Warming climate advances breeding and improves synchrony of food demand and food availability in a boreal passerine

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Abstract

Global climate change affects ecosystems via several trophic levels. We investigated changes in the timing of breeding in the willow tit (*Poecile montanus*) and timing of its caterpillar food resource in relation to warming springs in a boreal forest. We used generalized linear mixed effect models to study the importance of synchrony between the timing of breeding in willow tits and the caterpillar food availability on the breeding success, measured as nestling survival rate and mean nestling weight. Both the timing of breeding and the timing of the caterpillar peak advanced during the last decades, and were well explained by spring temperatures. Unlike in most passerine populations studied, synchrony has improved with rising spring temperatures. However, it had only a modest although statistically significant positive influence on breeding success. Spring temperatures do not seem to be used as cues for the timing of caterpillar food availability by willow tits. We conclude that responses to climatic warming seem to be population, species and habitat specific, necessitating research in a wide range of taxa in different climatic zones.

Keywords: breeding success, caterpillar abundance, climate change, frass-fall, *Poecile montanus*, rising temperature, timing of breeding

Introduction

Climate change has affected phenology both in plant and animal kingdoms (e.g. Walther *et al.*, 2002; Parmesan & Yohe, 2003; Menzel *et al.*, 2006). Rising spring temperatures have led to advanced onset of migration and breeding in many insectivorous bird species (e.g. Walther *et al.*, 2002; Parmesan & Yohe, 2003; Dunn, 2004), but not in all (Parmesan & Yohe, 2003). Temporal changes differ between populations (Sanz, 2002; Visser *et al.*, 2003; Both *et al.*, 2004). The timing of food resources, essential for feeding offspring, has also changed. In the Netherlands, climate change has led to asynchrony between the timing of breeding in great tits (*Parus major*), blue tits (*Cyanistes caeruleus*) and pied flycatchers (*Ficedula hypoleuca*) and the abundance of caterpillars feeding on oak leaves (Visser *et al.*, 1998; Visser *et al.*, 2006; Both *et al.*, 2009). The same has not happened with great tits in England (Cresswell & McCleery, 2003) nor with great tits and collared flycatchers (*F. albicollis*) in the Czech Republic (Bauer *et al.*, 2010). Differences are likely due to spatial variation in the intensity and detailed pattern of the climate warming (Walther *et al.*, 2002; Cresswell & McCleery, 2003).

In birds, timing of breeding is an important fitness-related life-history trait (e.g. Perrins, 1970; Dunn, 2004). Breeding should be timed so that enough food is available during the nestling feeding phase – in the temperate zone the appropriate time window is short (Lack, 1950; Visser *et al.*, 2004). The nestling period is mainly timed by the onset of egg laying (e.g. Cresswell & McCleery, 2003) that should occur long in advance to synchronize the nestling period with the food peak (Visser *et al.*, 1998). For Parids, caterpillars feeding on deciduous trees are the main food for nestling provisioning (Perrins, 1991; Rytkönen *et al.*, 1996). Proper timing is selectively advantageous to the parents, manifested by many and good quality fledglings with high local recruitment rate (Tinbergen & Boerlijst, 1990; Nager & van Noordwijk, 1995; Visser *et al.*, 2006).

In temperate zone, spring temperatures may affect the timing of breeding as a predictive factor, 'a cue' of the future food availability, as it affects the emergence of invertebrates (e.g. Visser *et al.*, 1998), or as a constraint affecting food availability and thermoregulatory costs in the early stages of breeding (Perrins, 1965; Bryant, 1975; Stevenson & Bryant, 2000). Perrins' (1965, 1970) energy limitation hypothesis suggests that constraining factors prevent birds from breeding earlier. Alternatively, one can consider the timing of breeding as a result of an optimization process, affected by fitness

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costs and benefits from breeding at a given time (Verhulst & Nilsson, 2008). Besides the temperature, photoperiodicity determines the timing of breeding via hormonal functions (e.g. Dawson, 2002).

