GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

Does the temporal mismatch hypothesis match in boreal populations?

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Abstract The temporal mismatch hypothesis suggests that fitness is related to the degree of temporal synchrony between the energetic needs of the offspring and their food supply. The hypothesis has been a basis in studying the influence of climate warming on nature. This study enhances the knowledge on prevalence of temporal mismatches and their consequences in boreal populations, and questions the role of the temporal mismatch hypothesis as the principal explanation for the evolution of timing of breeding. To test this, we examined if synchrony with caterpillar prey or timing of breeding per se better explains reproductive output in North European parid populations. We compared responses of temperate-origin species, the great tit (*Parus major*) and the blue tit (*Cyanistes caeruleus*), and a boreal species, the willow tit (*Poecile montanus*). We found that phenologies of caterpillars and great tits, but not of blue tits, have advanced during the past decades. Phenologies correlated with spring temperatures that may function as cues about the timing of the food peak for great and blue tits. The breeding of great and blue tits and their caterpillar food remained synchronous. Synchrony explained breeding success better than timing of breeding alone. However, the synchrony effect arose only in certain conditions, such as with high caterpillar abundances or high breeding densities. Breeding before good synchrony seems

advantageous at high latitudes, especially in the willow tit. Thus, the temporal mismatch hypothesis appears insufficient in explaining the evolution of timing of breeding.

Introduction

The temporal mismatch hypothesis proposes that fitness depends on the degree of synchrony between the phenology of a species and its food. Thus, the recruitment rate will be highest when the most energy-consuming part of the breeding cycle coincides with the peak availability of the food (Durant et al. 2007). As a consequence of warming springs, phenologies of several species in both aquatic and terrestrial ecosystems have shifted earlier (e.g. Parmesan 2006; Durant et al. 2007; Thackeray et al. 2010), changing the time window of food availability for higher trophic levels. Some predator populations now experience temporal mismatches with their prey, but the phenomenon is not universal (e.g. Visser and Holleman 2001; Cresswell and McCleery 2003; Donnelly et al. 2011; Visser et al. 2012). Actually, in a few cases synchrony has improved (Costello et al. 2006; Both et al. 2009; Vatka et al. 2011). Changes in synchrony between interdependent species can have far-reaching consequences throughout ecosystems, altering community structures and increasing the risk of population extinctions and biodiversity loss (Costello et al. 2006; Thackeray et al. 2010; Donnelly et al. 2011).

Availability of good-quality food during the nestling period is an important determinant of breeding success in birds (Martin 1987; Naef-Daenzer and Keller 1999). Seasonal environments provide high-quality food only for a

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short period each year. The breeding season is considered to be adapted to coincide with this period (Lack 1950). For insectivorous birds, timing of the food peak depends on spring temperatures, being earlier in warm springs than in cold springs (e.g. Visser et al. 1998). In order to time their breeding correctly with the food abundance peak, birds may use cues including day length, supplemented by other cues such as ambient temperature, rainfall, or food availability (Dunn 2004; Visser et al. 2004; Dawson 2008; Lyon et al. 2008). Temperature may have both direct (Stevenson and Bryant 2000; Dunn 2004; Visser et al. 2009) and indirect effects, e.g. through the phenology of other organisms and food availability (Perrins 1965; Bryant 1975; Nilsson and Källander 2006; Bourgault et al. 2010; Thomas et al. 2010). Thus, many birds breed earlier in warmer springs (Dunn 2004). The relative importance of different cues can vary among species, populations, and even among individuals in the same population (Lyon et al. 2008; Silverin et al. 2008).

A temporal mismatch can occur if unequal warming of different periods of spring deteriorates the temperature cue about the timing of the food availability (e.g. Visser et al. 2003). A mismatch can also appear when some timing-related factors restrain individuals from breeding at the best synchrony with the food peak (Visser et al. 2012). For example, lack of food and high thermoregulatory costs in cold weather during egg-laying and incubation periods can prevent birds from breeding early (Perrins 1965; Bryant 1975; Stevenson and Bryant 2000; Dunn et al. 2011). Thus, birds may not be able to adjust their breeding schedule according to the prey phenology. If breeding in good synchrony does not compensate the fitness costs of breeding early, a mismatch (i.e. breeding late in relation to the timing of food peak) can be considered adaptive (Jonzén et al. 2007; Lof et al. 2012; Visser et al. 2012).

Although matching the breeding time with an early food peak might be unfavorable or even impossible, sometimes the opposite seems to be true. In northern Europe, for example, some bird populations generally breed before the peak of food abundance (Eeva et al. 2000; Rytkönen and Orell 2001; Vatka et al. 2011; see also van Balen 1973 for a parallel mismatch for great tits *Parus major*, Linnaeus in the Netherlands). Early breeders are usually the most productive with larger clutches and higher recruitment rate (e.g. Perrins 1965; Nager and van Noordwijk 1992; Reed et al. 2013). Short summers may act as time constraints because late breeders would have less time for moulting and preparation for winter, which could decrease survival (Eeva et al. 2000). It is necessary, although challenging, to tease apart the effects of synchrony with food availability and other timing-related causes to understand which factors drive the evolution of timing of breeding, an important life-history trait.

In northern Europe, rising spring temperatures have advanced the insect caterpillar peak, improving synchrony between nestling food demands and caterpillar availability in a boreal species, the willow tit (*Poecile montanus*, Conrad; Vatka et al. 2011). Nevertheless, the positive effect on breeding success is modest, because willow tits easily exploit secondary food resources. A similar change in synchrony might have larger fitness effects in temperate-origin species that are more reliant on caterpillars (Rytkönen and Krams 2003). The great tit and the blue tit (*Cyanistes caeruleus*, Linnaeus) have expanded their ranges to northern Fennoscandia during the last few decades (Väisänen et al. 1998; Kvist et al. 1999). Great tits lay too large clutches with consequently low nestling survival in the north (Rytkönen and Orell 2001). Thus, it seems to be better adapted to temperate, broad-leaved forests where caterpillar availability is substantially higher during the breeding season than in boreal forests (Rytkönen and Krams 2003). The changes in synchrony and their effect on the breeding success of great and blue tits have been intensively studied in the mid-latitudes (Visser et al. 1998; Naef-Daenzer and Keller 1999; Cresswell and McCleery 2003; Charmantier et al. 2008; Both et al. 2009; Bauer et al. 2010; Matthysen et al. 2011), but previous studies in boreal populations cover only relatively short time periods (Eeva et al. 2000: 6 years; Rytkönen and Orell 2001: 2 years).

