than the rest of the population (Lehikoinen *et al*., 2004). Therefore, the almost complete lack of sexual-selection effects on FAD trends, as demonstrated by our relatively large sample overall, suggests that climatic responsiveness is not strongly influenced by the intensity of mating competition in birds. Similarly, Møller *et al*. (2008) found no relationship between sexual dichromatism and change in mean migration date in a diverse set of a hundred bird species.

To summarize, we have shown in a diverse set of avian species that the response of migration phenology to climate change (as reflected by the advancement of FAD) seems to be constrained by long-distance migration, specialized diet, and extensive prebreeding molt, and accelerated by selection for greater fecundity. These constraints and selection pressures appear to have greater effect on FAD trends than the strength of competition for mating and breeding opportunities. These findings demonstrate that characteristics of life history and ecology may play a fundamental role in how well the species can adapt to the environmental changes due to global warming.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. First arrival date (FAD) trends calculated as the slopes of linear regressions of the annual value (Julian day) of first sighting in Hortobágy against year.

Appendix S2. Data on life history, ecology and sexual selection used in the study.

Appendix S3. Component loadings of the principal components used as indices of sexual selection.

Appendix S4. Topology of the composite phylogeny and sources of phylogenetic information used.

Appendix S5. Bivariate phylogenetic relationships of FAD trends with life-history traits, controlled for potential confounding variables. The table reports *P*-values for overview.

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