Most of the phenological studies concerning timing of reproduction as well as food peaks are from temperate broad-leaved forests in the mid-latitudes of Europe (see Visser & Both, 2005 for a review; Both et al., 2009). Yet little is known about the effects of climate change on timing and synchrony or their impacts on breeding success of northern populations and boreal species (but see Visser et al., 2003; Ludwig et al., 2006; Waite & Strickland, 2006; Ahola, 2008; Lehikoinen et al., 2011). We used long-term data to study the shifts in timing of reproduction in a boreal forest sedentary passerine, the willow tit (*Poecile montanus*), and timing of the caterpillar abundance. We examined the synchrony of food demand and food availability and its impact to the breeding success, measured as nestling survival rate and mean nestling weight. As a sedentary species, the willow tit should be able to detect any environmental cues about the timing of the food peak. The study increases the knowledge concerning the effects of climate change on boreal ecosystems.

Material and methods

Study species

The willow tit is a small resident palearctic passerine, nesting in cavities the pair excavates in decaying stumps (Orell & Koivula, 1988; Orell et al., 1999). In the Oulu area, the average clutch size is 7.6 eggs, incubation takes ca. 14 days and the nestling period ca. 18 days (Orell & Ojanen, 1983a, b). During the nestling period, the parents feed the young with invertebrates, mostly caterpillars (e.g. *Epirrita autumnata*) if available but also with Diptera (Tipulidae, Culicidae), spiders Arachnoidea and aphids Aphidoidea. The proportion of caterpillars in the nestling diet is up to over 80% when the caterpillar peak matches with the nestling period (Rytkönen et al., 1996). Moulting takes place in late summer (Orell & Ojanen, 1980). Intensive hoarding of animal and plant food, which plays an important role in the winter diet, occurs in autumn (September–October) until the snow comes (Brodin et al., 1996). Willow tits spend the winter in small territorial flocks with a social hierarchy (e.g. Koivula & Orell, 1988).

Study area

The data were collected in the Oulu area, northern Finland (ca. 65°N, 25°30′E) during 1975–2009, in a habitat of coniferous, deciduous and mixed forests of varying ages, including young stands, swamps and clear cuttings (e.g. Lahti, 1997). The study area has expanded in size, starting from 0.57 km^2 in 1975 (Orell & Ojanen, 1983a) and gradually increasing to ca. 25 km^2 in 1996 and later.

Data

We determined the onset of egg laying, time of hatching (both in accuracy of 1 day) and the clutch size of the first clutches by routine visits to the nests as described in Orell et al. (1999). We weighed the nestlings at the age of 13 days to the nearest 0.1 g and recorded the number of fledged chicks. We used the annual median dates for the start of laying and hatching in the analysis, except for the breeding success analysis we used nest-specific values. Numbers of nests forming the data are presented in Appendix S1. We obtained the data of daily mean ambient temperatures for 1975–2009 from the Finnish Meteorological Institute, Oulunsalo observatory, situated ca. 20 km south of the study area.

The abundance of caterpillars foraging on birch (*Betula* spp.) was estimated for 1996–2009 using the frass-fall method (Zandt, 1994) according to Rytkönen & Orell (2001). By this procedure, the caterpillar biomasses were estimated in approximately weekly periods. We determined annual dates for caterpillar biomass peaks and initial and latter thresholds using a threshold limit of 0.1 g/m^2 to reflect the emergence and decline of the caterpillars. Visser et al. (2006) used 1 g/m^2 as a threshold value, but in our data the caterpillar biomass was always <1 g/m^2 (Rytkönen & Krams, 2003). The peak date is the day in the middle of the measurement period when the biomass is at its highest. The threshold date is the middle day of a measurement period if the average biomass value of the period equals 0.10 g/m^2. In case the threshold limit is in between of the average biomasses of two consecutive periods, the threshold date is the first day of the latter measurement period.

Temporal trends and a method to find the best correlative temperature periods

We studied temporal trends in the laying date, the initial caterpillar threshold date and the caterpillar peak date with linear regressions against the year using SPSS 15.0 for Windows and two-tailed P-values.

We used a correlation analysis to investigate the association between annual breeding time, ambient temperature and food availability, following e.g. Orell & Ojanen (1983a) and Visser et al. (2006). We calculated average temperatures (from daily mean temperatures) for all time periods with lengths varying from 7 to 181 days, by altering the beginning and end dates of the periods in 1-day interval between December 26 (previous year) and June 24, and computed Pearson's correlation coefficients between all of these temperature periods and the median laying dates, caterpillar initial threshold dates and peak dates. The temperature periods with the strongest correlations were chosen. In case of the caterpillar initial threshold dates and peak dates, temperature data from 1996 to 2009 were used. For the median laying dates, the best correlating temperature period was searched separately using data from the whole study period 1975–2009 and 1996–2009, from which caterpillar biomass data is available. To inspect climatic warm-

ing, we computed linear regressions for the temperature periods found with year as an explanatory variable.