We studied temporal changes in timing of breeding in relation to spring temperatures and caterpillar availability in boreal populations of two temperate-origin passerines, the great tit and the blue tit. We examined if spring temperatures can act as a cue for the timing of the food peak and if the premises of a mismatch hold. In the context of the mismatch hypothesis, we studied how the synchrony affects breeding success in boreal populations. We aimed to separate the effects of synchrony and timing of breeding per se and compared the effect of synchrony between temperate and origin species, and a boreal species, the willow tit.

Materials and methods

Data collection

The Oulu study area (65°N, 25°30′E) contains coniferous, deciduous and mixed forests of varying ages (Orell and Ojanen 1983a, c; Rytkönen and Orell 2001). The study area consisted of separate sub-areas of 2–4 km^2 total in 1969–1997, and since 1998, of four neighboring sub-areas in total of 8 km^2 (Online resource 1, Table S2; Orell and Ojanen 1983a, b, c; Rytkönen and Orell 2001; Karvonen et al. 2012). From 1969 onwards, 100–400 wooden nest boxes (with entrance hole diameter of 3.2–3.4 cm) were provided

for great tits, and since 1998, 75–100 nest boxes (entrance diameter 2.8 cm) for blue tits. Willow tit nests, excavated in rotten standing trees, were located each spring from an area of 25 km² (Orell and Ojanen 1983a; Lahti 1997).

Long-term breeding data on the great tit (1969–2011, excluding 1994), the blue tit (1998–2011), and the willow tit (1996–2011) were used. Nests were visited at least weekly from the end of April to July. Onset of egg-laying, clutch size, hatching date, number of hatched, and fledged young were determined (Orell and Ojanen 1983a, b, c). Only first nesting attempts per female in each season were used in the analysis (see Online resource 1, Tables S1 and S2 for sample sizes) since timing of re-nesting attempts are not opted by parents, and second clutches are infrequent in the study populations. Parents were identified by unique combinations of aluminum and plastic color rings. Non-marked parents were captured, marked, sexed, and aged as yearlings or older (Svensson 1992) when the nestlings were 9–16 days old. Nestlings were weighed to the nearest 0.1 g when ringed at the age of 13–15 days.

During the nestling period of ca. 18 days (Orell and Ojanen 1983b, c; del Hoyo et al. 2007), parents feed their young with invertebrates, mostly insect caterpillars (e.g. Perrins 1991; Rytkönen et al. 1996). Despite their relatively low abundance, caterpillars are the main food for nestling provisioning in Oulu populations (Rytkönen and Orell 2001). The food demand of the nestlings is estimated to be highest at the age of 8–13 days (van Balen 1973; Vatka et al. 2011). Caterpillar availability during breeding seasons was quantified with the frass-fall method (Zandt 1994) according to Rytkönen and Orell (2001) for 1996–2011. Biomasses of caterpillars foraging on birch (*Betula* spp.) were estimated in weekly periods. Annual caterpillar peak dates were determined as the middle day of a period when the biomass was at its highest, and dates of the emergence and the decline of caterpillars by using a threshold value of 0.1 g m^{-2} (Vatka et al. 2011).

Daily mean ambient temperatures were obtained from the Finnish Meteorological Institute, Oulunsalo observatory, 20 km S of the study area.

Temporal trends in the onset of egg-laying and the relationship with spring temperature

Temporal trends in the onset of breeding in the blue tit and timing of the caterpillar food were examined by regressing annual median first-egg dates and caterpillar peak dates against the year, as in Vatka et al. (2011) for the willow tit. For the great tit, sub-area-specific annual median first-egg dates were regressed against the year, including random intercepts for sub-areas in the model. This was done to allow for the possible artifact from the changing habitat composition of the study area. When dealing with time

series data, the assumption of independent residuals cannot be taken for granted. Temporal autocorrelation was tested with the function 'acf' in the package 'stats', program R (R Development Core Team 2011). The tests did not indicate any serious autocorrelations.

The relationships between phenologies and spring temperatures were studied as in Vatka et al. (2011). Average temperatures for all time periods of varying lengths (from 7 to 181 days at 1-day intervals) in January–June were calculated. Pearson's correlation coefficients between all of these temperature periods and annual median egg-laying dates in the great tit (sub-areas pooled) and the blue tit as well as caterpillar peak dates were computed. The periods with the strongest correlations were selected. Warming of these periods was inspected by regressing their mean temperatures against the year.

Synchrony of the caterpillar peak and timing of breeding, a population level examination

The changes in synchrony of the food peak and timing of breeding in great and blue tits were studied at population level. Synchrony was considered 'good' if the caterpillar peak date co-occurred with the period of the highest food demand for nestlings (8–13 days from hatching), defined according to annual median hatching dates. In addition, caterpillars were considered available during this period if the caterpillar biomass was over the threshold value of 0.1 g m^{-2}, regardless of the peak date itself (Vatka et al. 2011).

Effects of synchrony and timing on breeding success, an individual level examination

The effects of the synchrony with the caterpillars and timing of breeding on breeding success were analyzed in all three species using two response variables: mean nestling mass per brood and the number of fledged young, given that at least one young fledged. The number of fledged young was standardized ($y_i' = (y_i - \bar{y})/sd(y)$). Data from years 1996–2011 were used for great and willow tits, and 1998–2011 for blue tits (for which information of both breeding parameters and caterpillar food availability was available). Experimentally manipulated broods and nests of polygyny were excluded from the analysis. The numbers of observations for mean nestling mass and number of fledglings were 931 and 933 for the great tit, 310 and 301 for the blue tit, and 1,355 and 1,355 for the willow tit, respectively (Online resource 1, Table S1). A similar analysis was also carried out for a third response variable, the probability of producing at least one fledgling, but these results are not reported as even the 'best' models failed in predicting nesting failures accurately (major Type I error).

The analysis aimed at separating the effects of synchrony with the caterpillars and other timing-related factors, i.e. benefits or costs of breeding early vs. late. Thus, competing linear mixed-effect models (LMMs) with either synchrony or timing of breeding per se as explanatory variables were created. 'Synchrony' was defined for each nest as the difference between the day when the nestlings' food demands are the highest (at the age of 10 days) and the caterpillar peak date (see Online resource 1, Table S3 for elaborate variable definitions). Synchrony values of 0 indicate a perfect match and the more the value departs from zero, the greater the mismatch. 'Timing' was defined as the relative timing of hatching within the study population. Both linear and quadratic terms of 'synchrony' and 'timing' were tested. If a model contained a quadratic term, it must also include the linear term. 'Synchrony' and 'timing' were highly correlated ($r_s > 0.6$) in great and blue tits, and therefore, they were not allowed to enter the same model in any of the species for comparison's sake.

