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Climate warming, ecological mismatch at arrival and population decline in migratory birds

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Climate is changing at a fast pace, causing widespread, profound consequences for living organisms. Failure to adjust the timing of life-cycle events to climate may jeopardize populations by causing ecological mismatches to the life cycle of other species and abiotic factors. Population declines of some migratory birds breeding in Europe have been suggested to depend on their inability to adjust migration phenology so as to keep track of advancement of spring events at their breeding grounds. In fact, several migrants have advanced their spring arrival date, but whether such advancement has been sufficient to compensate for temporal shift in spring phenophases or, conversely, birds have become ecologically mismatched, is still an unanswered question, with very few exceptions. We used a novel approach based on accumulated winter and spring temperatures (degree-days) as a proxy for timing of spring biological events to test if the progress of spring at arrival to the breeding areas by 117 European migratory bird species has changed over the past five decades. Migrants, and particularly those wintering in sub-Saharan Africa, now arrive at higher degree-days and may have therefore accumulated a 'thermal delay', thus possibly becoming increasingly mismatched to spring phenology. Species with greater 'thermal delay' have shown larger population decline, and this evidence was not confounded by concomitant ecological factors or by phylogenetic effects. These findings provide general support to the largely untested hypotheses that migratory birds are becoming ecologically mismatched and that failure to respond to climate change can have severe negative impacts on their populations. The novel approach we adopted can be extended to the analysis of ecological consequences of phenological response to climate change by other taxa.

Keywords: climate change; conservation; ecological mismatch; migration; population trend

1. INTRODUCTION

Climatic variation is a major ecological and evolutionary force acting on populations both directly (via its effects on abiotic conditions) and indirectly (through interactions among species within biological communities) [1]. Organisms are selected to track this variation, and failure to adaptively respond to it may cause demographic decline and drive populations to the verge of extinction [2,3].

The Northern Hemisphere has undergone rapid warming during the past decades [4], and there is overwhelming evidence that the phenology and ecology of populations, the distribution of species and the

composition of communities show coherent symptoms of climate change effects [5–8]. The increase in winter and spring temperatures at medium and high latitudes [9] has led to a generalized advancement of spring phenological events (e.g. leaf unfolding and flowering) [7,8]. Populations of consumers must track such changes in order to retain an appropriate matching to extrinsic conditions and to the phenology of the organisms to which they are ecologically linked. However, response to climate change may not occur at the same pace among species [7,10,11]. This can be speculated to occur because differences in genetic variance affect the rate of their microevolutionary change, behavioural or physiological traits constrain phenotypic plasticity in phenology, the patterns of climate change in the wintering and passage areas of migratory species differ, or a combination of these conditions (see [12–15]). Phenological shifts in ecological communities may therefore result in directional

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selection for earlier arrival and breeding [11,16], and those species that lag behind are expected to suffer increasing levels of ‘ecological mismatch’.

Migratory birds breeding in temperate and high-latitude habitats with strong seasonal variation in ecological conditions must optimize the timing of spring arrival [17]. Arriving too early can entail considerable viability costs because of the risk of facing adverse weather or still-poor food supply [17]. On the other hand, late arrival can depress fitness because of reduced success in competition for mates and territories, and mistiming of reproduction with respect to seasonal peaks in food abundance [18]; several studies have indeed shown directional selection for early arrival and breeding of migratory birds [17].

In the Northern Hemisphere, migratory birds have advanced spring arrival to their breeding sites [19,20]. These changes may reflect either microevolution or phenotypically plastic responses to novel climatic conditions [12,13,21,22]. Whether advancement in arrival has allowed birds to fully compensate for advancement of spring events and retain the same level of matching to spring phenology as in the past or, conversely, only partial compensation has led to increasing levels of ecological mismatch (figure 1), however, remains largely unknown, as evidence exists for very few species and sites [14,23].

