Article:

Visser, M.E. orcid.org/0000-0002-1456-1939, Lindner, M. orcid.org/0000-0003-2931-265X, Gienapp, P. et al. (2 more authors) (2021) Recent natural variability in global warming weakened phenological mismatch and selection on seasonal timing in great tits (Parus major). Proceedings of the Royal Society B: Biological Sciences, 288 (1963). 20211337. ISSN 0962-8452

https://doi.org/10.1098/rspb.2021.1337

Recent natural variability in global warming weakened phenological mismatch and selection on seasonal timing in great tits (*Parus major*)

Marcel E. Visser[1,2], Melanie Lindner[1,2], Phillip Gienapp[1,3], Matthew C. Long[4] & Stephanie Jenouvrier[5]

[1] Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, 6700 AB Wageningen, the Netherlands m.visser@nioo.knaw.nl
[2] Chronobiology Unit, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, Groningen, The Netherlands
[3] Michael-Otto-Institut im NABU, Research and Education Centre for Avian and Wetland Conservation, Goosstroot 1, 24861 Bergenhusen, Germany
[4] Climate and Global Dynamics Laboratory, National Center for Atmospheric Research, P.O. Box 3000, Boulder, CO 80307-3000, USA
[5] Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA, USA

Keywords: seasonal timing, phenology, climate change, selection, great tit

Abstract

Climate change has led to phenological shifts in many species, but with large variation in magnitude among species and trophic levels. The poster child example of the resulting phenological mismatches between the phenology of predators and their prey is the great tit (*Parus major*), where this mismatch led to directional selection for earlier seasonal breeding. Natural climate variability can obscure the impacts of climate change over certain periods, weakening phenological mismatching and selection. Here, we show that selection on seasonal timing indeed weakened significantly over the past two decades as increases in late spring temperatures have slowed down. Consequently, there has been no further advancement in the date of peak caterpillar food abundance, while great tit phenology has continued to advance, thereby weakening the phenological mismatch. We thus show that the relationships between temperature, phenologies of prey and predator, and selection on predator phenology are robust, also in times of a slowdown of warming. Using projected temperatures from a large-ensemble of climate simulations that take natural climate variability into account, we show that prey phenology is again projected to advance faster than great tit phenology in the coming decades, and therefore that long-term global warming will intensify phenological mismatches.

Introduction

In climates with strong seasonality, life-cycle events, such as reproduction, can only successfully take place during a relatively short period in the annual cycle. In many species, the timing of this period to favourable conditions varies strongly between years as this timing is temperature dependent. Individuals therefore need to adjust the timing of their life-cycle events to these different annual conditions, and consequently these events exhibit a high degree of phenotypically plasticity[1]: individuals adjust their seasonal timing (or phenology[2]; the annual timing of life-cycle events) by responding to the relevant environmental variables or 'cues'.

Warmer temperatures due to climate change have led to the advancement of phenology in a wide range of species[3,4]. However, these phenological shifts are often insufficient to keep up with the changes in the species' environment[5]. Furthermore, the rates of phenological shifts often vary between species within the same food chain[4], leading to increased phenological mismatches[6]. Higher trophic levels generally advance at slower rates than lower trophic levels[7], which is consistent with theoretical predictions[8]. This increased phenological mismatch may have critical consequences for population viability[9–11], though in some instances mismatches can be buffered by ecological processes such as density dependence[12].

Climate-warming induced phenological mismatches often lead to a higher fitness for individuals being earlier or later than the population average, and these differences in fitness between individuals result in directional selection on phenology. To reduce the phenological mismatch, such selection will –in the long term– require that species adapt genetically to the changed phenology of their prey[13]. Only a few examples of genetic changes in response to phenological mismatch exist[14–16]. Importantly, monitoring the strength of directional selection on seasonal timing in order to estimate whether selection intensifies or weakens over time allows one to infer whether the population is catching up with phenological changes at other trophic levels. Such studies can be especially informative when conducted with long-term population studies. Moreover, identifying the ecological drivers of this selection enables the forecasting of the strength of directional selection under future climate scenarios.

One of the earliest and best-known examples of climate change induced phenological mismatches and resulting directional selection on seasonal timing, comes from a study of a Dutch great tit (*Parus major*) population[17]. That study showed that great tits were not advancing their laying dates despite a strong shift in the peak date of caterpillar biomass, a proxy for the phenology of the main nestling food. Great tit laying dates were affected by temperature during a different period of spring than caterpillar peak dates, and the temperatures during the temperature-sensitive period of the great tit increased at a slower rate than those of the temperature-sensitive period linked to the timing of the caterpillar biomass peak. As a result, the phenology of the caterpillar biomass peak advanced faster than the laying date of great tits, and the increasing phenological mismatch led to increasing directional selection for earlier laying[18].

Climate change is not a smooth process of continuously increasing temperatures. Instead, warming trends are characterized by significant slowdowns and speedups on decadal timescales. Indeed, while climate change is characterized by a global warming trend caused by elevated levels of greenhouse gases, other processes occurring over a broad range of temporal and spatial scales generate natural variability in the climate system (e.g. volcanoes[19]). This natural variability can generate period of slowdown in the rate of warming, such as observed during the decade of the 2000s due to a combination of volcanic influences and internal climate variability[20,21], while the climate forcing continued. Importantly, we can make use of this natural variability to better understand how temperature relates to the phenologies of trophically linked species in the food chain, as well as the resulting mismatches and strength of selection, as it overcomes the problem of spurious relationships due to a number of variables all changing undirectedly over time.