Breeding success is a complex phenomenon, thus, multiple factors must be considered to unmask the effects of interest. The analysis included the explanatory variables caterpillar peak height ('peak'), female age ('fage', that reflects female body condition), breeding density ('density', relating to the intensity of competition over resources) and brood size ('brood'). Terms 'synchrony', 'synchrony²', 'peak', and interactions 'synchrony × peak' and 'synchrony² × peak' together describe the availability of food for the nestlings. To find if effects of food availability or timing are inflected by other factors, selected interaction terms were included in the analysis (listed in Online resource 1, Table S3). Female identity was considered as a block random factor in all tested models, as many females bred in more than 1 year.

Continuous explanatory variables were centered to $\bar{x} = 0$ and scaled to SD = 0.5 to enable comparison of effect sizes of the factors (Grueber et al. 2011), as well as interpretation of the parameter estimates of the main effects when interaction terms are present (see Online resource 1, Table S4 for scaling factors). Sets of LMMs with all statistically relevant combinations of given explanatory variables were fitted to the data, using the function 'lmer' in package 'lme4' (Bates and Maechler 2010) in program R. The models were ranked with the Akaike information criterion (AIC). The models with ΔAIC ≤ 2 were considered as the best models and averaged with the function 'model.avg' in the package 'MuMIn' (Bartón 2011) by the so-called zero method (Burnham and Anderson 2002; Grueber et al. 2011). If both 'synchrony' and 'timing' models entered the best models, the averaging was done separately for them, resulting in two averaged models. Goodness-of-fit of the averaged models was defined as the squared Pearson
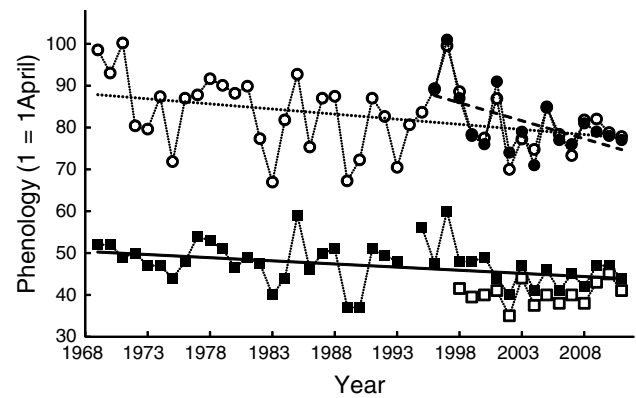

Fig. 1 Timing of the median onset of egg-laying of the great tit (*closed squares*) and the blue tit (*open squares*), and the caterpillar peak dates (*closed circles*) in the Oulu area. Temporal trends are significant for the caterpillar peak dates (*broken line*) and for the great tit (*solid line*), and non-significant for the blue tit. *Open circles* represent caterpillar peak dates estimated by the mean temperatures of 13 March–25 May, and the *dotted line* the corresponding temporal trend

correlation coefficient of the observed and predicted values ($r(y_i, \hat{y}_i)^2$).

Results

Temporal trends

The onset of great tits' egg-laying advanced 0.15 days per year during 1969–2011 (the sub-area-specific annual median first-egg dates, $b = -0.150$, SE = 0.033, $P < 0.001$; Fig. 1). A more pronounced shift earlier of 0.34 days per year was found for 1996–2011 ($b = -0.335$, SE = 0.113, $P = 0.005$). For the blue tit, no temporal trend in the onset of egg-laying was detected (1998–2011: $b = 0.153$, SE = 0.179, $P = 0.410$). Caterpillar peak date had an advancing trend, 0.86 days per year ($b = -0.860$, SE = 0.361, $P = 0.032$). However, when caterpillar peak dates were estimated for 1969–2011 by using the mean temperatures of the best correlative temperature period (see below), the trend was more gradual ($b = -0.243$, SE = 0.096, $P = 0.015$, Fig. 1). The observed trend of caterpillars did not differ significantly from the trend of the great tit ($t = 1.692$, $P = 0.095$) in 1996–2011.

The relationship between timing of breeding and spring temperatures

Timing of the caterpillar peak correlated best with the mean temperature of the period 13 March–25 May ($r = -0.955$). For the annual median onset of egg-laying in the great tit (with pooled data from all sub-areas), the corresponding
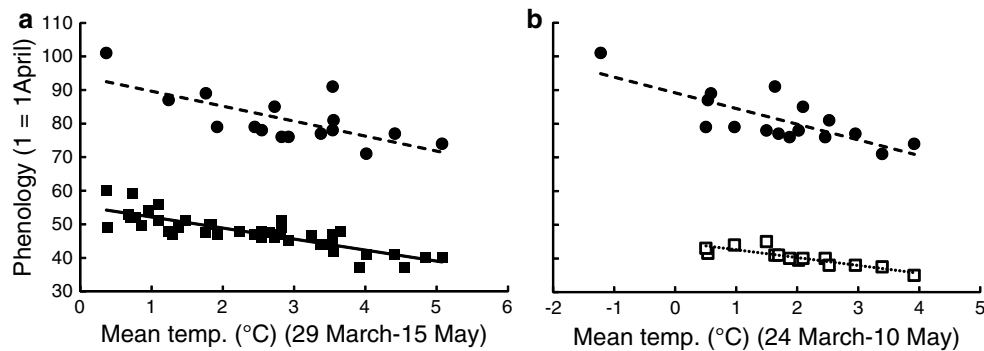
Fig. 2 The responses of the caterpillar peak dates (*closed circles*), the annual median laying dates of the great tit (*closed squares*), and the blue tit (*open squares*) to spring temperatures. **a** Great tits' laying date advances if the mean temperature of 29 March–15 May increases ($b = -3.40$, SE $= 0.51$, $P < 0.001$), as does the caterpillar

peak date ($b = -4.46$, SE $= 1.21$, $P = 0.003$). **b** Blue tits advance their breeding with the rise in the mean temperature of 24 March–10 May ($b = -2.32$, SE $= 0.39$, $P < 0.001$), in parallel with the caterpillar peak dates ($b = -2.86$, SE $= 1.29$, $P = 0.047$)
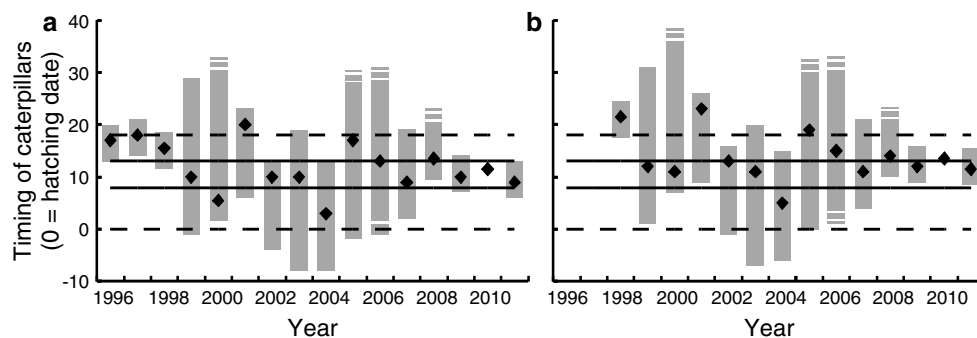

