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Which are the phenologically flexible species? A case study with common passerine birds

Jean-Pierre Moussus, Joanne Clavel, Frédéric Jiguet and Romain Julliard

J.-P. Moussus (moussus@mnhn.fr), F. Jiguet and R. Julliard, MNHN-CNRS-UPMC, UMR 7204, Conservation des espèces, Restauration et Suivi des Populations, 55 rue Buffon, FR–75005 Paris, France. – J. Clavel, Dépt Arts et Sciences de la communication, Faculté de Philosophie et Lettres, Place du 20 août, Univ. de Liège, BE-4000 Liège, Belgium.

One of the most consensual ecological effects of the current climate warming is the alteration of the environmental timing of ecosystems. Phenological shifts, at different levels of food webs, are predicted to have major effects on species assemblages. Indeed it is unlikely that all species should be able to respond to the phenological shifts of their environment evenly. Yet questions remain about the specific traits that predict the ability of a species to track the temporal fluctuations of its environment. In this study, we use data from the French Constant Effort Site ringing program over a 20 years period (1989–2008) to estimate the ability of 20 common passerine species to adjust their breeding phenology to spring temperature variations. We show that the sensitivity of species breeding phenology to climate relates to species mean migration distance, species' thermal and habitat niche breadth and brain mass. Species with the broadest ecological and thermal niches, the shortest mean migration distances and the largest brains were most able to adjust their breeding phenology to temperature variations. Our results thus identify long distance migrants and ecological specialists as species that could most suffer from the future expected climate change and suggests phenological adjustment as one possible mechanism underlying the replacement of specialist species by more generalist ones, the so called functional biotic homogenization.

Among important changes caused by the current global warming, changes in the timing of biological events, called phenological changes, have received particular attention during the last two decades (Parmesan and Yohe 2003). In terrestrial ecosystems, numerous studies show, among others, phenological shifts in the timing of budburst (Korner and Basler 2010), flowering (Menzel et al. 2006), caterpillar emergence (van Asch and Visser 2007), avian spring migration (Jonzén et al. 2006) or avian breeding (Crick and Sparks 1999, Both et al. 2004).

Because species interact within complex food webs, different phenological changes in different species can lead to resource mismatching between trophic levels (Durant et al. 2007, Both et al. 2009). Differences in the phenological responses to climate changes between organisms can relate to the physiological mechanisms by which a species responds to climatic fluctuations. In plants, budburst or flowering times are controlled by day length and temperature (Korner and Basler 2010). Insects spending winter in resistance forms also have time emergence dates based on temperature (van Asch and Visser 2007). In such organisms, phenological responses result from the influence of climatic parameters on physiology without important decision making processes (Both et al. 2009). On the contrary, bird breeding times are thought to be the result of decision making involving environmental information gathering (Both et al. 2009, Thomas et al. 2010). Laying dates should occur so that maximal resource requirements of the offspring match the resource abundance peak (Visser et al. 2006). Although temperature (Visser et al. 2009) and even solar activity (Visser and Sanz 2009) have been shown to directly influence laying dates in the great tit *Parus major*, more complex environmental cues particularly involving vegetation development, have also been thought to play a part in decision making (Bourgault et al. 2009, Thomas et al. 2010).

There is now accumulating evidence for birds, that a lack of phenological response is detrimental for populations. The resource match/mismatch hypothesis (Cushing 1990) offers an interesting framework to study the mechanisms underlying this relation because it replaces species within food webs and stresses the importance of inter specific relations. The absence of phenological trends has indeed been related to steeper population declines in migratory species (Møller et al. 2008) while weaker phenological responses of migratory return dates to spring temperatures are also correlated to lower population growth rates (Both et al. 2006).

The purpose of the present study is to look for potential correlates of species' ability to track climate fluctuations efficiently in order to identify groups of species susceptible of suffering most from the current climatic changes, which are predicted to amplify during the next decades (IPCC 2007). Because the predicted climatic changes not only consist in a linear increase in mean temperatures but also in an increase in climatic variability (IPCC 2007), the timing of resource abundance peaks could become less predictable in the future. Two different types of constraints could limit species efficiency in tracking phenological changes in their environment.

First, a number of life-history traits relate directly to the organization of species' lifecycles and set constraints on the breeding phenology. Among these traits, species' migration strategy could account for species' variable phenological adjustment capacities (Jones and Cresswell 2010). Indeed, if the timing of the breeding environments become increasingly variable and the tracking of such variability involves species' sensitivity to local cues, it can be expected that migrant species, especially trans-Sahara migrants should be less able to time their breeding phenology in relation with meaningful variables such as spring temperature on their breeding grounds (Gwinner 1996, Both 2010). Moreover, previous work has shown that migration strategy has a strong phylogenetical inertia (Bohning-Gaese and Oberrath 1999). Besides migration strategy, the number of brood a species raises during one breeding season could also be related to species' ability to track climate fluctuations, as the reproductive output of multi brooded species could be less dependent on the match between offspring requirements and the abundance peak of a single group of resources (Jiguet et al. 2007).

