

Marcel E. Visser · Leonard J. M. Holleman
Phillip Gienapp

Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird

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Abstract Timing of reproduction has major fitness consequences, which can only be understood when the phenology of the food for the offspring is quantified. For insectivorous birds, like great tits (*Parus major*), synchronisation of their offspring needs and abundance of caterpillars is the main selection pressure. We measured caterpillar biomass over a 20-year period and showed that the annual peak date is correlated with temperatures from 8 March to 17 May. Laying dates also correlate with temperatures, but over an earlier period (16 March – 20 April). However, as we would predict from a reliable cue used by birds to time their reproduction, also the food peak correlates with these temperatures. Moreover, the slopes of the phenology of the birds and caterpillar biomass, when regressed against the temperatures in this earlier period, do not differ. The major difference is that due to climate change, the relationship between the timing of the food peak and the temperatures over the 16 March – 20 April period is changing, while this is not so for great tit laying dates. As a consequence, the synchrony between offspring needs and the caterpillar biomass has been disrupted in the recent warm decades. This may have severe consequences as we show that both the number of fledglings as well as their fledging weight is affected by this synchrony. We use the descriptive models for both the caterpillar biomass peak as for the great tit laying dates to predict shifts in caterpillar and bird phenology 2005–2100, using an IPCC climate scenario. The birds will start breeding earlier and this advancement is predicted to be at the same rate as the advancement of the food peak, and hence they will not reduce the amount of the current mistiming of about 10 days.

Keywords Climate change · Fitness · Great tit · Phenology · Timing of reproduction

Introduction

Timing of reproduction is a life-history trait with important fitness consequences (e.g. Daan et al. 1990; Klomp 1970; Perrins 1970; Verhulst et al. 1995) because for many species there is a short time-window in the annual cycle where conditions are sufficiently good so that they can successfully reproduce. This time window is often set by the abundance of food necessary to raise offspring (Lack 1950; Martin 1987). As the seasonal pattern in the environmental conditions varies from year to year, also the optimal time window for reproduction varies annually. In accordance with this, timing of reproduction shows corresponding within-individual year-to-year variation, caused by phenotypic plasticity. To understand the selection acting on the timing of reproduction we need to identify the environmental factors, for example, prey phenology, which determine the optimal time window for reproduction. Only then we can understand why, in an ultimate sense, the animals reproduce early in one year and late in another, and why within a year late-reproducing animals do better or worse than early-reproducing conspecifics. What is more, it is the only avenue to a more predictive study on the impact of climate change on the reproductive output of animals.

There is ample evidence that climate change has led to changes in the phenology of many species (e.g. Beebee 1995; Brown et al. 1999; Crick et al. 1997; Parmesan et al. 1999; Penuelas et al. 2002). Parmesan and Yohe (2003) summarized the literature and concluded that there is "...'very high confidence' that climate change is already affecting living systems." It is however unclear how we should interpret this. If a species has shifted 10 days in 20 years, is that positive (adapting to changing conditions) or negative (climate change is affecting living systems)? What we need is a yardstick:

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M. E. Visser (✉) · L. J. M. Holleman · P. Gienapp
Netherlands Institute of Ecology (NIOO-KNAW),
P.O. Box 40, 6666 ZG Heteren, The Netherlands
E-mail: m.visser@nioo.knaw.nl
Tel.: +31-26-4791253
Fax: +31-26-4723227

how much should a species shift given the change in temperatures and other climate variables (Visser and Both 2005; Visser et al. 2004)? The yardstick is of course the shift in the moment in the year the environment is most suitable for reproduction; if this moment has shifted 10 days as well, the focus species is doing very well, if this moment has shifted 20 days, or not at all, then obviously climate change has a negative effect.

In many taxa the main variable determining reproductive success is the abundance of prey items (e.g. Dias and Blondel 1996; Durant et al. 2003; Pearce-Higgins and Yalden 2004; van Noordwijk et al. 1995; Verboven et al. 2001) affecting also the workload of the adults (Thomas et al. 2001). Yet, there are only a limited number of systems where data is collected on the annual cycle of a species and on the temporal variation of its prey abundance. We will focus on one of the more well-known systems of great tits (*Parus major*) relying on caterpillars in oaks as the main food source for their nestlings (e.g. Naef-Daenzer et al. 2000; Perrins 1991). In this system, the caterpillar prey appears after the trees have their bud burst and disappears when the caterpillars are fully grown and pupate in the soil and are thus no longer available. Hence, there is only a short period of ample food, and these insectivorous birds need to synchronise their breeding in such a way that the time of the maximal need of their offspring for food coincides with the time of maximal food abundance.