Fig. 3 Caterpillar availability in relation to the annual median timing of breeding in **a** the great tit and **b** the blue tit. *Grey bars* present the period when the caterpillar biomass exceeds the threshold level of 0.1 g m^{-2}. For some years, the threshold dates were not met during the frass-fall measurements—absent data is indicated with *broken*

bars. In 2010 the caterpillar peak was very low and did not exceed the threshold value at all. *Dots* indicate the caterpillar biomass peak dates. *Broken lines* mark the average nestling period (from hatching to 18 days old). The greatest demand for food takes place when the nestlings are approximately 8–13 days old (marked with *solid lines*)

period was 29 March–15 May ($r = -0.849$), and for the blue tit 24 March–10 May ($r = -0.866$). Phenologies were advanced by warm springs (Fig. 2). The caterpillars and great tits responded similarly to the mean temperature of 29 March–15 May (Fig. 2a, $t = 0.801$, $P = 0.430$), as did the caterpillars and blue tits to the mean temperature of 24 March–10 May (Fig. 2b, $t = -0.400$, $P = 0.692$). A year term did not improve the goodness-of-fit of the models on the basis of AIC values.

The mean temperatures of the defined spring periods did not rise during the comparison period of 1981–2010 (the caterpillar peak's impact period: $b = 0.009$, SE $= 0.026$, $P = 0.721$; great tit's period: $b = 0.030$, SE $= 0.027$, $P = 0.285$; blue tit's period: $b = 0.019$, SE $= 0.027$, $P = 0.496$), nor did they have differing warming rates when compared (for all pair-wise comparisons, $P > 0.500$). However, when considering the study spans (these cannot be compared between species as they

differ in length), the mean temperature of the caterpillar peak's impact period rose nearly significantly 0.12 °C per year ($P = 0.053$) during 1996–2011, and the great tit's period showed a temperature increase of 0.05 °C per year ($P = 0.004$) during 1969–2011. For the blue tit's impact period, no change was detected in 1998–2011 ($b = 0.001$, $P = 0.988$). These results agree with the observed temporal trends (Fig. 1).

Changes in synchrony

In the population level examination (Fig. 3), the peak date coincided with the period of the highest food demand in 8 out of 16 years for the great tit and 7 out of 14 for the blue tit. Caterpillars were available during the whole period of the highest food demand in 11 years for the great tit and 9 years for the blue tit. The synchrony has been rather good for both the species throughout the study, except the years

1996–1998 when caterpillars peaked later than the nutritional needs of parids. With these inspections, temporal match between caterpillars and the parids has remained unchanged.

Synchrony, timing of breeding, and breeding success

'Synchrony' models outcompeted 'timing' models in explaining breeding success in all three species, expect for the mean nestling mass in the blue tit where the top model set comprised both 'synchrony' and 'timing' models (Online resource 1, Tables S5 and S6).

Mean nestling mass

According to the averaged model, good synchrony improved nestling quality measured as mean nestling mass in the great tit only in years with high caterpillar abundances (Fig. 4a). This is indicated by the parameter estimate for 'synchrony^2' to be non-significant, and a significant negative value for 'synchrony^2 × peak' (see Table 1 for significant averaged parameter estimates and Online resource 1, Table S7 for full averaged model structures). Nestlings grew heavier if the caterpillar peak date coincided some days later than the expected timing of the highest food demand (Fig. 4a),
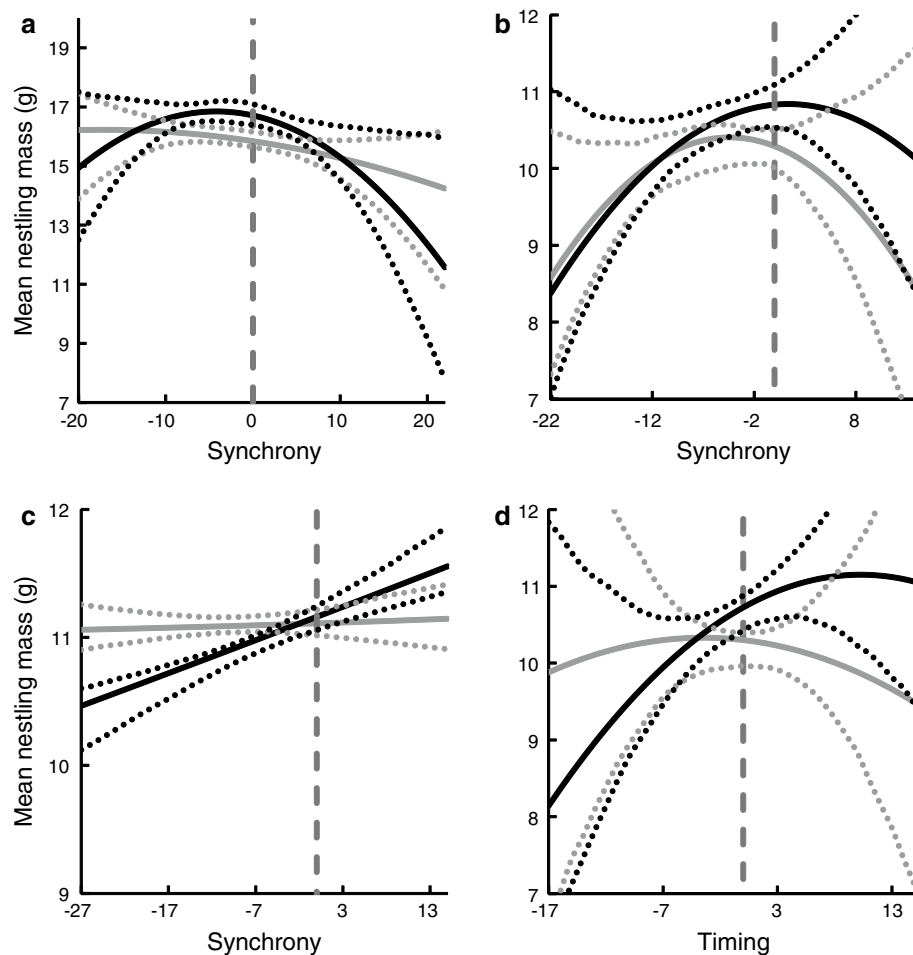