The second type of constraints on phenological adjustment emerges from the ecological niche history. Gathering information concerning the timing of the breeding environment should require important cognitive abilities. Yet such complex information gathering systems are unlikely to be uniformly distributed among species because of evolutionary contingence (Dall and Cuthill 1997). Species which evolved a broad ecological niche (Hutchinson 1957), the so called generalist species, tend to have more developed information tracking systems given the variety of resources they can exploit (Dall and Cuthill 1997). Such species have been shown to cope better with environmental changes than specialist species with narrower ecological niches (Kotze and O'Hara 2003, Julliard et al. 2004, Munday 2004). Thus, niche width could correlate positively with species' ability to adjust their breeding phenology to annual climatic fluctuations.

In this study, we estimate the phenological adjustment capacity (PAC) of the breeding time of 20 common passerine species to late winter and spring temperature averages. We use the data originating from the French Constant Effort Site ringing scheme (CES) to compute the phenology of the relative proportion of juveniles in total captures over the 1989–2008 period. We then use the estimated PAC to look for correlations with species' ecological and physiological features namely species' migration distance, average annual brood numbers, diet, brain size and ecological niche breadth.

Material and methods

Bird ringing data

Data originate from the French Constant Effort Site Program (CES) (Julliard et al. 2004). CES are standardized bird ringing schemes using mist nets during the breeding period. Standardization on CES relies on a fixed position and number of nets used per site (between 10 and 50), and on a fixed number and similar dates of capture sessions per site (usually between three and five, depending on the site, with dates ranging from the beginning of May to the end of July, and covering at least two months for a given site). The scheme started in 1989 and the data used in this study cover the period 1989–2008.

In the field, each captured bird is individually ringed to avoid double counting, and the species and age (breeding adults or young of the year) are determined unambiguously from plumage (including pattern of wear) by experienced volunteer bird ringers. All data for which there was uncertainty as to the age of birds were excluded ($<1\%$). Over the 20-year period the data were collected from 216 CES sites representing 1012 site-years. Species for which adults and juveniles were captured each year throughout the study period were included in the study. Thus, 20 species were considered for a total of 131 588 captured birds (*Acrocephalus scirpaceus* n = 11 715, *Aegithalos caudatus* n = 3926, *Certhia brachydactyla* n = 926, *Cyanistes caeruleus* n = 5707, *Erithacus rubecula* n = 10 904, *Fringilla coelebs* n = 2522, *Hippolais polyglotta* n = 2967, *Luscinia megarhynchos* n = 4741, *Parus major* n = 12 493, *Phylloscopus collybita* n = 12 672, *Phylloscopus trochilus* n = 2937, *Poecile montanus* n = 1298, *Poecile palustris* n = 1293, *Prunella modularis* n = 5167, *Sylvia atricapilla* n = 24 969, *Sylvia borin* n = 4035, *Sylvia communis* n = 5044, *Troglodytes troglodytes* n = 2976, *Turdus merula* n = 12 149 and *Turdus philomelos* n = 3147).

Estimating a breeding time index

For each species and each year, a breeding time index (BTI) was estimated using a curve fitting method (Moussus et al. 2009). The main features of this method will be described here but for further details concerning the algorithm and model justification please refer to (Moussus et al. 2010). It is assumed that the seasonal distribution of the proportion of juveniles within total captures reaches an inflexion point and that the shape of this distribution remains constant for different years. Under these assumptions seasonal distributions in the proportion of juveniles within total captures for two different years only differ in their timing (i.e. they match if a certain temporal shift is applied to one of them). This method aims at estimating this temporal shift necessary to make two different year's distributions match using an iterative algorithm. To achieve this, numbers of captures of juveniles and total captures were summed over all CES sites per species per year and per day (in days after 1 April). We will illustrate the functioning of the method with an example, the estimation of the temporal shift of the breeding time for the great tit *Parus major* in 2006 and 2007. In this case 2007 is set as the reference year and 2006 will be the year for which data are iteratively temporally shifted until they match the data of 2007. This is done by fitting the following generalized additive mixed effects model (GAMM) to the capture data of both years (2006 and 2007 for example): (no. of juveniles, no. of adults)~ spline function (date + t) with a Binomial error and where t is worth 0 for the 2007 data (set as the reference) and ranges between –30 and 30 days by 1-day increment for the 2006 data. To account for between years variations of the overall productivity, year was considered as a random categorical variable in the GAMM. The fit of each model corresponding to each value of t is monitored by its Akaike information criterion (AIC) (Akaike 1981). So, for one pairwise comparison (between two years) 61 AIC values are recorded. As the 61 models have the same number of parameters, minimizing AIC is equivalent to maximizing likelihood. This is achieved by fitting a quadratic regression ($AIC \sim t + t^2$) using the 10 AIC values around the smallest local minimum of AIC versus t function. If a is the second degree coefficient, b the first degree coefficient and c the intercept of the regression, then the AIC as a function of t is minimized for $t_{min} = -b/2a$ which is considered as an estimation of the temporal shift between the two breeding seasons. Moreover, the standard error of this estimation is given by the second derivative of the log-likelihood and is worth 1/a. For each year, temporal shifts were estimated with all the other years. Rarely, the GAMM fails to converge and the estimation of the phenological shift between the two compared years cannot be produced directly (167 out of 7600 estimations). These gaps were filled by recalculating the shifts using linear combinations of other pairwise comparisons. For example, if the temporal shift between year 2006 and 2007 could not be estimated for one species but the shifts between 2006–2003 and 2003–2007 were available, then the shift between 2006 and 2007 was calculated as the sum of shifts 2006–2003 and 2003–2007. All possible linear combinations involving two shifts were used and the reconstructed value was treated as the average of the sums. At the end of this first calculation step, the breeding phenology of each year is thus compared to the breeding phenology of the other 19 years.