Synchrony of the food peak and timing of breeding

To study the synchrony of the food peak and timing of breeding, we calculated the differences between the annual median hatching dates and initial and latter caterpillar threshold dates and the caterpillar peak dates. The food requirements of the willow tit nestlings are the highest at 8–13 days after hatching (Rytkönen *et al.*, 1996), so the food peak should coincide with this time for breeding to be the most successful. The synchrony is interpreted in two ways. First, we consider the peak dates only – for the timing of breeding to be advantageous, the caterpillar peak date should cooccur with the period of the highest food demand. In another way of thinking, the caterpillar food should be abundant during this period, regardless of the peak date itself. Here we define 'abundant' to be over the threshold value of $0.1\,g/m^2$ of caterpillars. Based on our unpublished data, we are able to tell that Parids do use caterpillars as the main food source already at this level of caterpillar biomass.

Caterpillar availability and breeding success

For the years 1996–2009 from which we have caterpillar data, we defined nest-specific synchrony values as the difference between the day when the chicks are 10 days old (in the middle of the period of the highest food demand) and the caterpillar peak date (synchrony = hatching date + 10−caterpillar peak date). We used nestling survival rate (derived from numbers of fledged chicks and dead chicks per brood) and mean nestling weight per brood as measures of breeding success. We included nestlings that died between the biometrics and fledging in the analysis but excluded predated broods and nestlings destroyed by human interference or unknown reasons (nest desertions). The dataset consists of 1192 nests (623 females) for the nestling survival and 1160 nests (615 females) for the mean nestling weight.

The relationship between the nestling survival and synchrony with the caterpillar peak was studied with generalized linear mixed models (GLMMs) (Bolker *et al.*, 2009) fit by the Laplace approximation with binomial distribution and logit link function, using function glmer in package lme4 in program R. We used female identity as a block random factor to control temporal pseudoreplication. We tested all possible statistically and biologically relevant models with different combinations of following fixed factors: synchrony and synchrony^2, log(peak height) (log transformation of maximum value of caterpillar biomass recorded that year), female age and male age (both as factorial: yearling or older) and interaction terms synchrony × log(peak height), synchrony^2 × log(peak height), synchrony × female age, synchrony^2 × female age, synchrony × male age, synchrony^2 × male age, log(peak height) × female age and log(peak height) × male age. Model selection was based on AIC values. Synchrony, synchrony^2 and log(peak height) were centred to evade high correlations of fixed effects. Interaction terms in the best

models were construed graphically from three-dimensional scatter plots (not shown).

In the case of mean nestling weight, we built linear mixed effect models using function lmer (library lme4). We included female identity as a block random factor and tested all statistically and biologically relevant models with different combinations of fixed factors [the ones listed for the nestling survival rate and in addition brood size (number of hatched chicks), synchrony × brood size, synchrony^2 × brood size and log(peak height) × brood size] and selected the best models. When selecting models, we fitted them by maximum likelihood (ML) method as AIC values were used as selection criterion, and the final model was fitted again using restricted maximum likelihood method (REML) for ML gives biased parameter estimates (Faraway, 2006).

We demonstrated the magnitude of the synchrony effect by estimating nestling survival rate and mean nestling weight with the average synchrony of −9.3 days and the best possible synchrony (synchrony = 0). We estimated the values for yearling and older parents separately. The caterpillar peak height and the brood size were kept constant, as the average values.

Results

Temporal trends in timing of breeding and food abundance

In 1975–2009, the average yearly median onset of egg laying was on May 13 (SD = 3.88), in 1996–2009 2 days earlier (SD = 2.86). The initial caterpillar threshold date and the caterpillar peak date occurred on average at 32 and 40 days after the median egg laying date, respectively. In general, willow tits bred too early to match the period of the highest food demand with the caterpillar peak – for a perfect match the time gap between the first egg day and the caterpillar peak date should have been 32 days (8 days of egg laying + 14 days of incubation + 10 days = 32 days, Orell & Ojanen, 1983a, b).

