

Climate change, breeding date and nestling diet: how temperature differentially affects seasonal changes in pied flycatcher diet depending on habitat variation

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Summary

1. Climate warming has led to shifts in the seasonal timing of species. These shifts can differ across trophic levels, and as a result, predator phenology can get out of synchrony with prey phenology. This can have major consequences for predators such as population declines owing to low reproductive success. However, such trophic interactions are likely to differ between habitats, resulting in differential susceptibility of populations to increases in spring temperatures. A mismatch between breeding phenology and food abundance might be mitigated by dietary changes, but few studies have investigated this phenomenon. Here, we present data on nestling diets of nine different populations of pied flycatchers *Ficedula hypoleuca*, across their breeding range. This species has been shown to adjust its breeding phenology to local climate change, but sometimes insufficiently relative to the phenology of their presumed major prey: *Lepidoptera* larvae. In spring, such larvae have a pronounced peak in oak habitats, but to a much lesser extent in coniferous and other deciduous habitats.

2. We found strong seasonal declines in the proportions of caterpillars in the diet only for oak habitats, and not for the other forest types. The seasonal decline in oak habitats was most strongly observed in warmer years, indicating that potential mismatches were stronger in warmer years. However, in coniferous and other habitats, no such effect of spring temperature was found.

3. Chicks reached somewhat higher weights in broods provided with higher proportions of caterpillars, supporting the notion that caterpillars are an important food source and that the temporal match with the caterpillar peak may represent an important component of reproductive success.

4. We suggest that pied flycatchers breeding in oak habitats have greater need to adjust timing of breeding to rising spring temperatures, because of the strong seasonality in their food. Such between-habitat differences can have important consequences for population dynamics and should be taken into account in studies on phenotypic plasticity and adaptation to climate change.

Key-words: demography, *Ficedula hypoleuca*, food web, foraging, glmmPQL, passerines

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Introduction

An important evolutionary factor that has shaped the decision when to reproduce is the seasonal variation in food availability. Seasonal fluctuations in food availability are especially important in temperate zones, where most bird species anticipate breeding in spring and summer when food is abundant (Lack 1966; Martin 1987). Both the breeding phenology of most organisms and the peak of their food resources are advancing with rising temperature (Dunn & Winkler 2010). Directional climate change is therefore predicted to result in long-term trends of advancements or delays of both phenologies (Parmesan & Yohe 2003; Visser, Holleman & Gienapp 2006). Rates of phenological shifts differ between species, depending on their trophic level (Thackeray *et al.* 2010). For example, Both *et al.* (2009) showed that over 20 years, caterpillar peak dates advanced faster than passerine hatching dates, while no advancement was found for predatory sparrowhawks (*Accipiter nisus*). One of the major challenges for species in coping with climate change is therefore to sufficiently match the timing of breeding with timing at other trophic levels. Several examples exist for increased trophic mismatches, but few studies are detailing the functional link between trophic levels and their consequences (Visser & Both 2005). Interestingly, even within these few studies, there is substantial variation in the results within the same trophic relationships. For example, whereas great tits *Parus major* and pied flycatchers *Ficedula hypoleuca* in the Netherlands advanced their breeding time less than the advance in the peak of their caterpillar prey (Visser *et al.* 1998; Both *et al.* 2009), great tits in Oxford adjusted their breeding time to be completely in synchrony with the timing of caterpillars (Cresswell & McCleery 2003; Charmantier *et al.* 2008), as did the great tits and collared flycatchers *Ficedula albicollis* in the Czech republic (Bauer *et al.* 2010). If we want to understand whether climate change has ecological consequences through differential changes in the phenology of both predators and prey, we need better insight into how different trophic levels are linked and any potential differences in resource use across habitats.