Eventually for each species and each year, the breeding yime index (BTI) was defined as the average temporal shift between one year and the others (as all pairwise comparisons were previously estimated). Therefore, it is the relative anomaly of the breeding phenology across the 1989–2008 period.

Because the method used in the present study is rather new it might raise several concerns particularly regarding the small number of visits per site in the French CES scheme compared to other European CES schemes and the restricted spread of visits (ending mid-July while not all young have fledged). Although these concerns are fully valid when trying to estimate productivity from CES data, it is not the case when trying to estimate phenological variation from these data. Actually, the crucial moment regarding the breeding phenology happens when the juveniles leave the nest and become catchable on CES sites. This crucial moment occurs during June when the young fledge. June is also the period when most visits are done in the French CES program. Regarding the low number of visits per site, the methodology was first developed for Breeding Bird Survey type of data where sites are visited only twice. The method takes advantage that the different sites are visited at different dates. By using the information for all sites together, we eventually are able to reconstitute accurately the phenology curve of what is measured. It works very well for BBS data, yet the phenological signal is even more complex with u- or n-shaped phenology (Moussus et al. 2009). For the 20 common passerine species (which were selected on the basis of the amount of information available) we feel thus that the French CES scheme brings sufficient phenological information regarding the breeding phenology of these species.

Estimating species' phenological adjustment to temperature

For each species, the phenological adjustment capacity (PAC) to climate was defined as the slope of the temperature effect in a generalized linear model (GLM) relating the BTI with temperature and linear year. Because all the phenological shifts were not estimated with the same accuracy, the inverse squared standard estimation errors of the BTI were used as weights in the regressions.

Climatic data

Temperature data were obtained from the website of the European Climate Assessment and Dataset (ECAandD) (<http://eca.knmi.nl/>). The monthly mean daily temperature data of 57 meteorological stations located across the entire country were averaged to produce the climate variable (Temp) used in the study. Temp was defined as the average mean daily temperature from January to May. A large temporal window for the temperature averages was chosen deliberately in order to limit the number of tests. Indeed, the breeding times of a majority of species seem to occur earlier when late winter or early spring temperatures are higher (Crick and Sparks 1999, Both and Visser 2001, Visser et al. 2006). The focus of this study was not to identify precisely the best fitting temporal window for each species but to find ecological correlates to the ability of these species to adjust their breeding phenology. In this respect, the climatic temporal window was defined broadly so that it could comprise the relevant information for all species. Moreover, if the study had been performed with the best fitting temporal window for each species, the interpretation of the results would not have been straightforward. We assume that this large temporal climatic window encompasses information regarding the timing of all the considered species.

Defining explanatory variables

We assumed that the potential drivers for species' PAC belonged to two very different categories. The first category of potential predictors for species' PAC relates to the life-history traits which are directly involved in species' lifecycle, particularly those which directly influence the timing of breeding. The mean annual number of broods was thus considered (Brood) and taken from Jiguet et al. (2007). Species' migratory strategy (MigrDist) was included in the study as the average log-distance between breeding and wintering grounds of the French breeding population based the French ringing database (Jiguet et al. 2007).

The second category comprises features the relations between species and their environment. We therefore tested the relations between the PAC and various continuous specialisation indices: first a habitat specialisation index (SSI) calculated as the variation coefficient (standard deviation/average) of a species density among 18 habitat classes

(Julliard et al. 2006) using the French Breeding Bird Survey (BBS) counts. This habitat specialization index has been shown to predict large scale population trends of common bird species in France (Julliard et al. 2004). This index represents a broad measure of species' realized ecological niche at the scale of a country.

Species' thermal range which represents a thermal specialisation index (TSI) as it measures a species thermal niche width, as the difference between the thermal maximum and thermal minimum (mean spring/summer temperature of 5% hottest/coldest atlas breeding cells in Europe, Hagemeijer and Blair 1997, Jiguet et al. 2006).

Species' diet could also influence PAC. It is possible that species relying on multiple resources like omnivorous species have better PACs than species relying on fewer resource types. Diet (as insectivorous or omnivorous, Diet) was thus also included in the set of explanatory variables and was taken from Gregory et al. (2007).

Lastly, several studies suggest that phenological adjustment in birds is based on the gathering of environmental cues providing information on the timing of the species' resources. It is likely that such information gathering systems relate to species' cognitive abilities (Bourgault et al. 2009, Thomas et al. 2010). To account for such effects, brain mass (BrainMass) available from Sol et al. (2010), were used as correlates to the PAC. Because there is an allometric relation between brain mass and body mass, the latter (BodyMass) was always included in the models testing the relationships between brain mass and other variables. The residuals of a linear regression between BrainMass and BodyMass were used to draw the figures related to BrainMass (Fig. 1a, 2c). Brain mass was not available for two species in the dataset, the melodious warbler *Hippolais polyglotta* and the short-toed treecreeper *Certhia brachydactyla*.