Here, we make use of a period of slowing down of spring temperature warming that affects the timing of peak caterpillar biomass. We show that in the 25 years after the data analysed in the 1998 study[17] (1973-1995, current study: 1973-2020), selection for laying date has weakened. We explore why this has happened by analysing changes in great tit laying date, the timing of maximal food abundance, the phenological mismatch, temperature during different periods in spring, and the strength of directional selection. We find that the increase in temperatures relevant to the caterpillar biomass peak has slowed down, and that this has led to a halt in the advancement of the timing of the food peak. At the same time, great tits laying dates continued to advance as the temperatures relevant for their phenology kept increasing. This has led to a decreased mismatch and a relaxation of selection on great tit laying dates. Further, our findings strongly suggest that the relationships described in the 1998 paper[17] are robust and not due to spurious relationships between different variables simply because they all change over time.

Furthermore, we project future timing of great tits laying dates, caterpillar biomass peak dates, and the phenological mismatch by using projected temperatures for several climate forcing scenarios, and thus include uncertainties in socio-economic pathways over the coming decades due to anthropogenic emissions as well as land-use changes. For this, we used a large-ensemble of climate outputs from a coupled atmosphere-ocean general circulation model which explicitly takes natural climate variability into account[22] and show that in the next decades the phenological mismatch will again intensify.

Methods

General fieldwork

We used 48 years of data (1973 to 2020) from a long-term study of a great tit population at the National Park de Hoge Veluwe (The Netherlands, 52°2'26.59" N, 5°51'20.63" E). The study area consists of mixed pine/deciduous wood covering 171 ha (1 ha = 10^4 m^2), and is supplied with approximately 450 nest-boxes. Nest-boxes were checked weekly to determine laying date and clutch size, and daily during the days immediately prior to predicted hatch date to determine specific hatching date of the young. Nestlings were ringed on day 7, and their parents identified. From these measurements, we obtained data on laying date of the first clutch for all females in the population (assuming that one egg a day was laid).

Phenological mismatch

Annual peak dates of caterpillar biomass were defined as the date on which the caterpillar biomass peaks using frass-fall samples from the Hoge Veluwe (1985-2020, excl. 1991)[23,24]. The annual phenological mismatch was defined as the difference in the mean laying date of the great tits plus 33 days minus the peak date of caterpillar biomass[24,25]. This measure of phenological mismatch has been shown to be a better predictor for both offspring recruitment and selection on timing than measures that aim to quantify the temporal overlap between the phenological distributions of laying dates and caterpillar biomass[24,26], primarily because the latter measure is based on assumptions that are hard to verify (see [24]). The addition of 33 days is based on mean clutch size, incubation duration, and taking into account that nestlings of 10 days old have the highest demand for food[23] and thus the absolute degree of mismatch may vary with a few days between broods. This largely depends on spring temperatures, as birds may already start incubating before the last egg is laid, thereby reducing the interval between laying date and hatching date. In addition, the use of hatching date, as done in some studies [10], has a major disadvantage in that any clutch where no chicks hatch (which will be a non-random group with respect to laying date) will be omitted from the analysis and thus selection will be underestimated.

Temperature and biotic environmental data

Temperature data were obtained from the De Bilt station of the KNMI (Royal Dutch Meteorological Institute), less than 50 km from the Hoge Veluwe field site. We used ClimWin[27] to find the best correlating temperature periods for both the great tit laying date (using mean annual laying dates and including year in the analysis to avoid spurious relationships [27]) and the caterpillar biomass peak date (using annual values). We used the ClimWin randomization test with 20 repeats to test the probability that we identified a temperature period by chance. Data on oak (*Quercus robur*) bud burst were available for 1988-2020[28] and data on beech (*Fagus sylvatica*) crop, the key environmental variable that affects winter survival in great tits, was available for 1977-2020[29].

Measuring selection

Annual standardised selection differentials were calculated by regressing relative fitness, i.e. individual fitness divided by annual mean fitness, against annually standardised laying dates following[30]. Laying dates were standardised within years by subtracting the annual mean and dividing by the annual standard deviation. For the selection analysis, broods that were manipulated (i.e. brood size manipulation) were excluded from the analysis. We estimated fitness as the number of offspring produced by a female in the breeding season (from first, replacement and second broods) that recruited (i.e. were recorded as breeders) in the study population in subsequent years (great tits already can recruit the year after they hatched), but note that this fitness estimate combines fitness components of the parent (number of offspring) with the fitness of their offspring (the survival to recruitment)[31].

Statistical analysis

All time trends were analysed with a Generalized Additive Model (gam), which allows the fitting of relationships without *a priori* expectations about the shape of the relationship. All gams were fitted with the package mgcv in R [32], allowing us to estimate the smoothness of model terms as part of the fitting procedure. To test whether the 'non-linear' fit of a gam was better than a linear fit, the AICs of the gam and the linear model were compared and the ΔAIC reported. If the estimated degrees of freedom (edf) for the smoothed term were 1, indicating a linear relationship, results from a linear regression are also reported. For relationships where the dependent variable was regressed against temperature or mismatch we have *a priori* expectations of linear relationships and thus linear regression was used. In the analysis of selection differentials, we weighted the datapoints by $1/\text{s.e.}^2$ [33]. In the analysis of laying date, we did not weight the datapoints as the variance in laying date is mostly biologically determined and not driven by sampling error.