The pied flycatcher has been studied extensively with respect to the timing of reproduction relative to one of their main prey groups, caterpillars (Both *et al.* 2006, 2009). In the Netherlands, this songbird breeds in oak *Quercus* spp., coniferous and mixed forests and forages for caterpillars and other arthropods. Oak forests show a sharp peak of caterpillar abundance in spring, which lasts for only about 3 weeks and is earlier (Visser, Holleman & Gienapp 2006) and narrower in warmer springs (Smith *et al.* 2011). The synchrony of brood rearing with the peak in this prey type has been suggested to be of major importance for reproductive success (Both & Visser 2001). Elevated spring temperatures of the last few decades have resulted in pied flycatchers increasingly mismatching the timing of breeding with the caterpillar peak (Both *et al.* 2006). As a consequence, an increasing proportion of later born nestlings are reared under suboptimal food condi-

tions and therefore are less likely to survive and recruit into the population (Both & Visser 2005). Across Europe, populations of pied flycatchers have advanced laying dates depending on the local degree of spring warming (Both *et al.* 2004). However, it is an open question whether the magnitude of these advancements is always sufficient to maintain synchrony with the peak in food abundance (Visser 2008; Goodenough, Hart & Stafford 2010). Observed local population declines both in the Netherlands and in the UK have been attributed to an increased phenological mismatch (Both *et al.* 2006; Goodenough, Elliot & Hart 2009).

An important assumption made in many of the previous studies is that caterpillar abundance is important for many passerine birds during reproduction. In a comparative study by Sanz (1998), Lepidoptera (adults and larvae) were the most common prey type in the nestling diets of different populations but only amounted 28.7%, followed by Diptera (18.8%) and Coleoptera (13.7%). Because caterpillars have a high-quality nutritional profile (Arnold *et al.* 2010), higher proportions in the diet should result in better nestling condition, as has been found in great tits (Wilkin, King & Sheldon 2009). However, it is not clear whether this relationship also applies to pied flycatchers. Eeva, Ryömä & Riihimäki (2005) found no correlation between the proportion of caterpillars and fledging success. In a study in Sweden, the number of fledglings in pied flycatchers was also not related to breeding synchrony with the caterpillar peak. In fact, even before the onset of severe climate warming, pied flycatchers were reported to breed during the declining slope of caterpillar abundance (Lack 1966), and early nests produced more recruits than late nests (but see Drent *et al.* 2003; who found a negative quadratic relationship). Moreover, perfect timing with the caterpillar peak might not be required as long as food availability does not drop below a certain threshold (Veen *et al.* 2010). Therefore, using caterpillar peak abundance dates as a yardstick for detecting mistiming might not be justified in all cases.

Timing of breeding with respect to a certain food source might be more or less important in its effects on reproduction depending upon the seasonality of different habitat types. Pied flycatchers usually prefer to breed in deciduous forest types (Lundberg & Alatalo 1992; Siikamäki 1995), and caterpillars form a main food source of nestling pied flycatchers in oak-dominated forests (Sanz 1998). However, while caterpillars are superabundant during a short period in many oak forests, their phenology is less seasonal in other types of forests. Birds breeding in pine *Pinus* spp.-dominated forests, a common breeding habitat in northern Europe, experience very different caterpillar phenologies, with much lower abundances and peaks occurring later in the season (van Balen 1973; Eeva, Veistola & Lehikoinen 2000; Veen *et al.* 2010). Pied flycatchers in such habitats rely more upon flying insects (*Diptera* and *Coleoptera*), which show a strong increase in numbers over the breeding season for both deciduous and coniferous habitats in southern Sweden (Lundberg *et al.* 1981). This underlines the need to consider habitat

differences in the timing and abundance of potential prey types when studying the effects of (mis-) matches on fitness and population dynamics for those birds.

By combining data sets on pied flycatcher nestling diets covering a large geographical scale, we were able to investigate the impact of spring temperatures on seasonal patterns of nestling diets and subsequent reproductive success in different habitats. Apart from directional climate change, annual fluctuations in spring temperatures could also cause pied flycatcher breeding dates to be mistimed in relatively cold or warm years, but only if those birds lack sufficient plasticity. As long-distance migrants, pied flycatchers seem unable to track spring phenology sufficiently before arrival to the breeding grounds (Coppack & Both 2002). Therefore, even in the absence of directional climate change, mistiming with the preferred prey types might occur in this species in warmer than in average years, and not in average or colder years.