The median egg laying date of willow tits advanced 0.16 days a year (SE = 0.060, $P = 0.012$) in 1975–2009 (Fig. 1). When considering the years 1996–2009, the trend was more pronounced although not significant ($b = −0.24$, SE = 0.185, $P = 0.217$) probably due to a small amount of years ($N = 14$). The initial caterpillar threshold dates had a non-significant advancing trend ($b = −1.20$, SE = 0.693, $P = 0.111$) and the caterpillar peak dates advanced by 1.02 days a year (SE = 0.470, $P = 0.050$) in 1996–2009. The regression coefficient of the median egg laying date does not differ significantly from the regression coefficient of the initial caterpillar threshold date ($t = −1.380$, SE = 0.695, $P = 0.181$) or from the one of the caterpillar peak date ($t = −1.552$, SE = 0.505, $P = 0.134$). An exceptionally cold spring in 1997 may result in an overestimation of caterpillar advancement rates on a longer time scale. When 1997 was excluded from the analysis, the slopes were less

pronounced both for the initial caterpillar threshold date and the peak date ($b = -0.66$, SE = 0.632, $P = 0.324$ and $b = -0.609$, SE = 0.414, $P = 0.169$, respectively).

Prebreeding temperatures related to timing of breeding and food abundance

The temperature period that correlated best with the median laying date of willow tits was March 27–May 6 when using data from the years 1975 to 2009, and for years 1996–2009 it was practically the same, March 25–May 5 (Table 1). For the initial caterpillar threshold date, the best correlative temperature period was March 22–May 27 and for the caterpillar peak date March 13–May 25 (Table 1). According to a linear regression model (Fig. 2) the median laying date advanced 1.77 days when the mean temperature of the period March 25–May 5 rose by 1 °C (SE = 0.264, $P < 0.001$, $r^2 = 0.788$). The initial caterpillar threshold date advanced 5.91 days (SE = 1.363, $P = 0.001$, $r^2 = 0.631$) and the caterpillar peak date 4.34 days (SE = 1.018, $P = 0.001$, $r^2 = 0.602$) per one centigrade increase in mean temperature. There were no significant

year factors for the median egg laying date, initial caterpillar threshold date or the caterpillar peak date. The regression coefficient for the median laying date differed from the regression coefficient for the initial caterpillar threshold date and for the caterpillar peak date ($t = -3.071$, SE = 1.350, $P = 0.005$ and $t = -2.446$, SE = 1.0519, $P = 0.022$, respectively). We suggest that willow tits and caterpillars respond with different rates to the warming of the spring period. If birds used the temperature of the spring period as a predictive cue for the timing of caterpillars as supposed by Visser et al. (2006) and acted accordingly, the regression slopes should be parallel. The mean temperatures of spring periods correlating best with the timing of breeding and the food abundance had rising nonsignificant trends (Table 1).

Synchrony between timing of breeding and food abundance

The timing of the caterpillar food peak in relation to median hatching dates fluctuated in 1996–2009 (Fig. 3). The caterpillar peak date coincided with the period of
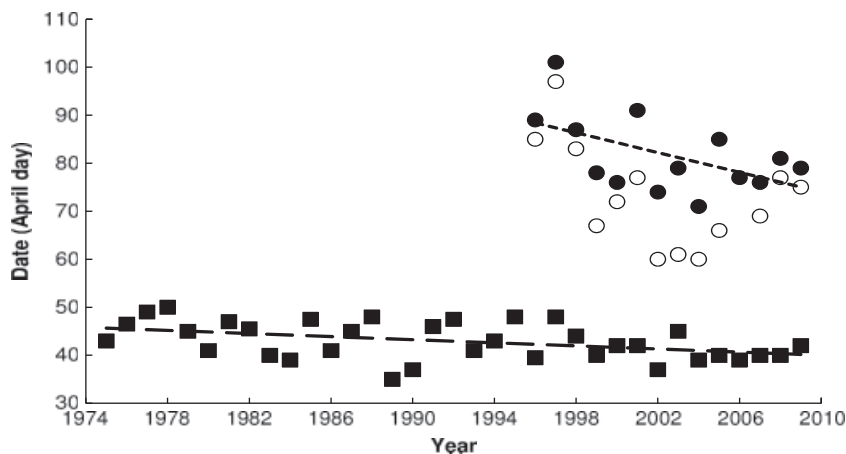
Fig. 1 Advancement of median egg laying date (closed square), caterpillar biomass threshold date (open circle) and caterpillar biomass peak date (closed circle) during the study period. The dashed line is the linear regression line for the laying date ($b = -0.160$, SE = 0.060, $P = 0.012$) and the dotted line for the caterpillar peak date ($b = -1.024$, SE = 0.470, $P = 0.050$). Advancement of the caterpillar biomass threshold date is not significant ($b = -1.199$, SE = 0.693, $P = 0.111$).