For the annual standardised selection differentials we then analysed whether phenological mismatch explained the year effect[18], and next, to explain the remaining year effect we substituted year with a number of annual variables: mean number of recruits produced (to test for the effect of mean fitness on the strength of selection[34,35]), total number of fledglings (testing for possible competition effects), the height of the caterpillar biomass peak (testing for possible harsh spring conditions), Beech Crop Index (testing for possible winter food conditions that affect both adult and juvenile survival[29]), and the spring temperatures in the following year when recruits need to settle (testing for harsh conditions when early recruits start breeding, c.f. [36] on Pied Flycatcher where there was such an effect). For annual laying date and annual biomass peak date, we tested whether changes over time were fully explained by the change in temperature over years. As this was not the case, we tested whether temperature fully explained the year effect and for the annual biomass peak date whether the remaining year effect could be explained by the variation in the annual Oak bud burst date. We report F statistics and p values for each variable at point of removal from the model. Note that the degrees of freedom can vary as the number of years an environmental variable was recorded varies among variables (see above). All analysis were done using R version 4.0.4 [37].

Climate scenarios

To forecast phenological mismatch over the period from 2021 to 2100, we projected the laying date of the great tits and the peak date of caterpillar biomass from the relationships between phenology and temperature using daily temperatures projected under five climate scenarios (see Appendix 1 for details on the climate scenarios, Appendix 2 for details on projection of temperatures, Appendix 3 for the validation of the climate scenarios, and Appendix 4 for the projection of laying dates and food peak dates). The RCP8.5 baseline scenario projects temperatures without policy intervention and RCP4.5 scenario projects temperatures with a pathway of various climate mitigation measures based on environmental, social, technical, economic, and cultural change. To explicitly evaluate future climate trajectories under the Paris Agreement temperature targets relevant to the 1.5 and 2°C goals, we used three additional climate scenarios developed by Sanderson et al.[38].

Including uncertainties related to natural climate variability required multiple climate ensemble members from a single fully coupled atmosphere-ocean general circulation model (AOGCM) in order to diagnose the influence of internal climate variability on projections[22]. To specifically use emissions scenarios designed to assess the Paris Climate Agreement targets, we used climate outputs from the Community Earth System Model. Appendices 2 and 3 detail the climate simulations, and the comparison of observed and simulated data demonstrating that the temperature and phenological trends simulated respectively by the AOGCM and climate-phenological model overlaped well with the range of observations over the "historical period" from 1985-2020.

Permission and licences for the field work

The research was carried out under license AVD801002017831of the Centrale Commissie Dierexperimenten (CCD) in the Netherlands. Fieldwork at the National Park de Hoge Veluwe was carried out with permission of the Park.

Results

In our long-term population of great tits, climate change initially led to increasing directional selection for earlier laying, followed by weakening selection (s(year): edf = 2.27, F = 3.31, n = 47, p = 0.04, ΔAIC = 5.10; Fig.1), where the year with the largest mismatch is around the year 1998. Mismatch showed a similar trend over time (s(year): edf = 1.84, F = 1.62, n = 35, p = 0.20, ΔAIC = 2.28, which is due to a continuous advance in mean laying date (s(year): edf = 1; $F_{1,46}$ = 20.56, p < 0.001, b = -0.248 (s.e. 0.055)) combined with an initial advance, followed by a period of no further advancement, in the phenology of the caterpillar peak date (s(year): edf = 1.89, F = 7.13, n = 35, p = 0.002, ΔAIC = 2.43 (Fig. 2a-c). See Table 1A for statistical details.

Selection differentials were negatively related with mismatch but in addition there was also a year effect (mismatch: b= -0.014 (s.e. 0.0054), $F_{1,31}$=9.60, p=0.004; year: b= 0.009 (s.e. 0.004), $F_{1,31}$=7.96, p=0.008: for the same degree of phenological mismatch, directional selection for laying date got weaker (Fig. 2d). To explain this year effect, we tested a number of hypotheses by fitting annual variables in a model with year to test whether they could explain the year effect. The year effect was not explained by the mean number of recruits produced (testing for the effect of mean fitness on the strength of selection[34,35]), the total number of fledglings (testing for possible competition effects), the height of the caterpillar biomass peak (testing for possible harsh spring conditions), Beech Crop Index (testing for possible winter food conditions that affect both adult and juvenile survival[29]), or the spring temperatures in the following year when recruits need to settle (testing for harsh conditions when early recruits start breeding, c.f. [36] on Pied Flycatcher where there was such an effect). See Table 1B for statistical details. Thus, we cannot offer an explanation for the year effect that, in addition to the mismatch, affects the strength of selection.