Fig. 4 The effects of synchrony with the caterpillar peak and timing of breeding on breeding success in Oulu populations. The effect of synchrony on the mean nestling mass in (**a**) the great tit with average (highest caterpillar biomass 0.3 g m^{-2}, *grey line*) and high caterpillar peaks (0.6 g m^{-2}, *black line*), (**b**) the blue tit for young (*grey line*) and older females (*black line*), and (**c**) the willow tit in low (4.1 pairs km^{-2}, *grey line*) and high breeding densities (5.4 pairs km^{-2}, *black line*). (**d**) The effect of timing of breeding in the blue tit for young (*grey line*) and older females (*black line*). The 95 % confidence limits (*broken lines*) are derived by non-parametric bootstrapping 1,000 times. Synchrony is defined as the difference in timing between the highest food demand of the nestlings (at the age of 10 days) and the caterpillar peak, thus the value 0 (marked with vertical *broken lines*) indicates perfect synchrony, negative synchrony values mean breeding early, and positive values breeding late in relation to the caterpillar peak. Negative 'timing' values denote hatching before and positive values breeding later than the population average. Point estimates of the averaged models were defined for females older than 1 year (if not mentioned otherwise) and other variables in the models were fixed to their average values

Table 1 Model averaged parameter estimates whose 95 % confidence intervals do not contain zero for variables explaining the mean nestling mass and the number of fledged young in the great tit (*Parus major*), the blue tit (*Cyanistes caeruleus*), and the willow tit (*Poecile montanus*) in the Oulu area

Variable	Mean nestling mass				Number of fledged young		
	Great tit	Blue tit		Willow tit	Great tit	Blue tit	Willow tit
		(a)	(b)				
(Intercept)	15.500 (0.10)	10.400 (0.11)	10.300 (0.10)	10.700 (0.04)			
Synchrony	−0.479 (0.13)				0.162 (0.05)		0.253 (0.06)
Synchrony^2		−0.682 (0.25)			−0.333 (0.11)	−0.332 (0.13)	−0.190 (0.08)
Peak	1.420 (0.17)	0.780 (0.17)	0.813 (0.16)	0.123 (0.05)	0.476 (0.08)	0.387 (0.12)	0.170 (0.05)
Female age (older)	0.408 (0.14)	0.333 (0.15)	0.429 (0.14)	0.320 (0.04)	0.177 (0.07)	0.290 (0.10)	
Female age (unknown)	0.534 (0.24)	−1.840 (0.50)	−1.210 (0.56)				−0.360 (0.17)
Density	−0.418 (0.14)			−0.276 (0.06)			−0.163 (0.05)
Brood size	−1.120 (0.13)	−0.592 (0.15)	−0.766 (0.13)	−0.111 (0.04)	0.924 (0.07)	0.972 (0.12)	1.480 (0.04)
Synchrony^2 × peak	−1.420 (0.43)				−0.638 (0.20)		−0.462 (0.19)
Synchrony × fage (older)		0.585 (0.27)					−0.245 (0.08)
Synchrony^2 × fage (unknown)		2.580 (1.03)					
Synchrony × density				0.533 (0.14)			0.343 (0.12)
Synchrony^2 × density					−0.517 (0.22)		
Synchrony × brood				0.269 (0.08)			
Timing × fage (older)			0.775 (0.27)				
Peak × density	−1.040 (0.31)						
Peak × brood	−0.573 (0.26)	0.755 (0.23)	0.761 (0.23)				
$r(y_i, \hat{y}_i)^2$	0.176	0.290	0.286	0.066	0.297	0.323	0.568

Standard errors are given in parentheses. For the mean nestling mass in the blue tit, two averaged models with a) 'synchrony' and b) 'timing' were created. Model averaging was done with the zero method, using models with ΔAIC < 2. Input variables were scaled to $\bar{x} = 0$ and SD = 0.5. $r(y_i, \hat{y}_i)^2$ is the squared Pearsson correlation coefficient of the observed values (y_i) and the predicted values ($\hat{y}_i$), expressing goodness of fit of the model

indicated by a significant negative parameter estimate of 'synchrony'. Technically, this parameter denotes that the fitness curve peaks before the population average value of synchrony (as the variables were scaled), but as the average is negative, the interpretation in relation to un-scaled synchrony values holds. In the blue tit, mean nestling mass can be explained with either synchrony or timing of breeding per se (Fig. 4b, d). Both models show a similar pattern: older females seemed to benefit from breeding later (in respect to timing of the caterpillars or timing of the population average) than the yearlings. Thus, the effects of synchrony and timing cannot be separated unequivocally. However, well-synchronous breeders seem to have heavier nestlings than both very early and very late breeders (Fig. 4b). Also, willow tits in better synchrony (synchrony values closer to 0) had heavier nestlings than birds breeding before the caterpillar peak (significant positive parameter estimate of 'synchrony', Table 1). The effect was more pronounced in high breeding densities (Fig. 4c) and in large clutches (Table 1). The lack of support for the quadratic synchrony term is likely due to low number of observations with positive synchrony values (only 69 out of 1,355).

In all three species, nestlings grew heavier in years of high caterpillar peaks (positive parameter estimates for 'peak', Table 1). Older females raised on average heavier nestlings than yearlings, and nestlings in large broods were lighter than in small ones. In the great tit, the effect of brood size was stronger, whereas in the blue tit it diminished with high caterpillar peaks. Nestlings were lighter in high breeding densities in the great and the willow tit, but not in the blue tit. In the great tit, the effect of density was stronger when caterpillar peaks were high.