The analysis of the consequences of climate change in terms of mistiming of avian arrival and breeding relative to spring phenological events is hampered by the diversity of the organisms (at different trophic levels) with which birds are ecologically interacting. Moreover, information on the progress of spring events on a daily basis obtained in a methodologically consistent way across decades and diverse geographical regions does not exist for individual plant and invertebrate species, not to mention entire communities. However, at medium and high latitudes, the phenophases and development of plants and ectothermic animals that birds use as, for example, food are strongly dependent on weather, and temperature qualifies as the most important factor [24–29], although other factors (e.g. photoperiod; see [30]) can also intervene. The phenology of several plants and animals integrates the thermal signal over periods spanning weeks to months, so that long-term changes in temperature during the first months of the year will result in a spring phenological response [8]. In addition, temporal shifts in plant phenology generate cascading effects on organisms at higher trophic levels [2,8,31]. The progress of spring at a given date can thus be conveniently expressed by degree-days (DD; the sum of mean daily temperatures above a given threshold from a biologically meaningful start date till the date of interest) indices, which summarize the thermal conditions affecting phenology ([27–29]; see also electronic supplementary material), although, to the best of our knowledge, this approach has never been applied in the studies of avian phenology [32].

By relying on DD indices, we here first provide a direct test of the hypothesis that the progress of spring phenological events at arrival of 117 European migratory bird species to the breeding quarters has changed during recent decades, indicating that birds are experiencing increasing levels of ecological mismatch (see also §3). The analyses are based on a large sample of 242 time series of mean/median spring arrival date (MAD)

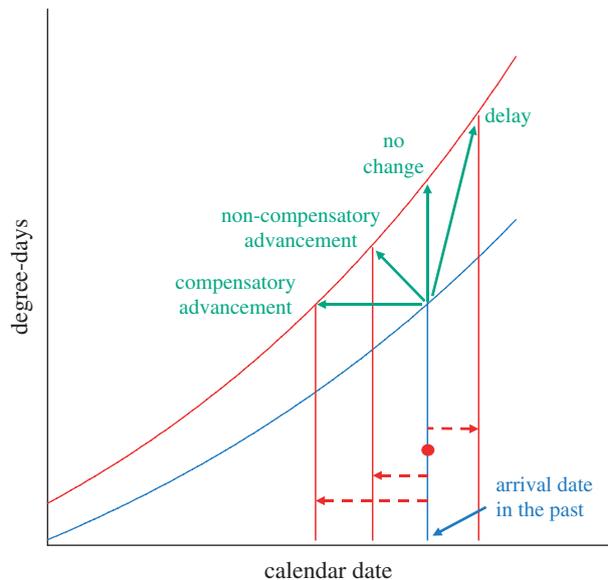


Figure 1. Potential effects of relative climatic and phenological changes on ecological mismatch of migratory birds. Curves represent the progress of spring (degree-days) in 2 years. The curve for the recent year (red line) lies above that for the past (blue line) because of winter and spring warming. Migratory birds show no change (red dot), advancement or delay (red arrows) in arrival date. Species that now arrive at the same or later dates face higher degree-days and are thus ‘thermally delayed’ relative to spring phenophases. Even species that have advanced their arrival may experience a thermal delay, if advancement does not fully compensate for increasing temperatures. Only large advancement in arrival can fully compensate for climate change.

recorded over 51 years (1958–2008) at four sites in northern Europe (figure 2). Migratory bird species show considerable variation in the timing and advancement of spring arrival, and this variation is partly associated with migration strategy—that is, whether a species is a ‘long-distance’ migrant (LDM) wintering south of the Sahara or it is a ‘short-distance’ migrant (SDM) wintering in Europe or in North Africa ([19,20]; but see [33]). We therefore also tested whether DD values at arrival have changed differently between these two groups of migrants, while predicting that LDMs have suffered larger thermal delay owing to their smaller rate of advancement of spring arrival.