To determine whether the advancement of laying date over time (Fig. 2a) is explained by an increase in temperature we first identified the window over which temperatures are correlated with laying date. The ClimWin analysis showed that laying date was strongly correlated with the mean daily temperature from 11 March to 20 April ($F_{1,45}$=75.9, p<0.001, Table 1C), with an additional year effect where laying date gets earlier for the same temperature over time ($F_{1,45}$=4.86, p=0.033, Table 1C; Fig.3a). The ClimWin randomization test clearly showed that this window was not selected by chance (P<0.0001). There is no change in temperature sensitivity over time ($F_{1,44}$ = 0.22, p = 0.64, Table 1C). The mean daily temperature from 11 March to 20 April increased linearly over the years (s(year): edf = 1, F1,46=14.1, p= 0.0005, ΔAIC = 0.0, see Table 1A; Fig. 3c,) leading to the earlier laying dates.

The caterpillar biomass peak date was also strongly correlated with mean daily temperature but for a different period: 6 March to 14 May ($F_{1,32}$=130.8, p< 0.001, Table 1C). This relationship did not change across years ($F_{1,31}$=0.53, p=0.47, Table 1C), but again an additive year effect was found, with an earlier food peak for a given temperature over the years ($F_{1,32}$=14.8, p=0.0005, Table 1C; Fig. 3b). The ClimWin randomization test clearly showed that this window was not selected by chance (P<0.0001). The year effect can be explained from the advancement of Oak bud burst date; when budburst date is fitted ($F_{1,29}$= 8.79, p=0.006) year is no longer significant (Table 1C); and budburst date strongly advances over time (s(year): edf = 1, F1,31= 11.35, p= 0.002, ΔAIC = 0.0, see Table 1A). When analysing the mean daily temperature for 6 March to 14 May over the same years as for mean daily temperature from 11 March to 20 April (1973-2020), temperature was significantly non-linearly related to year (s(year): edf = 2.03, F = 12.4, p < 0.001, ΔAIC = 3.16, see Table 1A), where temperature initially got warmer but then warming slowed down (Fig. 3d).

The five climate scenarios (RCP8.5, RCP4.5, 1.5degOS, 1.5degNE, and 2.0degNE) showed that temperatures relevant for the phenology of the great tit and for the food peak will increase from 2020 to 2100 (2020-2080 for the RCP4.5 climate scenario, Figure A1). As a consequence, the phenology of the birds and of their food will advance, but at different rates under the different scenarios. Specifically, the date of the food peak will advance faster and hence the phenological mismatch will again increase in the next 80 years (60 years for the RCP4.5 climate scenario). The mismatch is forecasted to be 14.6 days in 2100 under the RCP8.5 scenario, 10.0 days in 2080 under the RCP4.5 scenario, and 7.3, 8.0 and 8.7 days in 2100 under the 1.5degOS, 1.5degNE scenario, and 2.0degNE scenarios, respectively (Fig. 4, Table 2). Interestingly, under the Paris scenarios the mismatch stabilizes after 2050, while for the RCP8.5 and RCP4.5 the increase is continuously (and linearly) increasing.

Discussion

In our population of great tits, climate change has initially led to an increasing mismatch between the birds laying date and the timing of their caterpillar prey, leading to directional selection for earlier seasonal breeding[17]. Over the past 20 years, selection has significantly weakened (Fig. 1), likely driven by a slow-down in the increase in late spring temperatures resulting in a no longer advancing date of peak caterpillar food abundance. However, great tit laying dates continued to advance, resulting in a smaller phenological mismatch and hence weaker selection for earlier breeding. Importantly, all relationships between temperature, phenology of prey and predator, and selection on predator phenology are still present, as reported 25 years ago[17], demonstrating that these relationships did not arise spuriously through common time trends and that future dynamics can be projected with high confidence. We show, using five climate scenarios, that the current weakening of selection is likely to be temporary, as climate predictions indicate that spring temperatures will continue to increase and that phenology of the caterpillar peak date will again advance at a faster rate than bird phenology, resulting in increasing selection for early breeding.

We found an additive (negative) year effect on the relationships between temperature and the phenologies of prey and predator, as well as the selection on predator phenology, which we did not find in the benchmark 1998 study. Selection differentials were related to mismatch, as we found earlier[18]. While mismatch does not change significantly over years, selection differentials do. This may be due to the additional year effect in the relationship between the selection differentials and the mismatch: for the same degree of phenological mismatch, directional selection for laying date got weaker over time. We tested a number of hypotheses for why this could be the case (the mean number of recruits produced, total number of fledglings, the height of the caterpillar biomass peak, Beech Crop Index and the spring temperatures in the following year when recruits need to settle; see Methods) but none of these variables explained the year effect. Another possible mechanism is that the caterpillar frass used to estimate the caterpillar biomass[23] no longer accurately captures this biomass because other caterpillar species, that do not produce frass, have become more important. Although there is no direct data available to test this idea, it is striking that the annual height of the caterpillar biomass peak in spring correlates very well with the annual number of female winter moths caught on the trees the winter before ($b = 0.50$ (s.e. 0.10 (on a log-log scale), $p = 0.0001$, M.E. Visser, unpubl. data), indicating that winter moths, which produce frass collected in the frass nets, are to a large extent responsible for the caterpillar biomass peak.

Secondly, there was also an additive year effect in the relationship between laying date and spring temperature; laying date got earlier for the same temperature over the years. This could be because laying date is also affected by temperatures in another time of the season but the ClimWin analysis did not detect such a second period. There are numerous other environmental variables that will have changed over the years that may affect laying dates, including the phenology of the food used by the great tits at the time of egg laying (and thus lift a constraint for earlier laying[42]). Although the observation is consistent with a genetic response to selection, this is an unlikely explanation given the low heritability of laying date[43].