Statistical analyses

Treating species as independent replicates would not be correct given their phylogenetic relatedness (Harvey et al. 1991). It is therefore possible that some explanatory variables might be very similar between closely related species. To take phylogenetic relatedness into account in our dataset, we used the generalised least squares phylogenetic comparative method. We used package 'ape' of the R software (R Development Core Team 2008) to run the GLSs assuming a Grafen correlation structure (Grafen 1989) for the model dependence because branch lengths were not available (and therefore all set to 1). The phylogeny used to build the tree was taken from (Jonsson and Fjeldså 2006), see Appendix 1 for the phylogenetic tree used in this study). First, explanatory variables were tested alone in the GLSs. The effects of those variables with significant contributions to species' PAC were then tested including the other significant predictors. This approach allows testing direct correlations in the first place while the multiple regressions allow identifying more complex effects of the predictor variables. The inverse squared standard estimation errors of the PACs were used as weights in the GLSs. The relationships between the different explanatory variables were investigated using the same approach.

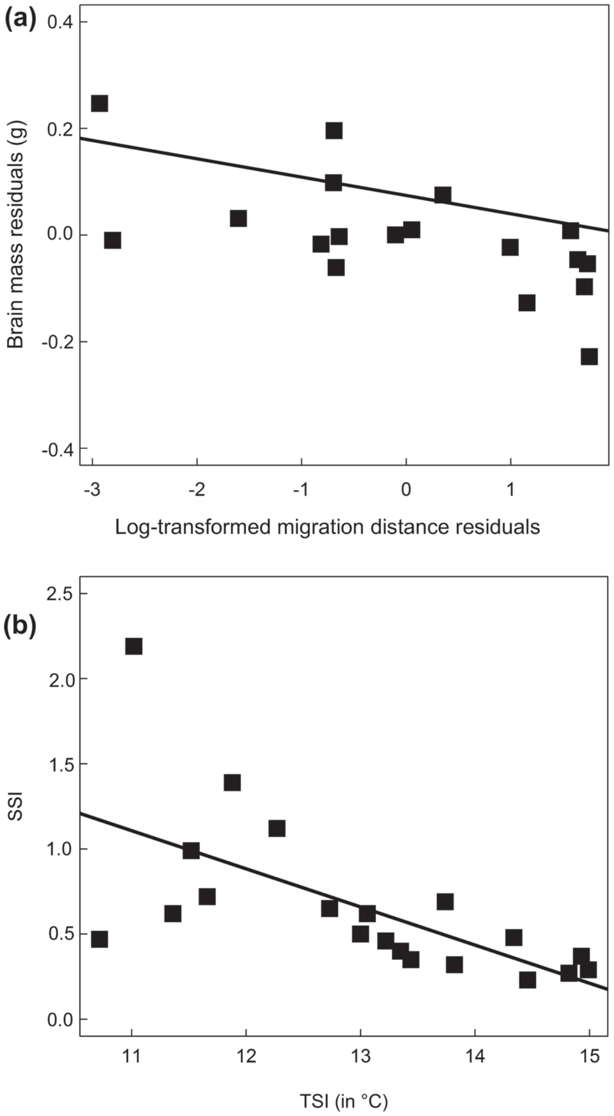

Figure 1. Significant relationships between the potential predictors of species' phenological adjustment capacity (PAC) for 20 common passerine species. (a) Relation between log-transformed migration distance and the average brain mass and (b) between thermal (TSI) and habitat (SSI) niche breadths. Regression lines from the GLS models are shown.

Results

For 15 species out of the 20 included in the study, the breeding time index was negatively correlated with average temperatures from January to May although this relation was significant for only three species namely the long-tailed tit (slope = –6.6, SE = 1.8), the great tit (slope = –2.68, SE = 1.05) and the winter wren (slope = –5.24, SE = 1.71), Table 1. There was a significant relation between two potential predictors considered for species' PAC. The relation between log mean migration distance and brain mass was marginally significant (slope = –0.03, SE = 0.02, $F_{1,16}$ = 4.34, p = 0.05, Fig. 1a), while species' habitat specialization index was negatively correlated to species' thermal niche breadth (slope = –0.22, SE = 0.06, $F_{1,18}$ = 12.56, p = 0.002,

Table 1. Phenological adjustment capacities (PAC), their standard errors (SE) and the different explanatory variables used in this study for 20 common passerine species. BrainMass: average total brain mass, Body Mass: average total body mass, SSI: species habitat specialization index, TSI: thermal specialization index, MigrDist: log mean migration distance, Brood: average annual number of broods and Diet: insectivorous (I) or omnivorous (O).