Increasing ecological mismatch can cause populations to decline. Under the assumption that higher DD at arrival imply increasing ecological mismatch, we thus also predicted that species with larger increase in DD at arrival showed more negative population trends, and tested this prediction using demographic data for northern Europe [34] as well as for Finland alone, as also obtained from a different source [35]. In the analyses, we controlled for the potentially confounding effects of species ecology, trophic level and migration strategy, as well as for similarity in response owing to common ancestry.

2. METHODS

(a) Avian phenological data

Phenological time series ($n = 242$) were obtained at four sites in northern Europe (Helgoland: 54.18° N, 7.88° E, $n = 24$;

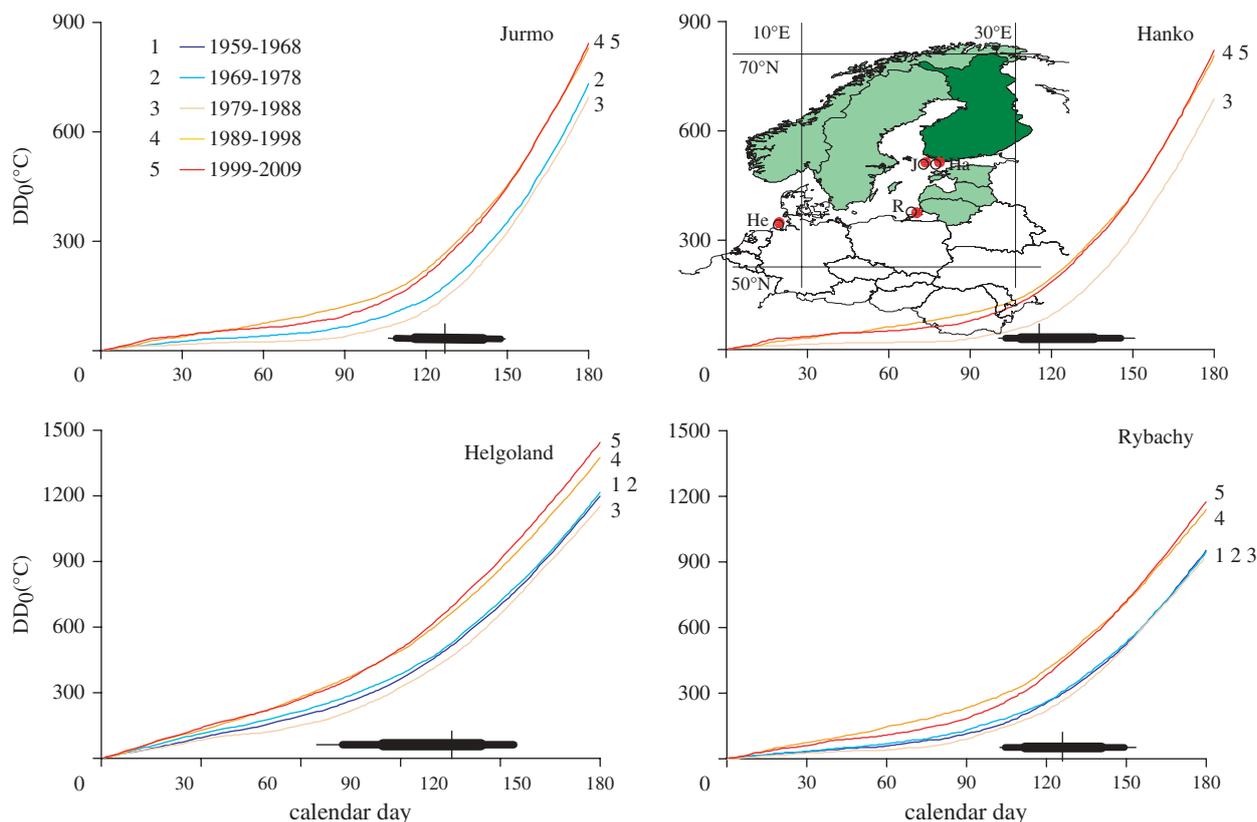


Figure 2. Temporal variation in winter and spring accumulation of degree-days (DD_0). Data refer to the period 1 January–30 June at four study sites and are averaged among years within five periods (1–5). Only periods with avian phenological data at individual sites are presented. Recent periods have markedly higher DD_0 values. Inset map shows the study sites (J, Jurmo; Ha, Hango; He, Helgoland; R, Rybachy), the temperature data grid points (blue dots) and the seven countries relevant to population trend analyses. Trends in Finland were also analysed separately; see text. Box plots indicate the frequency distribution of migration dates: thin boxes: 5–10% or 90–95% of the species; medium-size boxes: 10–25% and 75–90%; thick box: 25–75%; vertical line: median.