Table 1 (a) The best correlative temperature periods with timing of breeding and food abundance and (b) the rise ($b \pm$ SE) of the mean temperatures of these periods ($°C \, yr^{-1}$)

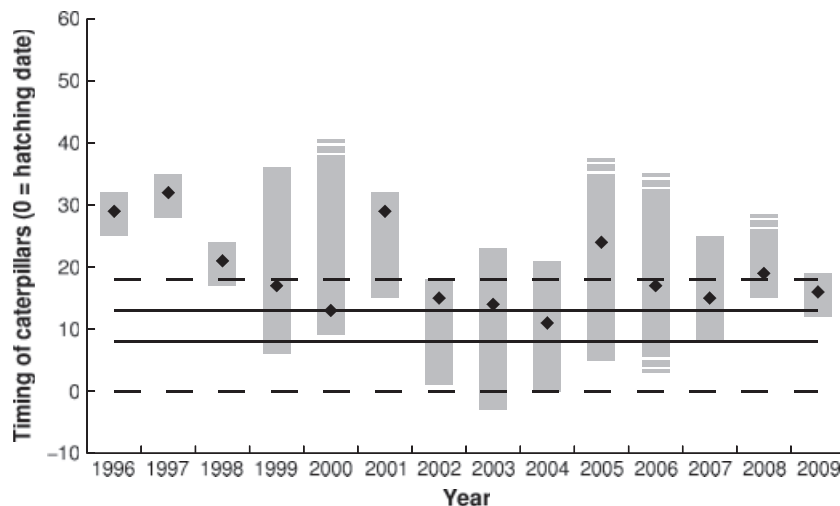| Variable | Years | (a) Best correlative period | | | (b) Rise of mean temperature | | |
		Temperature period	r	df	b	SE	P
Median laying date	1975–2009	27 March–6 May	−0.847***	34	0.042	0.023	0.074
	1996–2009	25 March–5 May	−0.888***	13	0.140	0.091	0.147
Initial caterpillar threshold date	1996–2009	22 March–27 May	−0.938***	12	0.141	0.071	0.068
Caterpillar peak date	1996–2009	13 March–25 May	−0.954***	13	0.145	0.073	0.070

***$P < 0.001$.

the highest food demand in 2 years (2000 and 2004, Fig. 3). Caterpillars were abundant (i.e. caterpillar biomass was over the threshold limit of $0.1 \, g/m^2$) during the period of the highest food demand in 7 years (1999, 2002, 2003, 2004, 2005, 2006 and 2007). By this contemplation, no signs of increasing asynchrony can be seen (Fig. 3). Actually, the timing of breeding has matched better with the food peak in the second half of the study period (2003–2009) than in the first half (1996–2002).

Caterpillar availability and breeding success

All models that best describe the nestling survival rate include: synchrony with the caterpillar food peak (both
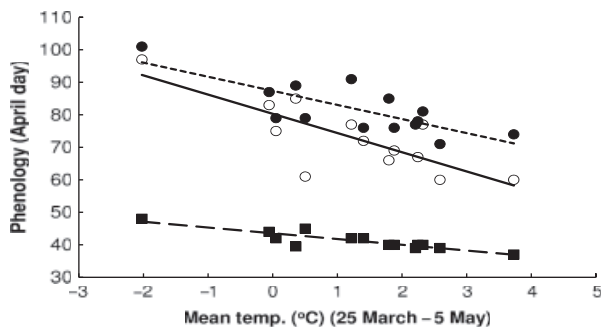
Fig. 2 Laying date (closed squares), caterpillar biomass threshold date (open circles) and caterpillar biomass peak dates (closed circles) against the mean temperature of March 25–May 5. The dashed line is the linear regression line for the laying date, the solid line for the caterpillar threshold date and the dotted line for the caterpillar peak date on temperature.

linear and quadratic terms), caterpillar peak height, female age and interactions synchrony^2 × log(peak height) and synchrony × female age (Appendix S2). Nests timed closer to the peak date had higher nestling survival. High caterpillar peaks resulted in better nestling survival, and the effect of synchrony was stronger when the caterpillar peaks were high. Nestling survival increased especially in the broods of yearling females when good synchrony, approaching the success of older females.