The phenology of caterpillars in trees is generally measured indirectly by collecting caterpillar droppings with so called frass-nets placed beneath a tree (e.g. Fischbacher et al. 1998; Verboven et al. 2001; Visser et al. 1998). The term *frass* stems from a mistranslation of the German word *Fraß* meaning 'amount eaten away' (from a certain food) rather than dropping. The biomass of the caterpillars is calculated from the mass of the droppings collect in the nets corrected for temperature (Tinbergen and Dietz 1994). Although this method has been validated (Fischbacher et al. 1998; Liebhold and Elkinton 1988a, b; Zandt 1994) it may be possible that weather conditions (wind, rain) and properties of the tree (height, size) introduce systematic errors. To validate the established relationship further and possibly to correct for the mentioned effects we compared caterpillar biomass calculated from collected droppings and from direct branch samples from trees.

We have reported on the impact of climate change on the synchronisation of great tit laying dates and caterpillar abundance in previous publications (Visser et al., 1998, 2004) where we showed that caterpillar peak biomass date has shifted forward over the past decades but that there has been no advancement of laying dates of great tits. Here, we will take our studies on this system a step further and predict how forecasted climate change will impact the phenology of both caterpillar biomass and bird reproduction in the next 100 years.

Our objectives are to describe the caterpillar biomass changes throughout a season, to construct a descriptive model of the peak date and width of the biomass curve.

We will also compare the temperature sensitivity of the great tit laying dates and of the food peak to assess the impact of changing temperatures on the synchrony of the birds with their main food. Furthermore, we correlate a number of great tit fitness parameters to the biomass distribution to demonstrate the importance of this synchronisation. Finally, we use a descriptive model to predict the future caterpillar biomass distributions and laying dates under IPCC scenarios and use these predicted caterpillar and bird phenologies to estimate the impact of the changing food phenology on the birds' breeding success.

Methods

Fieldwork

Fieldwork was carried out in the Hoge Veluwe, one of our long-term (1955–2004) study areas. This study area consists of 171 ha mixed woodland on poor sandy soils, dominated by oak and pine with about 400 nest boxes. Some additional comparisons are made with data from another long-term study area, Oosterhout, a smaller, isolated woodland (11 ha) on rich clay soils near the river Waal, in which 120 nest boxes are placed.

From 1993 to 2004 frass nets were placed under a varying number of trees on the Hoge Veluwe, but there is a fixed set of seven oak trees, located at different sites within the study area (> 500 m apart), which were sampled throughout these years. Furthermore, from 1985 to 1992 frass nets were used in the same area by J. M. Tinbergen, and we use these data on the phenology of the caterpillar biomass (see Verboven et al. 2001) to obtain a 20-year time series. For Oosterhout frass net data are available for the years 1957–1967 (van Balen 1973), 1986–1988 (Zandt 1994), 1996 and 2001–2004 (own data).

Frass nets (a cheese cloth of 0.25 m² in a metal frame, with a weight hung from the centre of the net, see Fig. 3a in Tinbergen 1960) were put up under oak trees (*Quercus robur*). Two of these nets are placed under a tree (about 1–1.5 m from the stem) and every 3–4 days all caterpillar droppings are collected, dried at 60° C for 24 h, sorted (i.e. all debris is removed), weighted and from this the caterpillar biomass is calculated (see below).

During 3 years (1994–1996) we took branch samples using a sky lift at the Hoge Veluwe. Branches of about 2 m were first put into a large plastic bag, then cut from the trees and later (within 36 h) sorted for insects. The length of the branches were measured to convert the total biomass to biomass/meter branch. We also measured height and stem diameter of these trees.

To analyse the spatial variation in the time of maximal caterpillar biomass we correlated the peak date of caterpillar biomass with bud burst date of the tree under which the nets were placed. Tree leaf phenology was scored twice a week and we use the date at which the leaves protruded from their buds in the

canopy of the tree as their bud burst date (Visser and Holleman 2001).

Data on laying dates and clutch sizes of great tits in the various populations was collected by weekly checks of the nest boxes. Laying dates are calculated back assuming that one egg per day is laid. All analyses of laying dates and clutch sizes were restricted to first clutches. Adults are caught during chick feeding and identified by their aluminium and colour-or ringed if not previously caught. All nestlings are banded at an age of 7 days and weighed at 15 days, which is a good approximation of their fledging weight. Laying dates are given as April-days (1 April is April-day 1, 24 May is April-day 54).

Temperature and other climatic data (precipitation, wind speed, sunshine duration) for 'De Bilt', the main weather station of the Royal Dutch Meteorological Institute (KNMI), were used and obtained from the KNMI's website (<http://www.knmi.nl/klimatologie/daggegevens/download.cgi?language=eng>).

Calibration of frass measurements

Caterpillar biomass was calculated from the raw frass data using the formula of Tinbergen and Dietz (1994), which essentially corrects the amount of frass produced per unit biomass caterpillar for the temperature. To calibrate these measurements we used data from 3 years (1994 – 1996) in which branches were sampled from trees that also had caterpillar frass nets ($n=60$ tree-sample days). The main species of caterpillars found were winter moth (*Operophtera brumata*) and oak leaf roller (*Tortrix viridana*). When correlating the biomass as recorded from the branch samples with the biomass as calculated from the frass samples we used a log transformation to normalise the data. We also used a repeated measures design with sample date repeated over trees to take into account that the same trees were sampled at different sampling dates (MIXED procedure SAS).