Rybachy: 55.08° N, 20.73° E, $n = 32$; Jurmo: 59.83° N, 21.62° E, $n = 95$; Hango: 59.82° N, 22.90° E, $n = 91$) for a total of 117 species. The average duration (first to last year) of the time series was 37.0 (6.85 s.d.) years. Data were not available for some species and years, yielding an average number of phenological data points per time series of 34.0 (9.11 s.d.). Their temporal spans (mean year of start to mean year of end across species within sites) were: Helgoland, 1960.1–2007.8; Rybachy, 1959.0–2003.3; Jurmo, 1970.7–2007.8; Hango, 1979.1–2007.9. Annual arrival dates were expressed as mean (Rybachy and Helgoland) or median (Hango and Jurmo) date of capture/observation (MAD). Methods of the trapping/observation procedures for estimating MAD are reported in [33,36,37].

(b) Degree-days data

Temperature data were obtained from the ERA-40 and ERA-Interim archives of the European Center for Medium Range Forecasts for the 1.125° latitude \times 1.125° longitude grid-point closest to individual sites (see electronic supplementary material). Because temperature thresholds relevant to the phenology of different organisms differ, we considered -3°C , 0°C or $+3^\circ\text{C}$ as thresholds, although only the analyses based on DD with the 0°C threshold (DD_0) are presented in the main text (see electronic supplementary material for a justification of these thresholds and for analyses based on DD_{-3} and DD_{+3}). For each year and j th day at each of the four sites, we thus computed degree-days (DD;

$i = -3^\circ\text{C}$, 0°C or $+3^\circ\text{C}$) as the sum of the instantaneous temperatures above -3°C , 0°C or $+3^\circ\text{C}$ from 1 January to day j , and divided it by 4 (i.e. the number of instantaneous temperature estimates per day). Each MAD datum (rounded to the nearest integer) for any given species, year and site was then matched to the pertaining DD_i data (see electronic supplementary material for analyses showing high correlation among DD_i computed at various temperature thresholds). Thus, species-specific DD_i for any given year and site is the sum of temperatures above threshold i from 1 January until MAD.

(c) Coding of species migration strategy, population trends, habitats and diet

Species were classified either as SDM or LDM migrants according to Cramp [38] (see electronic supplementary material).

Population trends for 1990–2000 were obtained from BirdLife International [34] for the countries where most of the populations migrating through the study sites breed (Denmark, Norway, Sweden, Lithuania, Latvia, Estonia and Finland). We excluded Russia because trends for this country refer to an area extending eastwards to the Ural Mountains, which has limited relevance for birds migrating through the study sites. In the original source, trends for each country and species are reported either as accurate trends (% change) or as trend classes (e.g. 20–29% change). We expressed trends as 11 trend classes, from -5 to $+5$ (0: no change; 1: $<20\%$ change; 2: 20–29% change;

3: 30–49% change; 4: 50–79% change; 5: $\geq 80\%$ change) [39]. Trends are classified according to three levels of data quality (i.e. trends based on qualitative, qualitative/quantitative or quantitative data; [34]). We considered only trend estimates based on qualitative/quantitative and quantitative data. Trend classes for each species were calculated as the mean trend class across the countries for which an estimate was available. For five species, trend estimates were not available. In addition, we used trend estimates from other sources for Denmark [40], Sweden [41] and Finland [35] (see electronic supplementary material).