Mean nestling weight was affected by synchrony with the food peak (both linear and quadratic terms), caterpillar peak height, age of the parents and brood size. The interactions included were synchrony × brood size and synchrony^2 × peak height (Appendix S3). Mistimed broods, those with nestlings well before the caterpillar peak, had lighter nestlings than broods in synchrony with the caterpillars when the caterpillar peaks were high. Nestlings were lighter in large broods and the positive effect of synchrony was clearer as brood size increased. Old parents produced heavier nestlings than yearlings.

Several good models were found for both response variables, all of them include the synchrony term. The models without synchrony and synchrony^2 have clearly higher AIC values than the best models: the lowest ΔAIC is 22.11 and 26.49 for the nestling survival and the mean nestling weight, respectively (Appendices S2 and S3).

The ranges of estimated nestling survival rates and mean nestling weights from the best models (ΔAIC ≤ 2) are expressed in Table 2. At average synchrony yearling

Fig. 3 Timing of the caterpillar abundance in relation to the median hatching date of willow tits (0 = the hatching date) in 1996–2009. Grey bars present the period when the caterpillar biomass tops the threshold level of $0.1 \, g/m^2$. For some years, the threshold dates were not met during the frass-fall measurements – absent data is indicated with broken bars. The caterpillar biomass peak dates are indicated with dots. Average nestling period (from hatching to 18 days old) is marked with broken lines. The greatest demand for food takes place when the nestlings are approximately 8–13 days old (marked with solid lines).

Table 2 The ranges of estimated nestling survival rates (a) and estimated mean nestling weights (b) derived from the best models ($\Delta AIC \leq 2$)

	Average synchrony	Best possible synchrony
(a)		
Yearling parents	0.796–0.855	0.904–0.933
Older parents	0.881–0.895	0.910–0.928
(b)		
Yearling parents	10.36–10.50	10.47–10.61
Older parents	10.70–10.76	10.75–10.86

Estimates are calculated for yearling and older parents separately with the average synchrony of −9.3 days and the best possible synchrony of 0 days. Other variables (peak height, brood size) were kept constant as the average values.

parents had a lower nestling survival rate than older parents, but with optimal synchrony the age of the parents had no effect. Yearlings benefited more from synchrony. The effect of synchrony was modest as the nestling survival rates were high already with the average synchrony. For the mean nestling weight the effect of synchrony was marginal, less than half a gram of increase in weight. As we did not vary the peak height or brood size but kept them constant (as the average values), these estimates demonstrate only the effect of synchrony *per se*, not the expected situation in the wild where peak heights and brood sizes do vary.

Discussion

Spring warming has advanced the caterpillar abundance and the onset of willow tit egg laying in the Oulu area. Both are highly correlated with spring temperatures, conforming many previous studies (e.g. Dunn, 2004; Visser *et al.*, 2006), but they respond at different rates to spring warming. We found no signs of emerging asynchrony. Instead, synchrony has improved during the study, with moderate positive effects on breeding success. The advancement in the onset of laying in willow tits had about the same rate ($b = -0.160$ in 1975–2009) as Gienapp *et al.* (2006) detected in the great tit in the Netherlands ($b = -0.182$). The observed change in better synchrony mirrors results from the coal tit (*Periparus ater*) in the Netherlands (Both *et al.*, 2009).

At high latitudes food availability has generally peaked later than the offspring needs of local Parids, suggesting that other important ultimate factors are affecting the timing of breeding (Eeva *et al.*, 2000; Rytkönen & Orell, 2001). Early breeders may gain from more time for moulting and hoarding (Orell & Ojanen, 1980) and from prior residency of their offspring (Koi-

vula *et al.*, 1993). Net benefits of early 'mismatched' breeding seem to outweigh the ones of breeding later with the caterpillar peak. The issue of local adaptations in timing of breeding may therefore be different at high latitudes (e.g. the willow tit in the Oulu area) vs. in the temperate zone (e.g. the great tit in the Netherlands).