Thirdly, in addition to the effect of spring temperature in the analysis of the phenology of the food peak, an additive year effect was found. This year effect was no longer significant when we included oak bud burst date in the model and hence the advancement of the oak bud burst date may have led to an earlier food peak date at the same temperatures indicating that the date of the food peak is affected both by the Oak bud burst date (start of caterpillar feeding) and temperature (rate of caterpillar growth).

While there was no significant advancement of laying date over time in the 1998 paper[17], we found such an advancement for the 1973-2020 period. It seems that the advancement is now significant simply due to the increased number of years as the two slopes of laying date versus year (years 1973-1995[17]: b = -0.215 +/- 0.152; years 1973-2020: b = -0.248 (s.e. 0.055) are not statistically different (t = 0.20, df=67, p = 0.58).

The projected mismatch for the end of the century differs under the different climate scenarios. Under the RCP8.5 scenario the mismatch is projected to be much larger than under the RCP4.5 scenario (in 2080, the last year of the RCP4.5 scenario). The projected mismatch increases is because the phenology of the birds advancing less rapidly than the phenology of their food (Fig. 4). In contrast, the three climate scenarios based on the Paris Agreement (1.5degOS, 1.5degNE, and 2.0degNE) show a smaller projected mismatch at the end of the century and, interestingly, the projected mismatch stabilizes after 2050 as under these scenarios the increase in temperatures end at that time point due to climate mitigation. Note also that the projected mismatch under the RCP8.5 scenario in 2100 (15 days, Fig. 4C) is 2-3 times larger than the peak mismatch observed in the past (5-10 days, Fig. 2C) and is in fact as large as the extreme mismatch observed in 2007. On the other hand, the three Paris Agreement scenarios project a mismatch of the same order of magnitude as the historical peak mismatch period (5-10 days). Thus, under all climate scenarios there will be sustained mismatches between the phenology of the birds and their prey, and thus sustained selection for earlier laying.

Our results show that the mismatch is forecasted to show the steepest increase under the RCP8.5 scenario, and thus leads to the largest phenological disruption. Schwalm et al.[39,40] concluded that RCP8.5 is the preferred choice for assessing climate impacts risks throughout the mid-century as RCP4.5 would be a definitive underestimate of physical climate risk. Indeed, the Climate Action Tracker reports that the current policy pathways have a greater than 97% probability of exceeding 2°C. The projected mean global warming is 2.4 °C (likely range: 1.7 to 3.2) under RCP 4.5 and 4.3 °C (likely range: 3.2 to 5.4) under RCP 8.5 above pre-industrial level[41].

The key reason why the directional selection on laying date has weakened over the past decades is that the temperatures correlated with great tit egg laying date have continued to increase, while the increase in temperatures correlated with food peak phenology has slowed down. The increase in greenhouse gases since the industrial revolution is imposing climate changes on timescales from decadal to centennial. In addition to an anthropogenic climate change signal characterized by a secular trend, there is a noise from unforced variability generated internally within the climate system (e.g. weather) or associated with external forces to the climate system (e.g. such as due to changes in aerosol loading or solar variations or volcanoes), referred to as natural or internal variability[44]. Such noise can lead to a slowdown in the increase in temperatures as observed recently in the 2000s due to a combination of volcanic influences and internal climate variability[20,21]. Taking this natural climate variability into account, we project that the temperatures correlating with food peak phenology will become warmer again, and that this will lead to an increased phenological mismatch, and as a consequence, increased directional selection for earlier laying dates. Our prediction of the mismatch does not take into account any potential evolutionary response in temperature-sensitivity of great tits, which will make only a small contribution at best[43], or other potential constraints on advancing laying or hatching dates[42]. Another weakness in our predictions is the unexplained year effect in the relationships between laying date and temperature (Fig. 3A) and food peak phenology and temperature (Fig. 3B).

Thus, we conclude that the relationships reported 25 years ago still hold, and that the recent weakening of the selection for earlier egg laying dates is caused by a recent, and probably temporal, slowdown of late spring temperature warming. The fact that our relationships are robust allows us to predict future mismatches from climate predictions with confidence, albeit this assumes that the relationships between phenology and temperature will remain as we have identified them. These future projections show that temperatures will continue to increase over the decades to come, and that the phenology of the caterpillar peak date will again advance, faster than great tit laying dates, and hence selection for early breeding will again increase. Climate change will thus continue to lead to an evolutionary lag, with potential effects on population viability[10,12]. Our results also make clear that the rate of climate change has been, and may will be again in the near future, too high to be matched by the rate of adaptation for our population, either through phenotypic plasticity or micro-evolution[13]. The Paris agreement is a first step in reducing the rate of climate change, which is important as only substantially reducing this rate to historical rates of warming, perhaps even by as much as a factor of 100[45], will allow species to keep up via genetic change, as they have always done on our ever-changing planet.

Acknowledgements

We thank the board of the National Park `de Hoge Veluwe' for their permission to work within their reserve for all these years. We also thank the numerous fieldworkers over the years, Louis Vernooij for managing the database and Tom Reed, Christiaan Both and Melissah Rowe for constructive comments on a previous version of the manuscript, and Ally Phillimore and an anonymous reviewer for their helpful comments. SJ and MaL acknowledge the support of NASA grant (19-IDS19-0028).