The two measures of caterpillar biomass were highly correlated (log biomass from branch samples versus log biomass calculated from frass in a repeated measures analysis of sample dates over trees: $F_{1,13}=19.35$, $P<0.001$). Biomass is expressed as gram caterpillar biomass per m^2 per day, and thus ignores the height of the tree under which the frass nets are placed. We therefore include height in the subsequent analysis where we correlate biomass as obtained from branch samples with the biomass as calculated from the frass nets. There were no additional significant explanatory variables, neither of the tree characteristics (height and width at breast height, $F_{1,50}<0.60$, $P>0.45$) nor of sample date characteristics (daily precipitation amount [Zandt 1994], sunshine duration, daily mean wind speed and daily mean temperature (note that the biomass as calculated from frass was already corrected for temperature according to Tinbergen & Dietz 1994; all $F_{1,3}<1.60$;

P -values >0.30 in a step-wise analysis). We therefore, used the biomass as calculated from the frass samples (using the Tinbergen and Dietz 1994 formula) without any further corrections as a measure for the biomass of caterpillars in the trees.

Caterpillar biomass distribution

The distribution of the biomass of caterpillars over the season cannot be fitted with a normal or any other distribution and hence we use three parameters to describe the food peak: the peak date is the date at which the largest biomass is recorded (also expressed in April-days), the peak height is the largest biomass recorded in a season ($g \text{ biomass } m^{-2} \text{ day}^{-1}$) and the peak width is the number of days where the biomass is above $1 g \text{ m}^{-2} \text{ day}^{-1}$. The date at which the biomass rises above and falls below this threshold value is estimated by fitting a cubic polynomial through the data points. In 3 years sampling either started after or ended before this threshold was reached and hence for these years we cannot estimate the peak width. Peak height and width depend on the trees sampled and hence were only calculated using the restricted set of seven trees that were sampled every year (1993 – 2004). The biomass peak date within an area is a much less tree-dependent measure and hence we used also the 1985 – 1992 period from Verboven et al. (2001).

We constructed a descriptive model for the peak biomass date ($n=19$ years, excluding 1991 as this was a year with a late frost, which damaged the leaves of the oak trees, Visser et al. 1998) by regressing the peak dates against the mean temperature in all periods of at least 10 day long between 1 January and the 31 May (in total 10,153 different periods) and selected the period which had the highest correlation with peak date. In the analysis of the spatial variation in caterpillar peak date, we used ANOVA and ANCOVA models (GLM procedure SAS) with peak caterpillar biomass date as dependent variable. Finally, we use the descriptive model and the predicted temperatures from an IPCC-SRES model, with an intermediate increase in temperature (SRES-B2) (Esch 2005), and use these to predict the caterpillar biomass distributions for 2005–2100.

Great tit fitness parameters

Synchrony with food peak

The synchronisation between the birds' breeding time and the timing of the food peak was defined as the difference between the hatching date plus 9 days and peak date (synchrony = hatching date + 9 – peak date) because great tit chicks grow fast at an age of 9 days and food demands are then highest (Gebhardt-Henrich 1990; Keller and van Noordwijk 1994).

Number and weight of fledglings

As part of our standard field protocol great tit chicks are weighed to the nearest 0.1 g when they are 15 days old and the number of fledged chicks is recorded by checking the nest for dead chicks after fledging. For all broods in the years 1985–2004 we calculated mean chick weight per brood and the number of fledged chicks. For some years clutch or brood size manipulations were carried out. Since these experiments possibly affected chick weight or the number of fledged chicks of a brood, manipulated broods were excluded from this analysis. The relationship between mean chick weight and the number of fledged chicks with synchrony with the caterpillar peak was analysed with GLMs in R 2.0.1. Full models included the following explanatory variables and all two-way interactions: synchrony, synchrony², peak height (maximum amount of caterpillar biomass recorded), peak width (number of days with caterpillar biomass above 1 g m⁻² day⁻¹) and brood size (number of hatched chicks). Identity link and normal error structure was used for analysing mean chick weight and log link and Poisson error structure for analysing the number of fledged chicks. Minimum adequate models were selected using step-wise backward deletion beginning with the interactions.

Selection differentials

Selection differentials are defined as the covariance between trait and relative fitness and quantify the strength of selection on the trait (e.g. Lande and Arnold 1983). We used the number of offspring breeding in our population (termed recruits) as a fitness measure. Fitness was converted to relative fitness by dividing the number of recruits by the mean number of recruits in a given year. To analyse whether the strength of selection is related to the synchrony of the population with the timing, the height or the width of the caterpillar peak, we regressed the annual selection differentials against these variables and all two-way interactions.