Willow tits are well capable of exploiting subsidiary food sources (Rytkönen *et al.*, 1996), which makes them less dependent on caterpillars compared with the great and blue tit (Rytkönen & Krams, 2003). This can be one reason for the small effect size of synchrony on the breeding success in the willow tit. Willow tits have adopted a clutch-size adjustment strategy (Orell & Ojanen, 1983b) independent of the synchrony with the caterpillars: nestling survival rates are high already with poor synchrony. The northern great tits suffer from higher nestling mortality (Orell & Ojanen, 1983b; Rytkönen & Orell, 2001 and references therein) and thus the effect size of synchrony can be larger (cf. Visser *et al.*, 2006).

If spring temperatures continue to increase, synchrony with the caterpillar peak is expected to improve (Fig. 2). Improved synchrony would have only modest effects on breeding success, at least if caterpillar peaks will remain as low as they were during the study period. Although, this study does not cover the possible effects of improving synchrony to the clutch size, which would contribute to the breeding success. Synchrony had larger impact on the nestling survival rate of broods attended by yearling females, perhaps due to increasing foraging ability with age (Desrochers, 1992 and references therein) or to the social hierarchy pattern in winter flocks (Koivula & Orell, 1988). If food is scarce, yearlings may not be able to allocate as much resources to breeding as old birds, but with a good synchrony they do as well.

The climate change may reduce the strength of factors that have previously determined early breeding in comparison with the food peak. As springs and autumns become warmer, the growing period becomes longer and snow fall will be delayed (Jylhä *et al.*, 2007; Ruosteenoja *et al.*, 2010). This gives more time for birds to moult and hoard and some of the costs of breeding late might be depressed (Eeva *et al.*, 2000). If timing of breeding is heritable and genetic variation exists, even small interindividual differences in life-time reproductive success may drive microevolutionary changes for timing of breeding to become more synchronous with the caterpillar peak with warming springs.

Visser *et al.* (2006) suggest that great tits' timing of breeding responses to spring temperatures because the temperature (or a correlating factor) is used as a cue for the timing of the food peak. This deduction is based on similar responses of phenologies in great tits and cater-

pillars to the warming of the spring period (Fig. 2 in Visser *et al.*, 2006). Our results show a contrasting pattern with different responses for the willow tits and caterpillars (Fig. 2). Willow tits do not use spring temperatures as a cue about the timing of the caterpillars or if they do, they do not act accordingly. Spring temperatures do have an impact on the timing of breeding, perhaps as a constraint (Perrins, 1965; Bryant, 1975; Stevenson & Bryant, 2000).

Some evidence for spatial variation in the timing of the caterpillars inside the study area exists, but unfortunately we were not able to consider that as for most of the years the caterpillar biomass has been measured from one site only. When modelling the breeding success, we used female identity as a block random factor to allow for temporal pseudoreplication. Some females are found only once in the data which leads to overparameterization and thus underdispersion (less variance than predicted by the model). Correcting for it would have led to severe anticonservatism. In the case of the nestling survival rate, the residual plot suggests dependency of individual observations, making the analysis somewhat inaccurate. The factors used in the models are doubtlessly not the only ones that contribute to it. However, we think that these sources of error do not severely undermine our results.

Proximate and ultimate factors affecting timing of breeding vary between populations and species (Ludwig *et al.*, 2006; Waite & Strickland, 2006; Lehikoinen *et al.*, 2011). These are important to understand to gain the general view of the effects of the climate change. Research is needed in different trophic levels in many climatic zones, habitats and species.

Acknowledgements

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Supporting Information

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

Appendix S1. The number of willow tit nests where the egg laying date (1st egg day), the hatching date (hatching day), and variables used in the breeding success analysis (the number of hatched chicks (#hatched), average chick weight (biometrics) and the number of fledgedchicks (#fledged) are known. Only the first clutches are included. In case of variables used in the analysis of the breeding success, nests were predation, human actions or nest desertion have caused nest failure are excluded. The number of nests is low for early years of the study period. We nevertheless consider our data adequate also for the early years, because the median egg-laying dates are practically equal to the ones from a more extensive data of Orell and Ojanen (1983a).

Appendix S2. Models to describe the nestling survival rate in willow tits. The table includes the best models with $\Delta AIC \leq 2$ (models 1–9), the best model without synchrony term (model 10) and the null model (model 11). Terms that are included in all the best models are bolded.

Appendix S3. Models to describe the mean chick weight in willow tits. The table includes the best models with $\Delta AIC \leq 2$ (models 1-20), the best model without synchrony term (model 21) and the null model (model 22). Terms that are included in all the best models are bolded.

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