Species	PAC (SE)	SSI	TSI (°C)	MigrDist (log km)	Brood	Diet	BodyMass (g)	BrainMass (g)
Acrocephalus scirpaceus	1.26 (1.83)	2.19	11.02	3.65	1.2	I	12.3	0.48
Aegithalos caudatus	–6.6 (1.80)	0.62	13.06	–0.89	1	I	8.2	0.5
Certhia brachydactyla	–2.58 (2.20)	0.62	11.36	0.05	2	I	NA	NA
Cyanistes caeruleus	–2.34 (1.95)	0.35	13.44	1.24	1.2	O	10.79	0.65
Erithacus rubecula	–1.3 (1.15)	0.48	14.34	2.03	2	I	16.75	0.66
Fringilla coelebs	–1.58 (2.69)	0.27	14.82	1.39	1	O	24.26	0.77
Hippolais polyglotta	1.37 (1.47)	0.72	11.66	3.7	1	I	NA	NA
Luscinia megarhynchos	1.15 (0.80)	0.47	10.72	3.58	2	I	21.17	0.73
Parus major	–2.68 (1.05)	0.29	14.99	1.29	1.5	O	17.02	0.85
Poecile montanus	–1.99 (3.07)	1.39	11.88	–1	1	O	10.2	0.79
Poecile palustris	–0.76 (2.25)	0.99	11.52	0.33	1	O	10.6	0.58
Phylloscopus collybita	–2.06 (1.45)	0.46	13.22	3.07	2	I	8.02	0.38
Phylloscopus trochilus	0.87 (1.07)	1.12	12.27	3.68	1	I	9.92	0.31
Prunella modularis	–2.42 (1.58)	0.5	13	1.9	2	I	20.41	0.71
Sylvia atricapilla	–1.36 (1.20)	0.32	13.82	2.99	1	O	19.37	0.67
Sylvia borin	0.25 (1.37)	0.69	13.74	3.72	1	O	18.22	0.62
Sylvia communis	–0.49 (1.34)	0.65	12.73	3.6	1	O	14.09	0.56
Troglodytes troglodytes	–5.24 (1.71)	0.37	14.93	1.11	2	I	9.27	0.51
Turdus merula	–1.13 (2.13)	0.23	14.46	1.88	2.5	O	98.17	1.92
Turdus philomelos	–2.83 (2.94)	0.4	13.35	2.7	2.5	O	69.64	1.59

Fig. 1b). Hence, habitat specialists are also thermal specialists because a high habitat specialization index refers to a narrow habitat niche. Log-transformed migration distance was significantly correlated to species' adjustment capacities. Species wintering further away from their breeding grounds are thus less able to time their breeding cycle in relation with spring temperature (slope = 1.29, SE = 0.20, Fig. 2b). The mean annual brood number was not significantly related to species' PAC (slope = –1.13, SE = 1.16). Species' niche habitat and thermal niche breadth measures were related to the PAC as species with wider thermal ranges and low habitat specialization indices were better able to cope with climatic variability (TSI: slope = –0.80, SE = 0.19; SSI: slope = 2.38, SE = 1.06, Fig. 2a, 2d). Species with larger brain mass were significantly more able to adjust their breeding phenology (slope = –10.4, SE = 4.75, Fig. 2c) while there was no evidence that PAC was influenced by species' diet ($F_{1,18} = 0.74$, $p = 0.40$). Because of the correlations between PAC predictors described here above (between both niche breadth measures and between log-transformed migration distance and brain mass), only the best univariate PAC predictors were kept in a multiple GLS model, therefore log-transformed migration distance and thermal niche width which effects on species' PAC remained significant (Table 2).

Discussion

Climate variability is going to increase during the next century. Hence the frequency of extremely mild winters and hot springs will increase as well as the frequency of cold episodes (IPCC 2007). Therefore, the phenology of birds breeding environment should become increasingly variable and difficult to anticipate. All species should not be able to track these increasing fluctuations similarly.

The scope of the present study is to document large scale correlations in order to identify ecological traits related to species' phenological adjustment capacity. Surely, the breeding phenology of individual bird pairs relates to the conditions they experience locally. However, an important part of local climate variations relate to large scale climatic variables. These large scale climatic indices then often outperform the local weather variables in explaining phenological variation in some components of the life cycle. This kind of approach necessarily excludes some (potentially interesting) local-scale phenomena, but this is common to all such large-scale studies. For example, regional variations of the phenological response to temperature cannot be addressed with the French CES dataset simply because estimating phenological variation requires pooling data originating from enough sites so that the phenology curve is meaningful.

This study identifies migration distance as the main ecological correlate of species' ability to time their breeding cycle in relation with temperature on their breeding grounds. All five species for which the PAC was positive are transsaharan migrants. Migratory species have long been considered as a group particularly vulnerable to climate change especially to resource mismatching (Jones and Cresswell 2010). Indeed, because the regional patterns of climate fluctuations are different (IPCC 2007), the rate of climate change on their wintering grounds can differ markedly from the one on their breeding grounds (Jones and Cresswell 2010). Yet migration phenology sets constraints on the breeding phenology in such species. In the pied flycatcher *Ficedula hypoleuca*, laying date has advanced over the past two decades but the selection differential towards earlier laying, and the absence of any temporal trend in migratory return dates suggest that migration phenology impairs adequate breeding responses to the local increase in temperatures (Both and Visser 2001). At least two different mechanisms can help understanding such