Predictive model of great tit laying dates

We used a Cox's proportional hazards model (Cox 1972) to build a descriptive model, based on the results of Gienapp et al. (2005). This kind of model describes the probability that an individual female will start with egg laying as a function of an unspecified baseline hazard and a set of explanatory variables. The explanatory variables included in the model were female age (first year breeder or older), temperature (calculated via a 'linear predictor'), day length and the interaction between temperature and day length. To avoid very small values of the baseline hazard and therefore possible computational inaccuracies in the used algorithms, the values for daily temperature and day length were

rescaled by subtracting their minimum value (i.e. effectively rescaling the smallest value to 0).

Temperature and day length data

We used an IPCC-SRES model, with an intermediate increase in temperature (SRES-B2) (Esch 2005) as temperature data for our prediction. The predictions of this climate model are available at a temporal resolution of 1 day and a spatial resolution of 50*50 km², in our case around Arnhem (the Netherlands). Day length data for every fifth year were obtained from the US Naval Office via its website (http://www.aa.usno.navy.mil/data/docs/RS_OneYear.html).

Simulation

The baseline hazard is only specified for days on which a laying date was observed. To be also able to predict laying dates outside this 'time window' we fitted an exponential function to the baseline hazard estimated by the proportional hazards model ($r^2=0.86$, $P<0.0001$) and used it for extrapolating the baseline hazard. We calculated the hazard for all days from 1 January to 31 May for all years from 2005 to 2100 using the temperature and day length data, assuming that 43% of the females are older than 1 year (which is the average percentage for 1973–2004) and the (extrapolated) baseline hazard. Using this hazard we simulated egg-laying dates of 100 females per year (see Gienapp et al. 2005 for details). From the obtained distribution of laying dates the annual mean simulated laying dates were calculated.

Results

Describing the caterpillar biomass changes throughout a season

In general, the peak in caterpillar biomass is narrow given the length of the nestling period of about 17 days as the number of days with a biomass above 1 g m⁻² day⁻¹ is on average 24.3 days ($n=9$, range 19–33.5). There is a correlation between the height of the biomass peak and the timing: in late years the peak is higher (Pearson's $r=0.76$, $P=0.004$). There is no correlation between the peak width and either the height or the timing of the peak (both Pearson's $r<0.55$; $P>0.13$).

There is clear annual variation in the peak dates: years differ when the caterpillar biomass peaks ($P<0.001$, correcting for site, see below) and the range is about 3 weeks, roughly equal to the width of the peak. There is also a significant advancement of the peak date over the years 1985 – 2004 of 0.74 days a year ($F_{1,17}=13.15$, $P=0.002$ excluding 1991; $F_{1,18}=10.88$, $P=0.004$ incl. 1991; Fig. 1a, Visser et al, 1998, 2005).

There is no significant change in the width or the height of the biomass peak over the years (both $F_{1,10} < 0.75$; $P > 0.40$).

There is clear spatial variation in the timing of the biomass peak of oaks: some sites within the Hoge Veluwe area are consistently early while others are late (site: $F_{6,65} = 17.52$, $P < 0.001$; year: $F_{11,65} = 22.35$, $P < 0.001$; Grieco et al. 2002). When site is replaced by characteristics of the sampled trees (retaining year as a factor in the model, $F_{1,34} = 19.78$, $P < 0.001$), then height of the tree and date of bud burst are not significant (both $F_{1,32} < 1.20$; $P > 0.28$), but there is a clear effect of the width of the tree at breast height ($F_{1,34} = 48.43$, $P < 0.001$): for every 10 cm of the diameter of a tree the biomass peak is 0.66 (SE 0.017) days earlier. Interestingly, trees with a large diameter also have an early bud burst ($F_{1,34} = 61.54$, $P < 0.001$; again controlling for year $F_{11,34} = 4.91$, $P = 0.002$): for every 10 cm of diameter the bud burst date is 0.51 (SE 0.065) days earlier.

Constructing descriptive model of food phenology

Of all periods tested, the correlation between peak biomass data and temperature was the highest for the period of 8th March to 17th of May ($r^2 = 0.78$, $P < 0.001$; Fig. 1b; Visser et al. 1998, but note different temperature period). The width of the peak (i.e. the number of days between caterpillar biomass above/below $1 \text{ g m}^{-2} \text{ day}^{-1}$) for which we have 9 years of data (1994, 1996, 1998–2004) also correlates with temperature. Here, the period with the highest correlation is 16th of March to 17th of May ($r^2 = 0.66$, $P = 0.005$).

There is also no interaction between site and temperature (over the best fitting period; $F_{6,69} = 0.42$, $P = 0.86$), but sites differ in timing ($F_{6,75} = 12.14$, $P < 0.001$, with temperature in the analysis: $F_{1,75} = 141.44$, $P < 0.001$), the earliest and the latest site differing by 9 days.