Number of fledged young

For all three species, the number of fledged young was on average higher in broods with good synchrony with the caterpillars than in the ones that were timed before or after the caterpillar peak (Fig. 5). Parameter estimates of 'synchrony$^{2\prime}$' are significant and negative for all the species (Table 1). For the great and the willow tit, the effect of synchrony was more intense with high caterpillar peaks ('synchrony^2 × peak', Fig. 5a, c). In addition, for the willow tit, the highest number of fledged young seemed to be

Fig. 5 The effect of synchrony on the number of fledged young in **a** the great tit, **b** the blue tit, and **c** the willow tit with average (highest caterpillar biomass 0.3 g m^{-2}, *grey lines*) and high caterpillar peaks (0.6 g m^{-2}, *black lines*). The 95 % confidence limits (*broken lines*) are derived by non-parametric bootstrapping 1,000 times. Point estimates of the averaged models were defined for females older than 1 year and other variables in the models were fixed to their average values
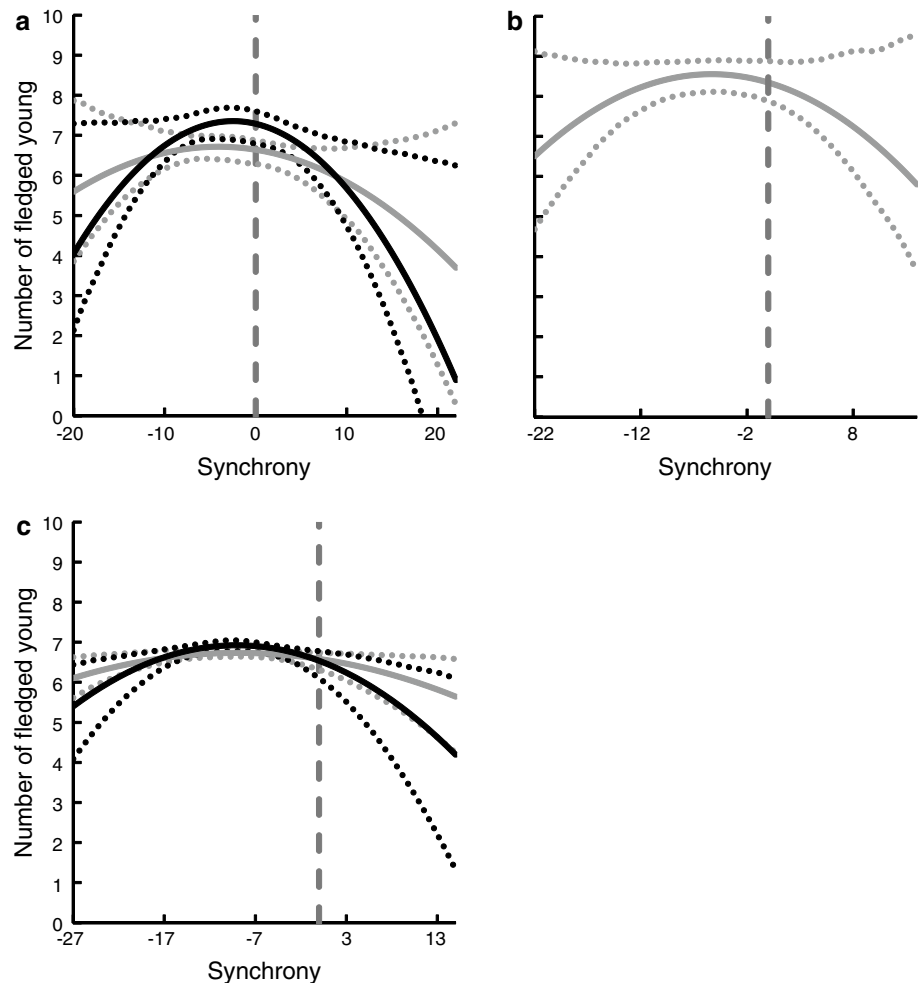
attained in different phases of synchrony in different breeding densities ('synchrony × density' has a significant positive parameter estimate, Table 1) and age groups: young females performed better when breeding a little later than older females in relation to the timing of the caterpillar peak ['synchrony × fage (older)' has a negative parameter estimate]. The number of fledglings was typically higher in years of high caterpillar peaks and in large broods in all studied species. Older females usually produced more fledglings than young females in the great and the blue tit. A negative effect of breeding density could be found only in the willow tit.

Discussion

<mark>The timing of breeding in the boreal great tit population has advanced during the last few decades, maintaining the synchrony with the food supply (caterpillars).</mark> The onset of breeding in the blue tit did not show any temporal trend, yet the synchrony with the caterpillar peak has remained close. Phenologies were highly correlated with spring

temperatures, thus temperature could provide a cue for when to start breeding in parids. The spring periods correlating with the two trophic levels did not have differing warming rates. Synchrony with the caterpillars affected reproductive output in the great, blue, and willow tit, and it seemed to explain breeding success better than timing of breeding per se. However, different levels of caterpillar abundance, female age, or breeding density resulted in differing responses to the degree of synchrony.

According to the temporal mismatch hypothesis, recruitment rate is expected to be at highest when the most energy-consuming breeding phase matches with the time of highest food abundance (Durant et al. 2007). Thus, an adaptive respond of timing the breeding to match with the food peak is expected. Yet, the adaptation may be disrupted by fast environmental changes, such as the anthropogenic climate warming. The studied boreal great and blue tit populations seem to breed in a rather good synchrony with their caterpillar prey. Our results show that climate warming has not caused temporal mismatches with the caterpillar peak in boreal parid populations so far (see also Vatka et al. 2011). Most other studies in parids have not found

increases in temporal mismatch, either (reviewed by Visser et al. 2012). Mismatch was found only in a Dutch great tit population (Visser et al. 1998, 2006). Temporal mismatches can be more common and vigorous in long-distance migrants (Visser et al. 2012 and references herein).

Visser et al. (2006, 2009) suggest that birds use spring temperatures as cues for the timing of the food peak. The idea is supported by similarity of phenological responses to spring temperatures between great tits and caterpillars and by birds responding to temperatures even when food availability does not constrain the onset of breeding. We found similar responses to spring temperature between the phenologies of great and blue tits and caterpillars. Thus, temperature could provide a cue for when to start breeding in parids. However, the willow tit does not seem to use spring temperatures as a cue about timing of the caterpillar peak, or at least does not act accordingly (Vatka et al. 2011). For the great and the blue tit in the Oulu area, the temperature cue has not deteriorated by unequally warming spring periods, which would be a prerequisite for a climate change-driven mismatch (e.g. Visser et al. 2003).