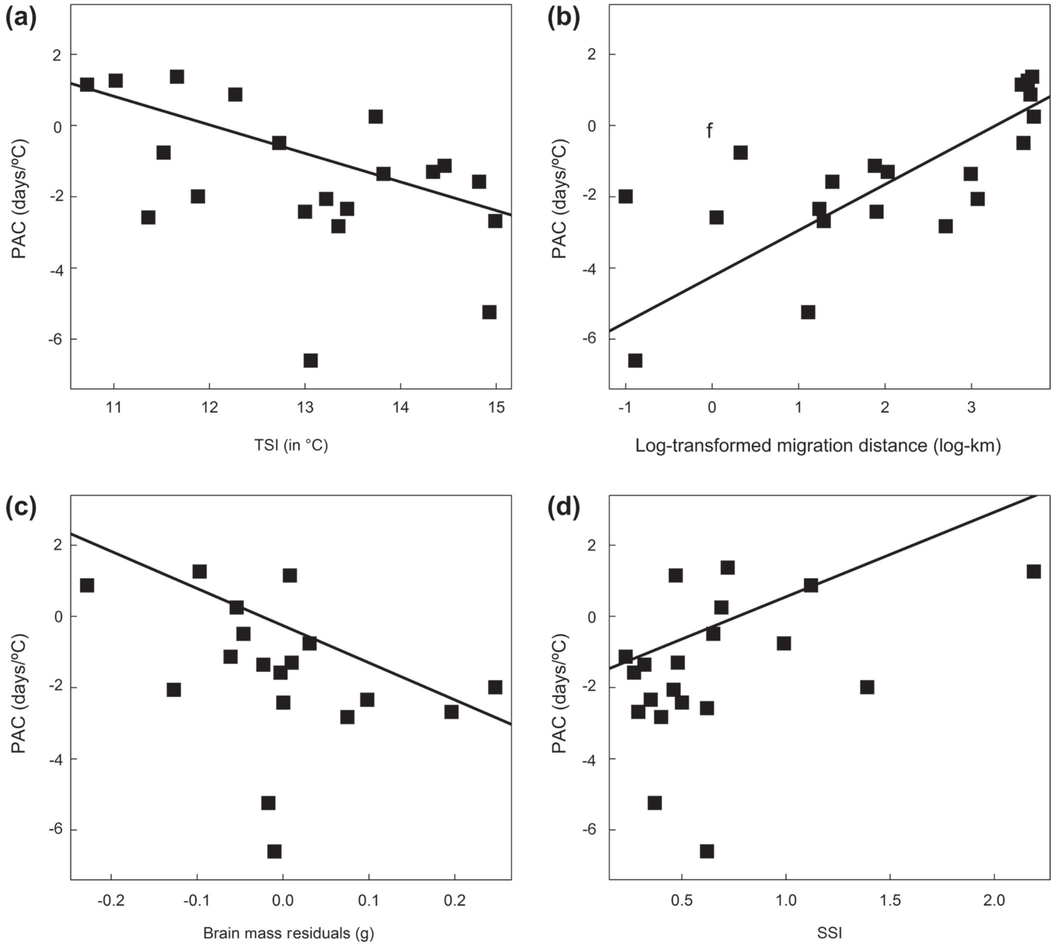

Figure 2. Relationships between species' phenological adjustment capacity (PAC) for 20 common passerine species and (a) the thermal niche breadth (TSI), (b) the log mean migration distance (MigrDist), (c) the average brain mass (BrainMass) and (d) the habitat specialization index (SSI). Regression lines from the GLS models are shown since the four relationships are statistically significant.

phenological inflexibility in long distance migrants. First, a number of studies show that migration timing is controlled endogenously by daily and circannual rhythms (Gwinner 1996) and relate to environmental information that is not related to climate change such as photoperiod (Both 2010). Such determinism is more pronounced in species wintering close to the equator because in these areas, environmental constancy does not provide valuable timing cues to the birds (Gwinner 1996). The wintering areas of the six trans-Sahara migrant species included in this study, namely the reed warbler, the common whitethroat, the garden warbler, the willow warbler, the melodious warbler and the common nightingale comprise equatorial regions. These species could thus time their migratory return based on such non informative cues and their laying date could therefore not relate to the climate on their breeding grounds. The second mechanism which could impair long distance migrant species to adjust their breeding times to local climate also relates to meteorological constraints during their journey back to their breeding grounds. In order to achieve such long return journeys, long-distance migrants rely on different stopover sites where they refuel before heading towards their breeding grounds (Saino et al. 2007). Climatic conditions might show substantial inter annual variations on these sites, thus altering the quality and quantity of resource which can delay the departure of the birds. Moreover, degraded meteorological conditions 'en route' can also force birds to stop (Tottrup et al. 2008). All climatic conditions the birds experience during their journey do not obviously relate to the climate conditions on their breeding grounds and could therefore act as severe constraints on phenological adjustment of the breeding time to climate fluctuations (Both 2010).

Table 2. Effects of different explanatory variables on species' phenological adjustment capacity (PAC) to spring temperature. The relationships between PAC and the different variables were investigated using generalized least squares (GLS) models. The effects of the variables significantly related to PAC were then tested in multiple predictor GLSs (TSI and MigrDist).

Explanatory variable	F	DF	p	slope (SE)
SSI	4.96	1.18	0.04	2.38 (1.06)
TSI	18.12	1.18	0.0005	–0.80 (0.19)
TSI MigrDist included	8.78	1.17	0.009	–0.49 (0.16)
Brood	0.95	1.18	0.34	–1.13 (1.16)
MigrDist	39.74	1.18	<0.0001	1.29 (0.20)
MigrDist TSI included	30.04	1.17	<0.0001	1.04 (0.19)
Diet	0.74	1.18	0.40	
BrainMass	4.77	1.16	0.045	–10.40 (4.75)

Species with smaller brain mass had reduced phenological adjustment capacities to climate on their breeding grounds.