The analyses that were run on mean population trends as derived from BirdLife International [34] were also run on population trends for Finland derived from the same source or from another source [35] in relation to the species-specific mean linear regression coefficient (DD_iYr) of DD_i at MAD on year recorded at Jurmo and Hanko, because these two sites are located in southern Finland, and MAD recorded there mainly refer to birds breeding in Finland [42]. Conversely, phenological data recorded at Helgoland and Rybachy cannot be associated to specific countries.

The main habitat of individual species was classified according to BirdLife International [34] as farmland versus non-farmland or as aquatic versus non-aquatic, because farmland and non-aquatic species have declined more than species from other habitats [43–47]. Because species at different trophic levels may differ in response to climate change, diet was also factored out in the analyses. Species were classified as mainly primary consumers, secondary/higher level consumers or omnivorous according to Cramp [38]. Finer-scale classification of diet in nine classes led to similar results (details not presented).

(d) Comparative analyses and phylogenetic information

In comparative studies, species cannot be considered as statistically independent because of their shared phylogenetic history. To control for the effects of common descent in the analyses of population trends, we calculated independent linear contrasts [48,49] using the CAIC library of the software R 2.8.1 [50]. Contrasts were analysed by regression analyses through the origin [49]. The sources of phylogenetic information are reported in the electronic supplementary material.

(e) Statistical analyses

Analyses reported in the main text, as well as those reported in the electronic supplementary material, were based on standard t -tests and on linear models or linear mixed models. In linear mixed models, species and site were included as random effect factors, whereas migration strategy was considered as a fixed factor. The analyses of mean population trends were run by weighted least-squares regression models using the number of countries for which population trend estimates were available as a weighting factor.

3. RESULTS AND DISCUSSION

(a) Temporal variation in arrival dates and degree-days at arrival

Owing to the rise in winter and spring temperatures, at all four study sites spring DD_0 showed a marked increase since 1958 (figure 2). Around 30 April, when bulk migration concentrates, average DD_0 between 1989 and

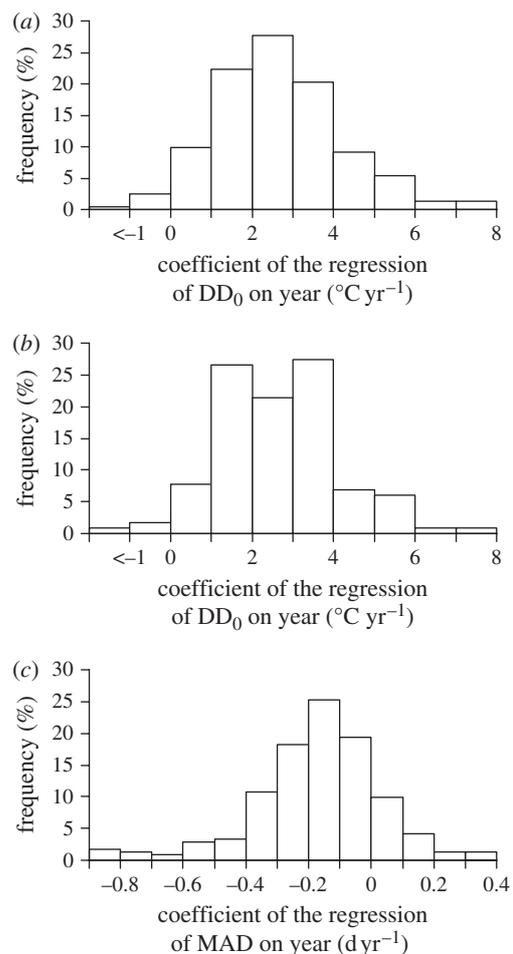


Figure 3. Temporal variation in DD_0 at arrival, and in arrival date. Frequency distribution of DD_0Yr for (a) phenological time series or (b) within-species means. (c) Frequency distribution of the mean species-specific $MADYr$.