Our results show that the synchrony with the caterpillar peak affected the quality and number of offspring produced in all three species. The effect is somewhat stronger in the temperate-origin great tit and blue tit than in the willow tit. However, synchrony or timing of breeding does not explain nesting failures (results not shown). Negative fitness effects of mismatched breeding have also been found in several previous studies, but not in all (e.g. Naef-Daenzer and Keller 1999; Thomas et al. 2001; Visser et al. 2012 and references herein). Visser et al. (2006) detected an effect of synchrony on the quality and number of fledglings in the great tit (Fig. 3 in their paper) that is approximately of the same magnitude as we found for high caterpillar peaks (Figs. 4a, 5a).

The effect of synchrony, however, arose only in certain conditions. According to our results, the mean nestling mass in the willow tit was higher when there was good synchrony with the caterpillar peak and breeding density was high (Fig. 4c, possibly referring to intensified competition over food) or the brood was large, entailing high nutritional needs of a brood (Table 1). Good synchrony raised the mean nestling mass in the great tit and the number of fledglings in the great and the willow tits only when the caterpillar peak was relatively high (Figs. 4a, 5a, f, see also Durant et al. 2005). Caterpillar availability is substantially lower in boreal forests than in temperate, broad-leaved forests (Rytkönen and Krams 2003). Indeed, in our study area, most of the years could be considered 'mismatched' due to low caterpillar abundances (Durant et al. 2007). The temporal mismatch hypothesis cannot be applied in environments with constant (Dunn et al. 2011) or low food availability. Thus, in boreal populations, synchrony with the caterpillars

may have substantial impact on the evolution of timing of breeding only in certain conditions, such as in years with infrequently high caterpillar abundances. Climate change is expected to lengthen the growing season (e.g. Ruosteenoja et al. 2011), which may lead to increases in biomass of insect caterpillars through changes in their life-history strategies (Kivelä et al. 2013). If so, synchrony may have a bigger role in determining timing of breeding in the future.

So-called adaptive phenological mismatch occurs when fitness does not peak at the best temporal match with food availability (Lof et al. 2012; Visser et al. 2012). Our analysis on breeding success gives some indications of possible adaptive mismatch (Figs. 4, 5). Thus, breeding success seems to be affected by some timing-related factor(s) (perhaps with varying effect sizes in different aged females or breeding densities) that we did not consider. Interspecific competition over food might be one candidate, as its intensity can change during the breeding season. Alternatively, if the tendency to breed early is inherited, the observed phenomenon might be caused by early fledged birds themselves breeding early and having high breeding success thanks to their prior residency status. Then again, an image of adaptive mismatch could be erroneous, caused by incorrect determination of the timing of the highest food demand, and thus synchrony. We expected the nestlings' highest food demand to occur at the age of 9–10 days (e.g. Visser et al. 2006; Reed et al. 2013). However, differing definitions exist: for example, Lof et al. (2012) suggest that 'good match' occurs when young fledge at the food peak.

Conclusions

The temporal mismatch hypothesis proposes that a good synchrony with a food peak results in high breeding success. Thus, in seasonal environments, the timing of breeding should be adapted to coincide with the peak of food availability, but this adaptation may be disrupted by climate warming. The studied boreal populations of the great and the blue tits breed in rather good synchrony with their main prey, foliage-dwelling insect caterpillars, and our results do not suggest climate warming-driven temporal mismatches. Ambient spring temperatures may function as a cue for birds to match their breeding schedule with the food peak. However, the positive effect of good synchrony on breeding success seems conditional, emerging only in certain conditions, such as in years of high caterpillar abundances. Thus, synchrony can only occasionally influence the evolution of timing of breeding. So, in the boreal zone, the temporal mismatch hypothesis alone is not a comprehensive explanation for the determination of the timing of breeding, an important life-history trait. Other timing-related factors (such as energetic constraints, inter-specific competition, or

prior residency) likely play a larger role, yet the power relationships of the factors may change with climate change.

References

Bartón K (2011) Multi-model inference R package version 1.0.0 http://cran.r-project.org/web/packages/MuMIn/index.html

Bates D, Maechler M (2010) lme4: Linear mixed-effects models using S4 classes R package version 0.999375-37 http://cran.r-project.org/web/packages/lme4/index.html

Bauer Z, Trnka M, Bauerová J, Možný M, Štěpánek P, Bartošova L, Žalud Z (2010) Changing climate and the phenological response of great tit and collared flycatcher populations in floodplain forest ecosystems in Central Europe. Int J Biom 54:99–111

Both C, van Asch M, Bijlsma RG, van den Burg AB, Visser ME (2009) Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? J Anim Ecol 78:73–83

Bourgault P, Thomas D, Perret P, Blondel J (2010) Spring vegetation phenology is a robust predictor of breeding date across broad landscapes: a multi-site approach using the Corsican blue tit (*Cyanistes caeruleus*). Oecologia 162:885–892

Bryant DM (1975) Breeding biology of house martins *Delichon urbica* in relation to aerial insect abundance. Ibis 117:180–216

Burnham KP, Anderson DR (2002) Model selection and multimodel inference. A practical information-theoretic approach, 2nd edn. Springer, New York

Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LEB, Sheldon BC (2008) Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320:800–803

Costello JH, Sullivan BK, Gifford DJ (2006) A physical–biological interaction underlying variable phenological responses to climate change by coastal zooplankton. J Plank Res 28:1099–1105

Cresswell W, McCleery R (2003) How great tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. J Anim Ecol 72:356–366

Dawson A (2008) Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. Phil Trans R Soc B 363:1621–1633

del Hoyo J, Elliott A, Christie D (2007) Handbook of the birds of the world, vol 12. Picathartes to tits and chickadees, Lynx Edicions

Donnelly A, Caffarra A, O'Neill BF (2011) A review of climate-driven mismatches between interdependent phenophases in terrestrial and aquatic ecosystems. Int J Biom 55:805–817

Dunn P (2004) Breeding dates and reproductive performance. Adv Ecol Res 35:69–87

Dunn PO, Winkler DW, Whittingham LA, Hannon SJ, Robertson RJ (2011) A test of the mismatch hypothesis: how is timing of reproduction related to food abundance in an aerial insectivore? Ecology 92:450–461

Durant JM, Hjerman DØ, Anker-Nilssen T, Beaugrand G, Mysterud A, Pettorelli N, Stenseth NC (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. Ecol Lett 8:952–958

Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33:271–283

Eeva T, Veistola S, Lehikoinen E (2000) Timing of breeding in subarctic passerines in relation to food availability. Can J Zool 78:67–78

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. J Evol Biol 24:699–711

Jonzén N, Hedenström A, Lundberg P (2007) Climate change and the optimal arrival of migratory birds. Proc R Soc Lond B 274:269–274