Correlation between great tit fitness parameters and biomass distribution

Laying date

When we analyse the relationship between the timing of the food peak and the start of egg laying by the birds within the Hoge Veluwe area we find a correlation: laying is earlier in years with an early food peak ($F_{1,17} = 4.52$, $P = 0.048$). Laying date however only advances with 0.3 days for every day the food peak is earlier (laying date = $8.23 + 0.30 \times \text{food peak date}$).

Verboven et al. (2001) have argued that the laying dates of great tits in the Hoge Veluwe and the Oosterhout areas differ in the way they correlate with the caterpillar biomass peak dates but we do not find this (effect of peak date on laying date: $F_{1,36} = 16.91$, $P < 0.001$ [combining the Oosterhout and Hoge Veluwe

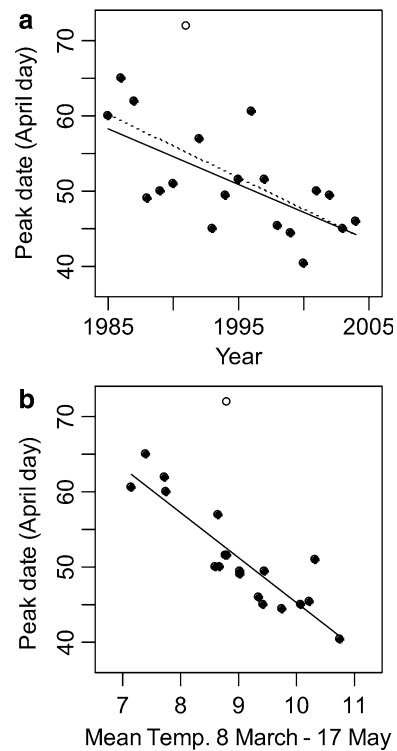


Fig. 1 Phenology of caterpillar biomass at the Hoge Veluwe (1985–2004), in 1991 (*open dot*) a late frost damaged the fresh oak leaves resulting in an extremely late peak date. **a** Advancement of caterpillar peak date over time (*broken line* for all 20 years, *solid line* with 1991 is excluded), and **b** caterpillar peak date (excluding 1991) versus the mean temperature from 8 March to 17 May (the period that correlates best with the caterpillar phenology)

data]), no effect of area \times peak date interaction ($F_{1,34} = 0.81$, $P = 0.37$) nor of area ($F_{1,35} = 0.01$, $P = 0.98$); it should be noted that the food peak data for Oosterhout came partly from much earlier years (1957–1967) than for the Hoge Veluwe.

Synchrony with food peak

The phenology of both the birds, their laying date, and of the food peak depend on temperature, but they differ in the temperature periods they correlate best with. However, if the temperatures used by the birds as cues to time their reproduction, we would expect these temperatures to predict the time of optimal conditions to raise their offspring, that is, caterpillar peak (Visser et al. 2004). We therefore used the temperatures for the best fitting period for the laying dates (16 March – 20 April, $r^2 = 0.61$ for 1973–2004) and determined how well these temperatures predict the food peak. When we restricted the analysis of the relationship between mean temperature and annual mean laying dates to the years for which we have measured caterpillar peak dates, this relationship still holds ($r^2 = 0.42$, $F_{1,17} = 12.22$, $P = 0.003$, no effect of year: $F_{1,16} = 0.26$, $P = 0.62$ or year \times temperature interaction: $F_{1,15} = 0.37$, $P = 0.55$). This

mean temperature over 16 March – 20 April also correlates with the timing of the food peak ($r^2=0.66$, $F_{1,16}=10.38$, $P=0.005$) but there is an additional effect of year ($F_{1,16}=11.18$, $P=0.004$, no significant year \times temperature interaction $F_{1,15}=1.26$, $P=0.28$). The sensitivity of the timing of laying and of the food peak to the temperatures over the period 16 March – 20 April is not significantly different (laying date: -3.34 ± 0.97 day $^{\circ}\text{C}^{-1}$, food peak: -4.01 ± 1.25 day $^{\circ}\text{C}^{-1}$, $F_{1,32}=0.23$, $P=0.63$). This means that the temperatures used by the birds as a cue are true predictors of the timing of the food peak and it is therefore meaningful for the birds to use them (Fig. 2). However, the year effect on the food peak shows that the timing of the food peak is advancing: for the same mean temperature over the period 16 March – 20 April the food peaks 0.57 days a year earlier.