References

1. Bradshaw AD. 1965 Evolutionary significance of phenotypic plasticity in plants. *Advan. Genet.* **13**, 115–155.

2. Visser ME, Caro SP, van Oers K, Schaper SV, Helm B. 2010 Phenology, seasonal timing and circannual rhythms: towards a unified framework. *Philosophical Transactions of the Royal Society B-Biological Sciences* **365**, 3113–3127.

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

4. Thackeray SJ *et al.* 2016 Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535**, 241-U94. (doi:10.1038/nature18608)

5. Radchuk V *et al.* 2019 Adaptive responses of animals to climate change are most likely insufficient. *Nature Communications* **10**, 3109. (doi:10.1038/s41467-019-10924-4)

6. Visser ME, Gienapp P. 2019 Evolutionary and demographic consequences of phenological mismatches. *Nature Ecology & Evolution* **3**, 879–885. (doi:10.1038/s41559-019-0880-8)

7. Thackeray SJ *et al.* 2010 Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology* **16**, 3304–3313.

8. Gienapp P, Reed TE, Visser ME. 2014 Why climate change will invariably alter selection pressures on phenology. *Proceedings of the Royal Society B-Biological Sciences* **281**. (doi:10.1098/rspb.2014.1611)

9. Post E, Forchhammer MC. 2008 Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B-Biological Sciences* **363**, 2369–2375. (doi:10.1098/rstb.2007.2207)

10. Simmonds EG, Cole EF, Sheldon BC, Coulson T. 2020 Phenological asynchrony: a ticking time-bomb for seemingly stable populations? *Ecology Letters* **23**, 1766–1775. (doi:10.1111/ele.13603)

11. Both C, Bouwhuis S, Lessells CM, Visser ME. 2006 Climate change and population declines in a long-distance migratory bird. *Nature* **441**, 81–83.

12. Reed TE, Grøtan V, Jenouvrier S, Sæther BE, Visser ME. 2013 Population growth in a wild bird is buffered against phenological mismatch. *Science* **340**, 488–491.

13. Visser ME. 2008 Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society of London Series B-Biological Sciences* **275**, 649–659.

14. Charmantier A, Gienapp P. 2014 Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary Applications* **7**, 15–28. (doi:10.1111/eva.12126)

15. van Asch M, Salis L, Holleman LJM, van Lith B, Visser ME. 2013 Evolutionary response of the egg hatching date of a herbivorous insect under climate change. *Nature Climate Change* **3**, 244–248. (doi:10.1038/nclimate1717)

16. Helm B, Van Doren BM, Hoffmann D, Hoffmann U. 2019 Evolutionary response to climate change in migratory pied flycatchers. *Current Biology* **29**, 3714-3719.e4. (doi:https://doi.org/10.1016/j.cub.2019.08.072)

17. Visser ME, van Noordwijk AJ, Tinbergen JM, Lessells CM. 1998 Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proceedings of the Royal Society of London Series B-Biological Sciences* **265**, 1867–1870.

18. Reed TE, Jenouvrier S, Visser ME. 2013 Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. *Journal of Animal Ecology* **82**, 131–144. (doi:10.1111/j.1365-2656.2012.02020.x)

19. Mann ME, Steinman BA, Brouillette DJ, Miller SK. 2021 Multidecadal climate oscillations during the past millennium driven by volcanic forcing. *Science* **371**, 1014. (doi:10.1126/science.abc5810)

20. Lewandowsky S, Cowtan K, Risbey JS, Mann ME, Steinman BA, Oreskes N, Rahmstorf S. 2018 The ‘pause’ in global warming in historical context: (II). Comparing models to observations. *Environmental Research Letters* **13**, 123007. (doi:10.1088/1748-9326/aaf372)

21. Risbey JS, Lewandowsky S, Cowtan K, Oreskes N, Rahmstorf S, Jokimäki A, Foster G. 2018 A fluctuation in surface temperature in historical context: reassessment and retrospective on the evidence. *Environmental Research Letters* **13**, 123008. (doi:10.1088/1748-9326/aaf342)

22. Kay JE *et al.* 2015 The Community Earth System Model (CESM) Large Ensemble Project: A community resource for studying climate change in the presence of internal climate variability. *Bulletin of the American Meteorological Society* **96**, 1333–1349. (doi:10.1175/bams-d-13-00255.1)

23. Visser ME, Holleman LJM, Gienapp P. 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.

24. Ramakers JJC, Gienapp P, Visser ME. 2020 Comparing two measures of phenological synchrony in a predator–prey interaction: Simpler works better. *Journal of Animal Ecology* **89**, 745–756. (doi:10.1111/1365-2656.13143)

25. Chevin L-M, Visser ME, Tufto J. 2015 Estimating the variation, autocorrelation, and environmental sensitivity of phenotypic selection. *Evolution* **69**, 2319–2332. (doi:10.1111/evo.12741)

26. Linden A. 2018 Adaptive and nonadaptive changes in phenological synchrony. *Proceedings of the National Academy of Sciences of the United States of America* **115**, 5057–5059. (doi:10.1073/pnas.1805698115)

27. Bailey LD, van de Pol M. 2016 climwin: An R Toolbox for Climate Window Analysis. *PLoS One* , e0167980. (doi:https://doi.org/10.1371/journal.pone.0167980)

28. Visser ME, Holleman LJM. 2001 Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London Series B-Biological Sciences* **268**, 289–294.