The aim of this study was to investigate: (i) the importance of caterpillars in nestling diets in terms of reproductive success; (ii) whether breeding date in areas with strong climate change is less well timed in relation to their caterpillar food; (iii) how susceptible populations are in their timing to between-year temperature fluctuations; and (iv) how the effects of temperature on seasonal patterns of caterpillars in the diet differ among habitat types (i.e. oak vs. coniferous and other woodlands).

Materials and methods

STUDY SPECIES

Pied flycatchers are long-distance migratory passerines breeding in temperate forests across Europe and Russia. They breed preferentially in deciduous forests, but also frequently occur in coniferous forests (Siikamäki 1995). The species is single-brooded with clutch sizes normally ranging from five to eight eggs. Usually, bi-parental care is provided to the young (Lundberg & Alatalo 1992). Populations used in this study almost exclusively breed in nest boxes where nestling diet can be measured in a standardized way.

NESTLING DIET

Proportions of prey types in the nestling diet are an easy way of quantitatively measuring diet but do not generally reflect food availability in the birds' habitat (Naef-Daenzer, Naef-Daenzer & Nager 2000). However, for a preferred food type like caterpillars, a seasonal decline in the diet may be expected to correspond to a decline of caterpillar biomass in the environment, although the relationship might be nonlinear (e.g. environmental decline stronger than the decline in diet, van Balen 1973). We tested the assumption whether the seasonal decline in proportion of caterpillars in the diet indeed was because of the temporal match with the caterpillar peak for 5 years (1998–2002) for which we had data on nestling diets and the timing of the caterpillar peak in the HogeVeluwe area (NL, Appendix S1, Supporting information). The caterpillar peak varied between 10 and 20 May in these years, and mean hatch dates between 20 and 27 May. A model with proportion of caterpillars in the diet for each brood as dependent and the relative timing to the caterpillar peak as covariate

performed much better than a model with actual date (AICs: 489 vs. 497, Table S2, Fig. S1, Supporting information). This analysis supports our assumption that an observed seasonal decline of caterpillars in the nestling diet indicates mismatching of the population with the caterpillar peak rather than a seasonal change in food preference.

DIET DATA SETS

For this study, data sets from nine areas in Europe and Russia, collected in different years between 1998 and 2008 (resulting in 22 individual 'seasons'), were analysed (Table 1). The data sets were collected with the use of cameras taking pictures ($n = 2$) or videos ($n = 6$), or by using neck collars to retrieve prey items from the nestlings' throats ($n = 1$). For all data sets, sampling took place when the young were between 8 and 12 days old (7 days for 30 nests in North Wales), which is in the late nestling phase (chicks fledge between 14 and 16 days of age). When analysing the seasonal change, we only included data sets where diet data were collected over a period of > 1 week and where at least eight nests were sampled. The number of observed prey items per nest was on average 65 (± 62 SD, range: 7–600). Diet information was used from one time-point per nest (sampling duration was *c.* between 30 min and 3 h during 1 day) except for 30 nests in North Wales in 2001, where also a second, 5-day earlier measurement was used to achieve a greater seasonal spread. Heterogeneity between data sets was considerable, and because most data were collected for other purposes, different collecting and diet analysis methods were used and sample sizes differed substantially (for additional information, see supplementary material). For this reason, the analysis was restricted to investigate seasonal changes in the proportions for the presumably most important food type in the diet, caterpillars. In most, but not all cases, the term 'caterpillars' also included *Hymenoptera* larvae (mostly *Symphyla*, which also have herbivorous larvae), as at least some of them can be hard to distinguish from *Lepidoptera* larvae. Therefore, the comparison of average values of proportions of caterpillars between areas might be associated with a small error.