We also have 19 years of data on the timing of the food peak of Oosterhout, but 11 of these are from an earlier period (1957–1967). We do find however also for this area that the laying dates and the food peak correlate well with the temperatures from 16 March to 20 April (Fig. 2, temperature effect on laying date: $F_{1,17}=107.30$, $P<0.001$; temperature effect on food peak: $F_{1,17}=16.17$, $P<0.001$) and here also there is

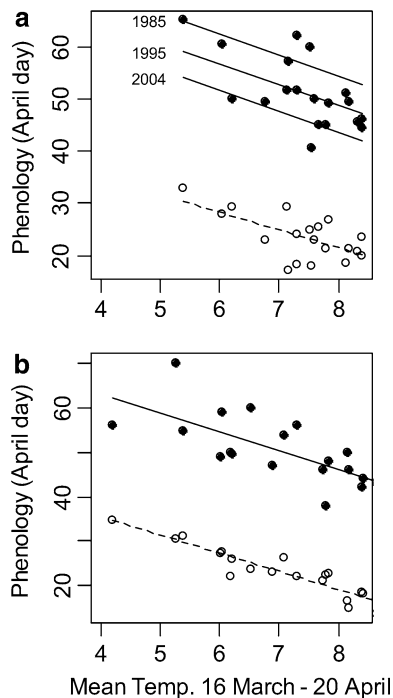


Fig. 2 Laying date (open symbols) and peak biomass date (closed symbols) for **a** Hoge Veluwe (1985–2004, excluding 1991) and **b** Oosterhout (1957–1967, 1986–1988, 1996, 2001–2004) against the mean temperature for 16 March – 20 April (period that best correlated with mean annual laying date). The dashed lines are the regression lines for the laying dates. The solid lines are the regression lines for the food peak as obtained from a model with temperature and, for the Hoge Veluwe, year as explanatory variables. The significant year effect for the Hoge Veluwe is indicated by plotting the regression lines as obtained from the model for 1985, 1995 and 2004. The difference in elevation for the 1985 and 2004 line is 10.9 days

no significant difference in the temperature sensitivity of the two phenological variables (laying date: -4.14 ± 0.40 day $^{\circ}\text{C}^{-1}$, food peak: -4.22 ± 1.05 day $^{\circ}\text{C}^{-1}$, $F_{1,32}=0.01$, $P=0.91$). But in contrast to the Hoge Veluwe, there is no significant year effect for the food peak ($F_{1,16}=0.76$, $P=0.40$). This may reflect actual differences between these areas but it is perhaps more likely that this is due to the large number of years from the earlier period for Oosterhout.

Clutch size

There was no effect of the height of the peak caterpillar biomass on the mean annual clutch size (9.23 eggs; $F_{1,10}=0.33$, $P=0.58$) for the 12 years of the Hoge Veluwe (1993–2004) where we sampled the same trees for a number of years, making the peak height data comparable over the years. The relationship between laying date and clutch size varies significantly between years (interaction between laying date and year: $F_{18,2062}=3.99$, $P<0.001$ in a model with year and laying date, no significant quadratic terms) but the estimates for these annual slopes do not correlate with the biomass peak date ($F_{1,17}=3.46$, $P=0.08$) as was found for the pied flycatcher (*Ficedula hypoleuca*) at the Hoge Veluwe area (Both and Visser 2005).

Reproductive success

The number of fledged chicks was strongly determined by brood size (number hatched: $X^2_1=646.0$, $P<0.001$; $n=1,368$ broods) and by synchrony with the caterpillar peak (Fig. 3a): when corrected for brood size, fewer chicks fledged from broods raised before or after the food peak (synchrony²: $X^2_1=97.0$, $P<0.001$; $n=1,368$ broods) and this relationship did not reach its maximum at a synchrony of 0 days but 1.7 days later, that is, when the chicks are 10.7 days old (synchrony: $X^2_1=10.9$, $P<0.001$).

Mean chick weight is significantly influenced by the synchrony with the caterpillar peak (Fig. 3b): chicks raised before or after the caterpillar peak are lighter (Verboven et al. 2001). This effect is influenced by brood size and the height of the caterpillar peak (synchrony² \times number hatched: $F_{1,529}=18.3$, $P<0.001$; synchrony² \times peak height: $F_{1,529}=5.3$, $P=0.02$): the effect of synchrony on chick weight becomes weakened with an increasing maximum caterpillar biomass but becomes stronger with increasing brood size. The linear synchrony term of the model means that maximum chick weight is not reached at 0 days synchrony (i.e. chicks are 9 days at the date of the biomass peak) but 1.1 days later (when the chicks are 10.1 day old). This relationship is also affected by the width of the caterpillar peak, the wider is the peak the earlier becomes the date relative to the caterpillar peak when chick weight is maximal (synchrony \times peak width: $F_{1,529}=7.1$, $P=0.007$; correcting for the brood size: $F_{1,529}=66.0$, $P<0.001$).