Karvonen J, Orell M, Rytkönen S, Broggi J, Belda E (2012) Population dynamics of an expanding passerine at the distribution margin. J Avian Biol 43:102–108

Kivelä SM, Välimäki P, Gotthard K (2013) Seasonality maintains alternative life-history phenotypes. Evolution 67:3145–3160

Kvist L, Ruokonen M, Lumme J, Orell M (1999) Different population structures in northern and southern populations of the European blue tit (*Parus caeruleus*). J Evol Biol 12:798–805

Lack D (1950) The breeding seasons of European birds. Ibis 92:288–316

Lahti K (1997) Social status and survival strategies in the Willow Tit *Parus montanus* PhD thesis, Department of Biology, University of Oulu, Oulu, Finland

Lof ME, Reed TE, McNamara JM, Visser ME (2012) Timing in a fluctuating environment: environmental variability and asymmetric fitness curves can lead to adaptively mismatched avian reproduction. Proc R Soc Lond B 279:3161–3169

Lyon BE, Chaine AS, Winkler DW (2008) A matter of timing Sci 321:1051–1052

Martin TE (1987) Food as a limit on breeding birds: a life-history perspective. Annu Rev Ecol Syst 18:453–487

Matthysen E, Adriaensen F, Dhondt AA (2011) Multiple responses to increasing spring temperatures in the breeding cycle of blue and great tits (*Cyanistes caeruleus*, *Parus major*). Glob Change Biol 17:1–16

Naef-Daenzer B, Keller LF (1999) The foraging performance of great and blue tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. J Anim Ecol 68:708–718

Nager RG, van Noordwijk AJ (1992) Energetic limitation in the egg-laying period of great tits. Proc R Soc Lond B 249:259–263

Nilsson J-Å, Källander H (2006) Leafing phenology and timing of egg laying in great tits *Parus major* and blue tits *P. caeruleus*. J Avian Biol 37:357–363

Orell M, Ojanen M (1983a) Effect of habitat, date of laying and density on clutch size of the Great Tit *Parus major* in northern Finland. Holarctic Ecol 6:413–423

Orell M, Ojanen M (1983b) Breeding biology and population dynamics of the willow tit *Parus montanus*. Ann Zool Fenn 20:99–114

Orell M, Ojanen M (1983c) Timing and length of the breeding season of the great tit *Parus major* and the willow tit *P. montanus* near Oulu. North Finl Ardea 71:183–198

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637–669

Perrins CM (1965) Population fluctuations and clutch-size in the Great Tit, *Parus major* L. J Anim Ecol 34:601–647

Perrins CM (1991) Tits and their caterpillar food supply. Ibis 133(suppl. 1):49–54

R Development Core Team (2011) R: A language and environment for statistical computing R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Reed TE, Jenouvrier S, Visser ME (2013) Phenological mismatch strongly affects individual fitness but not population demography in a woodland passerine. J Anim Ecol 82:131–144

Ruosteenoja K, Räisänen J, Pirinen P (2011) Projected changes in thermal seasons and the growing season in Finland. Int J Clim 31:1473–1487

Rytkönen S, Krams I (2003) Does foraging behaviour explain the poor breeding success of great tits *Parus major* in northern Europe? J Avian Biol 34:288–297

Rytkönen S, Orell M (2001) Great tits, *Parus major*, lay too many eggs: experimental evidence in mid-boreal habitats. Oikos 93:439–450

Rytkönen S, Koivula K, Orell M (1996) Patterns of per-brood and per-offspring provisioning efforts in the Willow Tit *Parus montanus*. J Avian Biol 27:21–30

Silverin B, Wingfield J, Stokkan K-A, Massa R, Järvinen A, Andersson N-Å, Lambrechts M, Sorace A, Blomqvist D (2008) Ambient temperature effects on photo induced gonadal cycles and hormonal secretion patterns in Great Tits from three different breeding latitudes. Horm Behav 54:60–68

Stevenson IR, Bryant DM (2000) Climate change and constraints on breeding. Nature 406:366–367

Svensson L (1992) Identification guide to european passerines, 4th edn. British Trust for Ornithology

Thackeray SJ, Sparks TH, Frederiksen M, Burthe S, Bacon PJ, Bell JR, Botham MS, Brereton TM, Bright PW, Carvalho L, Clutton-Brock T, Dawson A, Edwards M, Elliott JM, Harrington R, Johns D, Jones ID, Jones JT, Leech DI, Roy DB, Scott WA, Smith M, Smithers RJ, Winfield IJ, Wanless S (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. Glob Change Biol 16:3304–3313

Thomas DW, Blondel J, Perret P, Lambrechts MM, Speakman JR (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. Science 291:2598–2600

Thomas DW, Bourgault P, Shipley B, Perret P, Blondel J (2010) Context-dependent changes in the weighting of environmental cues that initiate breeding in a temperate passerine, the Corsican blue tit (*Cyanistes caeruleus*). Auk 127:129–139

Väisänen RA, Lammi E, Koskimies P (1998) Distribution, numbers and population changes of Finnish breeding birds. Otava, Helsinki

van Balen JH (1973) A comparative study of the breeding ecology of the great tit *Parus major* in different habitats. Ardea 61:1–93

Vatka E, Orell M, Rytkönen S (2011) Warming climate advances breeding and improves synchrony of food demand and food availability in a boreal passerine. Glob Change Biol 17:3002–3009

Visser ME, Holleman LJM (2001) Warmer springs disrupt the synchrony of oak and winter moth phenology. Proc R Soc Lond B 268:289–294

Visser ME, van Noordwijk AJ, Tinbergen JM, Lessells CM (1998) Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proc R Soc Lond B 265:1867–1870

Visser ME, Adriaensen F, van Balen JH, Blondel J, Dhondt AA, van Dongen S, du Feu C, Ivankina EV, Kerimov AB, de Laet J, Matthysen E, McCleery R, Orell M, Thomson DL (2003) Variable responses to large-scale climate change in European *Parus* populations. Proc R Soc Lond B 270:367–372

Visser ME, Both C, Lambrechts MM (2004) Global climate change leads to mistimed avian reproduction. Adv Ecol Res 35:89–110

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

Visser ME, Holleman LJM, Caro SP (2009) Temperature has a causal effect on avian timing of reproduction. Proc R Soc Lond B 276:2323–2331

Visser ME, te Marvelde L, Lof ME (2012) Adaptive phenological mismatches of birds and their food in a warming world. J Ornithol 153:S75–S84

Zandt HS (1994) A comparison of three sampling techniques to estimate the population size of caterpillars in trees. Oecologia 97:399–406