29. Perdeck AC, Visser ME, Van Balen JH. 2000 Great Tit *Parus major* survival, and the beech-crop cycle. *Ardea* **88**, 99–108.

30. Lande R, Arnold SJ. 1983 The measurement of selection on correlated characters. *Evolution* **37**, 1210–1226.

31. Thomson CE, Hadfield JD. 2017 Measuring selection when parents and offspring interact. *Methods in Ecology and Evolution* **8**, 678–687. (doi:10.1111/2041-210X.12795)

32. Wood SN. 2011 Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **73**, 3–36. (doi:10.1111/j.1467-9868.2010.00749.x)

33. Aitken AC. 1936 IV.—On Least Squares and Linear Combination of Observations. *Proceedings of the Royal Society of Edinburgh* **55**, 42–48. (doi:10.1017/S0370164600014346)

34. Pelletier F, Coulson T. 2012 A new metric to calculate the opportunity for selection on quantitative characters. *Evolutionary Ecology Research* **14**, 729–742.

35. Reiss JO. 2013 Does selection intensity increase when populations decrease? Absolute fitness, relative fitness, and the opportunity for selection. *Evolutionary Ecology* **27**, 477–488. (doi:10.1007/s10682-012-9618-7)

36. Visser ME, Gienapp P, Husby A, Morrisey M, de la Hera I, Pulido F, Both C. 2015 Effects of spring temperatures on the strength of selection on timing of reproduction in a long-distance migratory bird. *Plos Biology* **13**, e1002120. (doi:10.1371/journal.pbio.1002120)

37. R_Core_Team. 2021 *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

38. Sanderson BM *et al.* 2017 Community climate simulations to assess avoided impacts in 1.5 and 2\\,\degreeC futures. *Earth System Dynamics* **8**, 827–847. (doi:10.5194/esd-8-827-2017)

39. Schwalm CR, Glendon S, Duffy PB. 2020 RCP8.5 tracks cumulative CO_2 emissions. *Proc Natl Acad Sci USA* **117**, 19656. (doi:10.1073/pnas.2007117117)

40. Schwalm CR, Glendon S, Duffy PB. 2020 Reply to Hausfather and Peters: RCP8.5 is neither problematic nor misleading. *Proc Natl Acad Sci USA* **117**, 27793. (doi:10.1073/pnas.2018008117)

41. IPCC. 2014 *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva: IPCC.

42. Visser ME, Te Marvelde L, Lof M. 2012 Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology* **153**, S75–S84.

43. Ramakers JJC, Gienapp P, Visser ME. 2019 Phenological mismatch drives selection on elevation, but not on slope, of breeding time plasticity in a wild songbird. *Evolution* **73**, 175–187. (doi:10.1111/evo.13660)

44. Marotzke J, Forster PM. 2015 Forcing, feedback and internal variability in global temperature trends. *Nature* **517**, 565–570. (doi:10.1038/nature14117)

45. Diffenbaugh NS, Field CB. 2013 Changes in Ecologically Critical Terrestrial Climate Conditions. *Science* **341**, 486–492. (doi:10.1126/science.1237123)

Figure ledgends

Figure 1. Annual standardized selection differentials for great tit laying date between 1973-2020. Negative values indicate selection for earlier laying. Error bars are s.e. of the annual regression slopes of relative fitness on standardized laying dates. The line is the fit of the generalized additive model (Table 1A).

Figure 2. A: Great tit laying date (in April dates, i.e. 31 March is day 0) over years. **B:** Date of the peak in caterpillar biomass (in April dates, i.e. 31 March is day 0) over years. **C:** Annual phenological mismatch between great tit laying date and date of peak caterpillar biomass (in days) over years. The annual phenological mismatch is defined as the difference in the mean laying date of the great tits plus 33 days minus the peak date of caterpillar biomass, positive values thus indicate that the birds breed too late to be matched with their food. **D:** Annual standardized selection differentials are linearly related to mismatch with an additive year effect. This effect is illustrated by the three lines, each illustrative for a particular period: blue line 1985, green line 2002 and magenta line 2019.

Figure 3. A: Great tit laying date (in April dates, i.e. 31 March is day 0) versus temperature (mean daily temperature from 11 March to 20 April, in C). The additive year effect is illustrated by the three lines, each illustrative for a particular period: blue line 1985, green line 2002 and magenta line 2019. **B:** Date of the peak in caterpillar biomass (in April dates, i.e. 31 March is day 0) versus temperature (mean daily temperature from 6 March to 14 May, in C). The additive year effect is illustrated by the three lines, each illustrative for a particular period: blue line 1985, green line 2002 and magenta line 2019. **C:** The temperature best correlating with great tit laying date temperature (mean daily temperature from 11 March to 20 April, in C) over time. **D:** The temperature best correlating with the date of the peak in caterpillar biomass (mean daily temperature from 6 March to 14 May, in C) over time.