There is accumulating evidence that cognitive abilities are related to population trends in birds. In British birds, long term population growth rates were related to brain size and more specifically to telencephalon size (Shultz et al. 2005). Yet the marginally significant relation between brain mass and log-transformed migration distances rather points out another underlying mechanism for the poor PAC of long-distance migrants. Indeed, previous work has shown that migrants have smaller brain sizes than resident species (Sol et al. 2010). Contrary to resident species which have evolved costly cognitive strategies to cope locally with seasonality and climate fluctuations, migrants face these issues by leaving inhospitable grounds which probably involved the development of different costly physiological abilities. Whereas migratory species do not face adverse winter conditions on their wintering grounds, this is the case for resident species which often have to change resources. Such cognitive abilities could then be useful when timing the breeding phenology in relation with local climate (Sol et al. 2010). Different evolutionary pathways could have lead to such differences. The high degree of phylogenetical inertia of the migratory behavior could rapidly lead to important declines in long distance migrants because of a lack of response to the current directional selection, and could well account for part of their current observed declines (Møller et al. 2008).

The last important predictor of species' PAC was their ecological niche breadth. Hence, species with wide thermal or habitat niches, in other words ecological generalists, were more able to track climate fluctuations in their breeding phenology than ecological specialists. The pattern of ecological generalists better able to cope with ongoing global changes has been ascertained by a number of studies concerning fish (Munday 2004), insects (Kotze and O'Hara 2003), birds (Julliard et al. 2004) and mammals (Fisher et al. 2003). It is also known that habitat, as well as thermal generalists suffer smaller population declines than both habitat and thermal specialists (Jiguet et al. 2007, 2010). Species with wide thermal ranges are also able to face extreme climatic events such as heat waves (Jiguet et al. 2006). Ecological generalism involves the development of complex information gathering systems which costs can outweigh the benefits in environments where resources' abundance and distribution are predictable (Dall and Cuthill 1997, Tosh and Ruxton 2008). Moreover, living on a variety of resources requires the development of physiological abilities such as digestive flexibility (Futuyma and Philippi 1987). The general pattern is thus that generalist species will be favored during substantial changes in the environment or in highly heterogeneous environments where specialist species are expected to decline. Our results show that different forms of flexibilities are to some extent correlated. This suggests the existence of an 'ecological flexibility syndrome', where on average habitat generalists are thermal generalists and phenological generalists (Clavel et al. 2011). This hypothesis is reinforced by the significant correlation found between habitat and thermal niche breadth. Moreover, habitat generalists, thermal generalists and phenological generalists currently seem to experience smaller declines on the long term (Julliard et al. 2004, Jiguet et al. 2010). Given the predictions under which such generalists should perform better in changing environments (Futuyma and Moreno 1988), their current fate brings evidence about how intensively global changes impact ecosystems. Moreover, because the gradual changes in phenology (Møller et al. 2008) as well as the phenological response to the migratory return to spring temperatures (Both et al. 2006) have both been related to species large scale population growth rates, these results provide evidence for one of the numerous putative mechanisms by which functional biotic homogenization is currently contributing to alter plant and animal communities (Devictor et al. 2007, Clavel et al. 2011).

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References

Akaike, H. 1981. A new look at the statistical-model identification. – Curr. Cont./Engin. Tech. Appl. Sci. 22–22.

Bohning-Gaese, K. and Oberrath, R. 1999. Phylogenetic effects on morphological, life-history, behavioural and ecological traits in birds. – Evol. Ecol. Res. 1: 347–364.

Both, C. 2010. Flexibility of timing of avian migration to climate change masked by environmental constraints en route. – Curr. Biol. 20: 243–248.

Both, C. and Visser, M. E. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. – Nature 411: 296–298.

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.

Both, C. et al. 2006. Climate change and population declines in a long-distance migratory bird. – Nature 441: 81–83.

Both, C. et al. 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? – J. Anim. Ecol. 78: 73–83.

Bourgault, P. et al. 2009. Food supplementation in distinct Corsican oak habitats and the timing of egg laying by blue tits. – J. Field Ornithol. 80: 127–134.

Clavel, J. et al. 2011. Worldwide decline of specialist species: toward a global functional homogenization? – Front. Ecol. Environ 9: 222–228.

Crick, H. Q. P. and Sparks, T. H. 1999. Climate change related to egg-laying trends. – Nature 399: 423–423.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations – an update of the match mismatch hypothesis. – Adv. Mar. Biol. 26: 249–293.

Dall, S. R. X. and Cuthill, I. C. 1997. The information costs of generalism. – Oikos 80: 197–202.

Devictor, V. et al. 2007. Functional homogenization effect of urbanization on bird communities. – Conserv. Biol. 21: 741–751.

Durant, J. M. et al. 2007. Climate and the match or mismatch between predator requirements and resource availability. – Climate Res. 33: 271–283.

Fisher, D. O. et al. 2003. Extrinsic versus intrinsic factors in the decline and extinction of Australian marsupials. – Proc. R. Soc. B 270: 1801–1808.