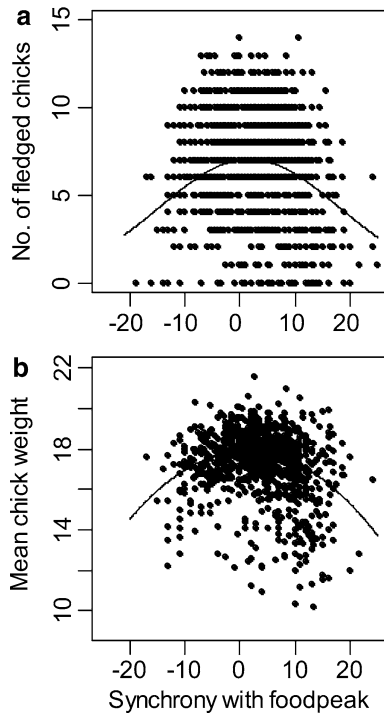


Fig. 3 Number of fledged chicks **a** and mean chick weight **b** of great tits on the Hoge Veluwe in relation to synchrony with caterpillar peak (synchrony = hatching date + 9 – peak date). In **a** fitted lines show relationship between number of fledged chicks and synchrony for different brood sizes, in **b** the fitted line shows the relationship between chick weight and synchrony for the average number of hatched chicks, peak width and peak height

Selection differentials

We could neither find a relationship between width nor height of the caterpillar peak and annual selection differentials (peak width: $F_{1,3} = 0.02$, $P = 0.90$; peak height: $F_{1,4} = 0.0008$, $P = 0.98$). There was a trend of a negative relationship between population mean synchrony and the selection differential, however not significant ($F_{1,15} = 1.27$, $P = 0.28$).

Constructing descriptive model of laying date

Our proportional hazards model explained a significant amount of variation in egg laying dates (Likelihood-ratio = 1,549, $df = 4$, $P < 0.001$, see also Gienapp et al. 2005). All included explanatory variables were highly significant (age: $b = 0.35$, $P < 0.001$; temperature: $b = 1.60$, $P < 0.001$, day length: $b = 5.03$, $P < 0.001$, temperature \times day length: $b = -1.03$, $P < 0.001$). Older females laid earlier than young females (i.e. Perdeck and Cave 1992; Wheelwright and Schultz 1994; Robertson and Rendell 2001) as indicated by the positive regression coefficient. Both temperature, calculated as ‘linear predictor’, and day length had a positive effect on the probability that a female starts with egg laying (both regression coefficients are positive). The negative

regression coefficient of the interaction between temperature and day length means that the effect of temperature decreases with increasing day length. Late in the season, thus, lower temperatures trigger laying than in early in the season (see also Gienapp et al. 2005).

Predicting future caterpillar biomass distributions and laying dates

Over the period 2005–2100, caterpillar peak dates are predicted from the linear regression against spring temperature and an IPCC-SRES temperature scenario. Peak dates will advance by 0.20 days per year, which will add up to a total advancement of 18 days (linear regression: $F_{1,94} = 50.0$, $P < 0.001$; Fig. 4). The predicted width of the caterpillar peak will significantly decrease (linear regression: $b = -0.13 \pm 0.020$, $F_{1,94} = 40.0$, $P < 0.001$).

From 2005 until 2100 mean laying dates are predicted to advance by 0.16 days (± 0.02) per year (linear regression: $F_{1,94} = 47.1$, $P < 0.001$) (Fig. 4). This amounts to a total advance of 15 days over the whole period. Simulated standard deviations show no significant time-trend (linear regression versus year: $F_{1,94} = 2.28$, $P = 0.13$).

The predicted time trends for laying dates in birds and caterpillar phenology are however not significantly different (linear regression: year \times species interaction: $F_{1,188} = 0.99$, $P = 0.32$).

Discussion

The optimal time for reproduction in the great tit is clearly set by the time the biomass of the caterpillars peak: birds that have 11–12-day old chicks in their nest at the annual peak date in biomass fledge the most chicks (for their clutch size, Fig. 3a) and these are also the heaviest (Fig. 3b), increasing the chance that they will survive and breed (Verboven and Visser 1998).

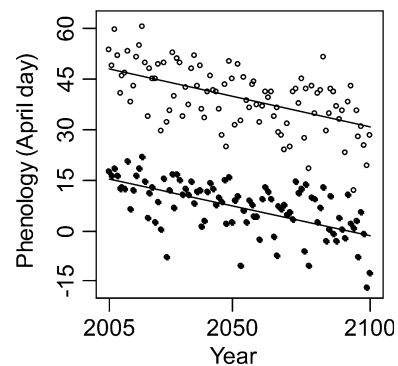


Fig. 4 Predicted phenology based on an IPCC-SRES scenario for the Hoge Veluwe area. Annual means of predicted laying dates (filled dots), and predicted dates when the caterpillar biomass reaches its maximum (peak date) (open dots)

There is both spatial and annual variation in the time of maximal caterpillar biomass and hence the optimal time of breeding for the birds varies in space and time. The annual variation in the date of the biomass peak is as large as the width of the peak (about 3 weeks) emphasising the need for phenotypic plasticity.