2009 was as much as 58 per cent larger than in the previous three decades. However, migrants have not kept track of this change. In fact, linear regression coefficients (DD_0Yr) of DD_0 recorded at MAD for individual species and springs on year were positive for 97.1 per cent of the 242 phenological time series, and 109 (=45.0%) of them were significantly larger than 0. When included in polynomial regression models to account for nonlinear trends in change of DD_0 , the squared term of year never attained significance ($p > 0.05$ in all cases). Mean DD_0Yr ($=2.66^{\circ}C yr^{-1}$ (0.099 s.e.m.)) computed across all time series was significantly larger than 0 (one-sample $t_{241} = 26.97$, $p < 0.001$, $n = 242$ series; figure 3a). The mean species-specific DD_0Yr values were also positive in 97.4 per cent of the cases and their mean ($2.70^{\circ}C yr^{-1}$ (0.136 s.e.m.)) was significantly larger than 0 ($t_{116} = 19.82$, $p < 0.001$, $n = 117$ species; figure 3b). These results imply that migrants arrive at larger DD_0 now than in the past, therefore showing that they have accumulated a ‘thermal delay’ upon arrival.

During the same period, in 83.5 per cent of the 242 time series the linear regression coefficient ($MADYr$) of MAD on year was smaller than 0, and significantly so ($p < 0.05$) in 100 (=41.3%) of the cases, whereas in only seven cases it was significantly positive. Hence, most time series showed earlier arrival of migrants in

recent years. On average, MAD_{Yr} values were significantly smaller than 0 (mean = -0.166 d yr^{-1} (0.0138 s.e.m.); $t_{241} = -12.02$, $p < 0.001$, $n = 242$). The mean within-species values of these phenological trends were negative for 88 per cent of the species and their mean (-0.162 d yr^{-1} (0.0216 s.e.m.)) was also significantly negative ($t_{116} = -7.49$, $p < 0.001$, $n = 117$ species; figure 3c). Thus, advancement of arrival date may have not been sufficient to compensate for climate change (figure 1), as DD₀ at arrival have increased, and birds are now arriving at later spring phenophases.

(b) Arrival dates and degree-days at arrival of SDMs or LDMs

LDM species have advanced their arrival less than SDM (mean MAD_{Yr}, estimated by averaging the species means computed across sites, for LDM = -0.073 d yr^{-1} (0.0252 s.e.m.); SDM = $-0.214 \text{ d year}^{-1}$ (0.0294 s.e.m.); two-samples $t_{115} = 3.25$, $p = 0.002$, $n = 43$ LDM and 74 SDM). Both LDM and SDM species have suffered a thermal delay at MAD, as the mean value of the mean species-specific DD₀Yr was significantly larger than 0 for both type of migrants (SDM: one-sample $t_{73} = 13.92$, $p < 0.0001$; LDM: $t_{42} = 19.31$, $p < 0.0001$). However, smaller advancement of MAD by LDM than SDM has translated into larger mean DD₀Yr values for the former, implying that they have accumulated larger thermal delay than SDM (mean DD₀Yr for LDM = $3.62^\circ\text{C yr}^{-1}$ (0.188 s.e.m.); SDM = $2.17^\circ\text{C yr}^{-1}$ (0.156 s.e.m.); two-samples $t_{115} = 5.85$, $p < 0.001$, $n = 43$ LDM and 74 SDM).

When run on DD₋₃ or DD₊₃, all the above analyses led to results similar to those obtained using DD₀. Moreover, the analyses of DD_{Yr} or MAD based on linear mixed models with species and site as random factors and migration strategy as a fixed effect also led to qualitatively identical results (see electronic supplementary material).

(c) Thermal delay and population trends

As inability of birds to track climate change may cause their populations to decline [3,51], we predicted that species with larger ‘thermal delay’ at arrival have experienced larger population declines. By using population trends reported for 1990–2000 in BirdLife International [34] for migrants breeding in seven countries north of the study sites, we found this prediction to be supported (table 1 and figure 4a). To check for robustness of this result, we first tested if DD₀Yr at the Finnish sites of Hanko and Jurmo alone (which mostly refer to birds breeding in Finland) negatively predicted population trends in that country, and again found that this was the case (table 1 and figure 4b). Moreover, estimates of population trends in Finland during 1983–2005 [35] were also found to negatively covary with DD₀Yr recorded on that time interval at Hanko and Jurmo (table 1 and figure 4c).