Futuyma, D. J. and Philippi, T. E. 1987. Genetic variation and covariation in responses to host plants by *Alsophila pometaria* (Lepidoptera, Geometridae). – Evolution 41: 269–279.

Futuyma, D. J. and Moreno, G. 1988. The evolution of ecological specialization. – Annu. Rev. Ecol. Syst. 19: 207–233.

Grafen, A. 1989. The phylogenetic regression. – Phil. Trans. R. Soc. B 326: 119–157.

Gregory, R. D. et al. 2007. Population trends of widespread woodland birds in Europe. – Ibis. 149: 78–97

Gwinner, E. 1996. Circadian and circannual programmes in avian migration. – J. Exp. Biol. 199: 39–48.

Hagemeijer, E. J. M. and Blair, M. J. 1997. The EBCC atlas of European breeding birds: their distribution and abundance. – T & AD Poycer.

Harvey, P. H. et al. 1991. The comparative method in evolutionary biology. – Oxford Univ. Press.

Hutchinson, G. E. 1957. Concluding remarks. – Cold Spring Harbor Symp. Quant. Biol. 22: 415–427.

IPCC 2007. Climate Change 2007: the physical scientific basis. Contrib. Working Grp I 4th Assess. Rep. Intergovernmental Panel on Climate Change 2007. – In: Press, C. U. (ed.), Intergovernmental Panel on Climate Change Cambridge.

Jiguet, F. et al. 2006. Thermal range predicts bird population resilience to extreme high temperatures. – Ecol. Lett. 9: 1321–1330.

Jiguet, F. et al. 2007. Climate envelope, life history traits and the resilience of birds facing global change. – Global Change Biol. 13: 1672–1684.

Jiguet, F. et al. 2010. Population trends of European common birds are predicted by characteristics of their climatic niche. – Global Change Biol. 16: 497–505.

Jones, T. and Cresswell, W. 2010. The phenology mismatch hypothesis: are declines of migrant birds linked to uneven global climate change? – J. Anim. Ecol. 79: 98–108.

Jonsson, K. A. and Fjeldså, J. 2006. A phylogenetic supertree of oscine passerine birds (Aves: Passeri). – Zool. Scripta 35: 149–186.

Jonzén, N. et al. 2006. Rapid advance of spring arrival dates in long-distance migratory birds. – Science 312: 1959–1961.

Julliard, R. et al. 2004. Common birds facing global changes: what makes a species at risk? – Global Change Biol. 10: 148–154.

Julliard, R. et al. 2006. Spatial segregation of specialists and generalists in bird communities. – Ecol. Lett. 9: 1237–1244.

Korner, C. and Basler, D. 2010. Phenology under global warming. – Science 327: 1461–1462.

Kotze, D. J. and O'Hara, R. B. 2003. Species decline – but why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. – Oecologia 135: 138–148.

Menzel, A. et al. 2006. European phenological response to climate change matches the warming pattern. – Global Change Biol. 12: 1969–1976.

Møller, A. P. et al. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. – Proc. Natl Acad. Sci. 105: 16195–16200.

Moussus, J.-P. et al. 2009. A method to estimate phenological variation using data from large-scale abundance monitoring programmes. – Bird Study 56: 198–212.

Moussus, J.-P. et al. 2010. Featuring 10 phenological estimators using simulated data. – Meth. Ecol. Evol. 1: 140–150.

Munday, P. L. 2004. Habitat loss, resource specialization, and extinction on coral reefs. – Global Change Biol. 10: 1642–1647.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – Nature 421: 37–42.

Saino, N. et al. 2007. Temperature and rainfall anomalies in Africa predict timing of spring migration in trans-Saharan migratory birds. – Climate Res. 35: 123–134.

Shultz, S. et al. 2005. Brain size and resource specialization predict long-term population trends in British birds. – Proc. R. Soc. B 272: 2305–2311.

Sol, D. et al. 2010. Evolutionary divergence in brain size between migratory and resident birds. – PLoS One 5: e9617.

Thomas, D. W. et al. 2010. Context-dependent changes in the weighting of environmental cues that initiate breeding in a temperate passerine, the Corsican bue tit (*Cyanistes caeruleus*). – Auk 127: 129–139.

Tosh, C. R. and Ruxton, G. D. 2008. Notes and comments – body plan of consumed organisms influences ecological range of consumers through neural processing bias. – Am. Nat. 171: 267–273.

Tottrup, A. P. et al. 2008. Avian migrants adjust migration in response to environmental conditions en route. – Biol. Lett. 4: 685–688.

van Asch, M. and Visser, M. E. 2007. Phenology of forest caterpillars and their host trees: the importance of synchrony. – Annu. Rev. Entomol. 52: 37–55.

Visser, M. E. and Sanz, J. J. 2009. Solar activity affects avian timing of reproduction. – Biol. Lett. 5: 739–742.

Visser, M. et al. 2006. Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. – Oecologia 147: 164–172.

Visser, M. E. et al. 2009. Temperature has a causal effect on avian timing of reproduction. – Proc. R. Soc. B 276: 2323–2331.

Appendix 1

Phylogenetic relations between the species included in the study. This tree was used to specify the taxonomic correlation in the generalized least squares (GLS) models.