Figure 4. A. Projected laying dates, **B**. food peak dates, and **C.** phenological mismatch from 2006-2100 for five climate scenarios (RCP8.5, RCP4.5, 1.5degOS, 1.5degNE, and 2.0degNE). For each scenario and phenotype, the running mean over an eleven-year period over ensemble runs within the respective scenario with 90% confidence interval (CI) is plotted (note: for illustration purposes only, the analysis was done on annual values as plotted, see figure A4 in the Appendix for plots of these annual values). Please note, that the RCP4.5 scenario provides projected temperatures until 2080 (rather than 2100).

Table 1: Details of statistical analyses of (A) time trends, (B) variables potentially affecting the relationship between selection differentials and mismatch, and (C) relationships between phenology and temperatures. For non-significant variables significance and coefficients are given at the point of removal from the model.

A Details of generalised additive model of the different dependent variables *vs*. year. Given are the estimated degrees of freedom (edf), F-ratio (*F*), p-value (*p*), the minimised generalised cross-validation score (GCV), all for s(year), the sample size (n) and in case the model yielded a linear fit the slope (*b*).

Dependent variable	**edf**	***F***	***p***	**GCV**	**n**	***b* (s.e.)**
Selection differential	2.272	3.308	0.044	1.47	47	
Laying date	1	20.56	< 0.001	28.9	48	-0.248 (0.055)
Food peak date	1.893	2.361	0.002	49.2	35	
Mismatch	1.843	1.167	0.203	48.56	35	
Oak budburst date	1	11.35	0.002	37.8	33	-0.367 (0.109)
Temperature correlating with laying date	1	14.14	< 0.001	1.66	48	0.050 (0.013)
Temperature correlating with food peak date	2.031	12.42	< 0.001	0.965	48	

B *F*-ratios (*F*), degrees of freedom (df), p-values (*p*) and coefficients (*b*) of the variables that were tested to explain the year effect in the relationship between selection differentials and mismatch.

Variable	***F***	**df**	***p***	***b* (s.e.)**
Beech Crop Index	0.0324	1, 19	0.86	0.0016 (0.0086)
Spring temperatures in following year	0.377	1, 20	0.55	-0.0203 (0.0330)
Total number of fledglings	0.223	1, 21	0.64	-0.000094 (0.00020)
Height of the caterpillar biomass peak	2.07	1, 22	0.16	0.0039 (0.0027)
Mean number of recruits	3.57	1, 30*	0.068	0.21 (0.11)

** Denominator d.f. increase by more than one because additional years can now be included in the analysis.*

C *F*-ratios (*F*), degrees of freedom (df), p-values (*p*) and coefficients (*b*) of the variables determining laying dates and food peak phenology

	Variables				
dependent	**independent**	***F***	**df**	***p***	***b* (s.e.)**
Laying date	temperature*year	0.283	1,44	0.60	-0.012 (0.024)
	temperature	75.89	1,45	< 0.001	-3.31 (0.38)
	year	4.86	1,45	0.033	-0.085 (0.039)
Food peak date	temperature*year	0.526	1,31	0.47	-0.038 (0.052)
	temperature	130.8	1,32	< 0.001	-6.03 (0.53)
	year	14.8	1,32	< 0.001	-0.210 (0.055)
Food peak date	year	2.88	1,28	0.10	-0.121 (0.072)
	temperature*	31.5	1,29	< 0.001	-4.42 (0.79)
	bud burst date	8.79	1,29	0.006	0.356 (0.120)

** Note that the temperature effect differs between the two models because fewer years are included in the analysis due to missing bud burst data.*

Table 2: Mean with 90% confidence interval (CI) of projected laying dates (A), food peak dates (B) and phenological mismatch (C) for five climate scenarios (RCP8.5, RCP4.5, 1.5degOS, 1.5degNE, and 2.0degNE) in 2075 (left panel) and 2095 (right panel). Mean corresponds to the eleven-year running mean over ensemble runs within the respective scenario. Please note, that the RCP4.5 scenario provides projected temperatures until 2080 (rather than 2100).

	2075			**2095**		
Scenario	**Mean**	**Start 90% CI**	**End 90% CI**	**Mean**	**Start 90% CI**	**End 90% CI**
(A) Projected laying dates						
RCP8.5	101.49	101.21	101.76	99.70	99.39	100.02
RCP4.5	105.49	105.04	105.93			
1.5degOS	108.51	108.01	109.01	109.03	108.24	109.82
1.5degNE	109.02	108.43	109.61	108.90	108.55	109.25
2.0degNE	107.72	106.95	108.50	107.48	106.88	108.09
(B) Projected Food peak dates						
RCP8.5	121.12	120.71	121.53	118.07	117.61	118.53
RCP4.5	128.50	127.90	129.09			
1.5degOS	133.50	132.55	134.46	134.70	133.64	135.75
1.5degNE	134.46	133.74	135.18	133.90	133.34	134.46
2.0degNE	132.71	131.77	133.66	131.80	131.08	132.52
(C) Projected phenological mismatch						
RCP8.5	13.37	13.11	13.63	14.63	14.37	14.90
RCP4.5	9.99	9.57	10.41			
1.5degOS	8.01	7.39	8.62	7.33	6.90	7.76
1.5degNE	7.56	7.25	7.87	8.00	7.55	8.44
2.0degNE	8.01	7.59	8.42	8.68	8.31	9.05