These results and the fact that population trends during 1990–2000 are positively correlated with those recorded over longer time periods at continental as well as national scales [39] (see electronic supplementary material) show that increased DD₀ at arrival negatively predicts population trends. Analyses where we controlled for ecological variation among species in terms of habitat and trophic level, and/or for similarity in response owing

Table 1. Population trends in relation to DD₀Yr (regression coefficient of DD₀ at MAD on year). The effects of DD₀Yr on population trends are obtained from a model including a binary factor migration strategy but excluding the effect of the non-significant interaction. Full models are reported in electronic supplementary material, tables S1 and S2. Finland DD₀Yr data were averaged between Hanko and Jurmo. Population trends for the seven countries and for Finland (a) are derived from BirdLife International [34]. Population trends used in model Finland (b) are derived from Väisänen [35]. The number of short-distance or long-distance migrants for which population trend data were available was 70 and 42 for the seven countries, 65 and 39 for Finland (a), and 35 and 27 for Finland (b).

	<i>t</i>	d.f.	<i>p</i>	estimate
species-specific data				
seven countries	-2.30	109	0.023	-0.222(0.097)
Finland (a)	-2.39	101	0.019	-0.379(0.159)
Finland (b)	-2.53	59	0.014	-0.654(0.258)
independent contrasts				
seven countries	-2.72	106	0.008	-0.221(0.081)
Finland (a)	-3.13	98	0.002	-0.458(0.146)
Finland (b)	-2.90	58	0.005	-0.753(0.259)

to common ancestry, led to consistent results (table 1; see electronic supplementary material). Moreover, analyses run on DD₋₃Yr or DD₊₃Yr both on ‘raw’ species data and while controlling for phylogenetic effects largely confirmed the results of analyses based on DD₀Yr (see electronic supplementary material, tables S1 and S2).

Several previous studies of migratory birds have provided evidence that migrants have advanced their arrival to the breeding areas during recent decades [19,20]. Conversely, very few studies have investigated whether the rate of change in migration and breeding phenology has compensated for generalized phenological shifts owing to climate change [10,11,16]. Here, we have adopted an approach based on degree-days accumulation to investigate whether the progress of spring at the time when migratory birds arrive to their breeding areas has changed over the last five decades. This approach is novel and can be extended to studies of the ecological consequences of phenological response to climate change in studies of birds and other taxa, owing to the ubiquitous nature of the effects of temperature on the phenology of plants and ectothermic organisms (see §1).

Advancement in arrival date to the breeding areas, which has indeed occurred for most species, has not fully compensated for climate change, and larger degree-day values at arrival in recent years may imply that birds have become ecologically mismatched. This is the case because the phenophases of plants and ectothermic animals, including those relevant to bird ecology, are mostly regulated by temperature [24–29,52]. The present study thus rests on the assumption that long-term increase in degree-days at arrival causes an (increasing) ecological mismatch. This would *not* be the case if birds were arriving too early (i.e. at too low degree-days) in the past, as an increase in degree-days at arrival would ensure smaller, rather than larger, ecological mismatch. Although no unequivocal