One way the birds can cope with the spatial variation is to learn when best to breed at the place they have established themselves (Grieco et al. 2002). They cope with the temporal variation by phenotypic plasticity of their laying dates: the same individual lays at different times in different years. Obviously, the birds need to start reproduction quite some time before their chicks are 11–12 days, that is, when they need to be synchronised with the food peak. They, therefore, use cues from their environment at the time of laying. We have shown that laying dates correlate very well with temperature (from 16 March to 20 April), and that the food peak also correlates with these temperatures and that the phenology of the birds and the caterpillar biomass respond very similar to these temperatures. Hence, the birds seem to be able to respond adequately to the temporal variation in biomass peak date.

The observed mismatch between bird and caterpillar biomass phenology at the Hoge Veluwe seems to be at variance with the observation that both phenologies respond in the same way to temperature. The reason for this is that the timing of the food peak is also affected by temperatures after 20 the April (note that the best fitting period for the food peak is 8 March – 17 May) and that these temperatures have also increased (Visser et al. 1998). It turns out that this is more or less additive so that the change of 1° C in the earlier period still leads to a food peak that is 0.3 days earlier, but that the food peak has advanced because the temperatures in the later period have increased (see Fig. 2a). As the phenology of the food is now earlier for the same temperatures over the early period, but the phenology of the birds is not, the consequence is that the interval between laying and the food peak has become shorter. For a mean temperature of 7° C over the period 16 March – 20 April, this interval was 37.5 days in 1985, but is only 26.6 days in 2004 (a shift of 10.9 days). Given a clutch of ten eggs (= 10 days), 12 days of incubation and chicks of 12 days when they should synchronise with the food peak (= 34 days), the result is that many of the birds have their offspring in the nest too late to profit from the short peak in caterpillar biomass. In the statistical model this leads to a significant year (as a continuous variable) effect in the analysis of the food peak.

The changed relationship between early spring temperature (16 March – 20 April) and caterpillar peak date will lead to selection for a changed reaction norm. However, there is no need for the birds to become more sensitive to temperature (the slope of the reaction norm) but just that they have to lay earlier over the whole range of temperatures (the intercept of the reaction norm). We have indeed detected selection on the reaction norm for the Hoge Veluwe population, but surprisingly the

selection was stronger on the temperature sensitivity, that is, the slope of the reaction norm, than on the laying date in the average environment, that is, the intercept (Nussey et al. 2005). At present, we cannot explain this from the changes in the caterpillar biomass phenology as this has not become more temperature sensitive (no significant year \times temperature interaction). We can only propose several different explanations. A time series of 20 years may not be long enough to detect such an interaction. For a meaningful description of reaction norms it is crucial to identify the correct explanatory variable, against which phenotypes are regressed. Mean temperatures are only a proxy for the real cues used by the birds (Gienapp et al. 2005) and describing reaction norms using a different explanatory variable may give different results. Another explanation could be that there are other selection pressures that select for a steeper reaction norm, such as earlier settlements in warmer years, and hence an earlier competition for territories among the fledged offspring.

Great tits are facultative multi-brooders at the Hoge Veluwe but over the past 20 years the proportion of birds producing a second brood has strongly declined (Visser et al. 2003). A potential explanation for this decline would be a reduction in the width of the food peak; a narrow food peak means a short time-window for reproduction and hence fewer broods. However, we cannot demonstrate a reduction in the width of the food peak. Moreover, it is also likely that for the second brood offspring caterpillars in oak are not the main food source (Verboven et al. 2001).

Annual mean laying dates are correlated to annual mean food peak dates, both on Oosterhout and the Hoge Veluwe. This is what is expected if the phenotypic plasticity in laying date is adaptive. Our results are in contrast to those of Verboven et al. (2001) who claim that there is such a relationship in Oosterhout and Marley Wood (UK), where birds are generally not multi-brooded, but not on the Hoge Veluwe and Vlieland (NL), where part of the birds use to be double-brooded. A major problem with the analysis of Verboven et al. (2001) is, however, that they compare two areas for which they have data from the fifties and sixties (Oosterhout and Marley Wood) with two areas for which they have data from the eighties and nineties (Hoge Veluwe and Vlieland), and find a difference. Given the disrupted synchrony in the recent two decades this could well explain their results, rather than the incidence in second broods in these two pairs of areas. In our analysis, with more recent years for both areas, there is no longer a statistical difference between Oosterhout and the Hoge Veluwe.

We have shown that the current reaction norm of great tit laying date against temperature is no longer adaptive. Given that laying dates reaction norms are heritable (Nussey et al. 2005), we expect a response to this selection and thereby a change in the reaction norm of the birds. We predicted laying dates and food phenology for 2005–2100 and found that both advance over

the next 100 years (Fig. 4) and are predicted to do so at the same rate. However, this prediction is for a great tit population in which no micro-evolution occurs. Obviously, what is needed is a predicted rate of change in laying dates due to selection. Next, we should then compare the rate of change in ecological conditions with the rate of micro-evolution. In the absence of a change in reaction norm we predict that the current mistiming will not increase, which might mean that selection may occur fast enough for the synchrony between the birds and the caterpillar biomass phonologies to be restored, and thereby reducing the negative impact of global climate change.

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