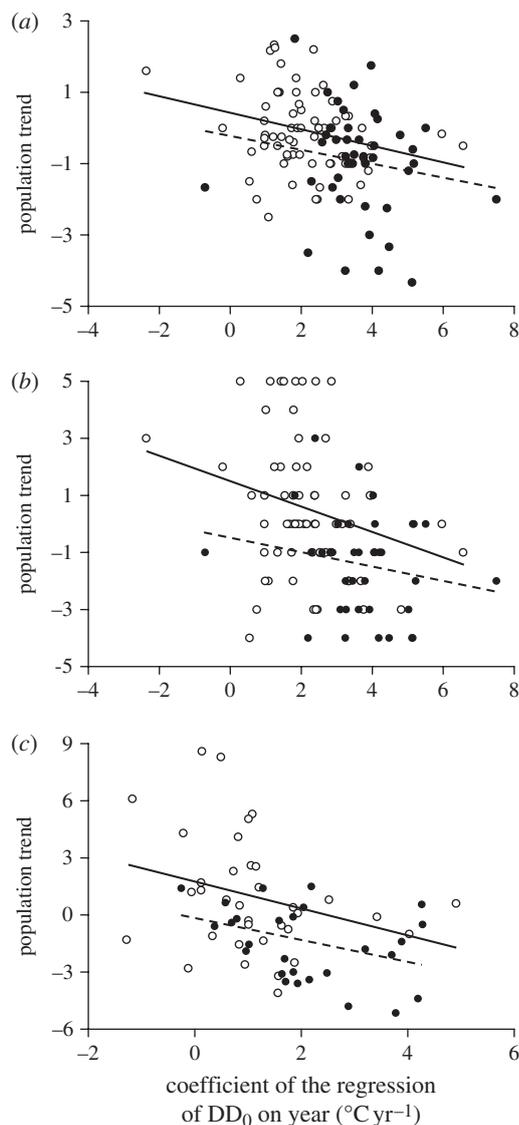


Figure 4. Population trends in relation to thermal delay. (a) Mean species population trends [34] in the seven countries in relation to species DD_0Yr . (b) Population trends in Finland [34] in relation to species DD_0Yr computed for the Finnish sites (Jurmo and Hanko). (c) Population trends in Finland obtained from a different source [35] in 1983–2005 in relation to species DD_0Yr calculated over the same period for the Finnish sites. Regression lines fitted to short-distance (empty circles, solid line) or long-distance (filled circles, dashed line) migrants show that the slopes are similar.

reference for optimal conditions (in terms of degree-days at arrival) is known for any bird species, we consider the possibility that ecological matching increases with increasing degree-days at arrival a remote one. First, selection for earlier arrival and breeding has been repeatedly documented in bird studies [17], implying that birds arrive on average too late, rather than too early. Second, birds are advancing their arrival date, whereas they should be expected to delay it if they were arriving too early. Third, temperature changes have been occurring at faster pace during recent decades than in the previous ones [4] (see also figure 2). If birds show a constant latency in responding to climate change, more rapid recent climate change *per se* justifies the expectation of

larger ecological mismatch. We thus consider the assumption that higher degree-days at arrival are associated with stronger ecological mismatch as warranted. Obviously, the extent of ecological mismatch arising because of a unit increase in degree-days may widely vary among species according to their trophic level and habitat. However, we found no statistical evidence that the effect of DD_0Yr on population trend depended on diet or habitat, suggesting that any negative consequence of change in degree-days at arrival on population trends was independent of variation in major ecological traits of the species.

The ability of birds to cope with climate change by adjusting their migration phenology may be constrained by the timing of life-cycle phases preceding migration, which may limit the scope for phenotypically plastic response, by different climatic variation in the wintering areas and *en route*, and/or by depleted genetic variance in migration traits, which can hinder microevolutionary response [14]. All these scenarios are compatible with the observation that LDMs, having advanced their arrival less, have accumulated a larger ‘thermal delay’ when compared with SDMs.

We have also shown that species with larger ‘thermal delay’ at arrival have undergone the largest population decline, while species with small-to-moderate thermal delay have barely shown a decline. Previous studies have shown that LDMs have declined more than SDMs [39]. Although this difference may also be caused by factors operating differently on their wintering grounds or along the migration route, the present results suggest that the larger thermal delay they have accumulated may contribute to their larger decline.

Hence, ecological mismatch at arrival from spring migration may be a general condition among birds breeding in northern Europe, and failure to adjust phenological events to rapidly changing climatic conditions may be an important factor causing negative demographic and conservation effects.

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