Data came from different forest habitat types, including deciduous, coniferous and mixed forest. Previous work on timing of breeding in pied flycatchers has mainly been conducted in oak-dominated forests (Both *et al.* 2006) and in far northern birch–pine forests (e.g. Eeva, Veistola & Lehikoinen 2000). Oak habitats seem to differ largely from other types of habitat with regard to caterpillar phenology and abundance (Rytkönen & Orell 2001; Mägi *et al.* 2009). The caterpillar peak in oak forests is usually much higher compared with other habitats (van Balen 1973; Fischbacher, Naef-Daenzer & Naef-Daenzer 1998; Veen *et al.* 2010), and we therefore chose to use two categories of breeding habitat for our analysis: (i) oak (mainly *Quercus robur*) and oak-mixed forest and (ii) other, non-oak habitat, consisting of coniferous species (mainly pine, *Pinus* spp.) and/or other deciduous species (mainly birch, *Betula* spp.), subsequently termed 'coniferous/other' habitat. For areas where both habitat types occur, habitat classification was based on a radius of about 100 m around the nest box, which is presumably the range within which most foraging of pied flycatchers occurs (von Haartman 1956).

VALIDATION OF USING PREY NUMBERS AS DIET MEASURE

Estimated caterpillar prey lengths (in mm) from two areas (Drenthe and Turku) were used to validate the use of numbers of caterpillars alone, rather than numbers corrected for the size of caterpillars in the main data analysis. A linear model with caterpillar size (length

Table 1. List of study areas where nestling diet of pied flycatchers was sampled, and their features

Country	Area	Latitude	Longitude	Habitat	Years with data	Total number of broods	Δ Spring T (in °C, per year, between 1980 and 2008)	References to original sources of diet data
Netherlands	Hoge Veluwe	52°7'N	5°53'E	Oak, Coniferous/other	1998–2002	94	0.077	
Netherlands	Drenthe	52°50'N	6°22'E	Oak, Coniferous/other	2007–2008	74	0.074	
Sweden	Öland	56°44'N	16°40'E	Oak, Coniferous/other	2004	32	0.069	Wiley <i>et al.</i> (2007)
Wales	North Wales	53°14'N	4°1'W	Oak	1998–1999, 2001	66 ^a	0.058	
Estonia	Kilingi-Nõmme	58°7'N	25°5'E	Coniferous/other	2006	36	0.047	Sisask <i>et al.</i> (2010)
Norway	Oslo	59°59'N	10°38'E	Coniferous/other	2003, 2005–2007	72	0.038	Wiebe & Slagsvold (2009)
Finland	Harijavalta	61°20'N	22°10'E	Coniferous/other	2000, 2002	68	0.003	Eeva, Rymmä & Riihimäki (2005)
Finland	Turku	60°26'N	22°6'E	Oak, Coniferous/other	2008	51	0.003	
Russia	Revda	56°48'N	59°28'E	Coniferous/other	2005–2007	31	−0.006	Belskii & Belskaya (2009)

^aOf 30 broods, a second measurement was used (553 observations in total).

in mm) as dependent variable and date, area and the interaction of date and area as fixed effects showed no significant change of size with date (GLM, d.f. = 71, interaction area × date: estimate = 0.007 ± 0.17 , $t = 0.05$, $P = 0.96$; date: estimate = 0.088 ± 0.062 SE, $t = 1.42$, $P = 0.16$). However, mean caterpillar length in Turku (16.7 mm) was significantly smaller compared to Drenthe (20.5 mm; model estimate (GLM) = -3.78 ± 0.604 SE, $t = -6.26$, $P < 0.001$). Accounting for prey size could be important, especially if diet information of nestlings of different ages is used (van Balen 1973), if different prey types are included in the analysis or if the main focus is on comparing average proportions of prey. In our data set, ingestion constraints were unlikely to affect diet as only older nestlings were filmed (Slagsvold & Wiebe 2007). We also show that caterpillar size selected by the birds over time was consistent within habitat types. So, for comparisons of seasonal changes in proportions of different prey types, this justifies the use of prey numbers here. Differences in mean prey size between areas might depend on habitat type (Lundberg *et al.* 1981), but can be assumed to occur randomly with regard to the degree of climate warming in the respective area.

BREEDING PARAMETERS

In addition to diet information, breeding parameters were also analysed, such as laying date, clutch size, nestling condition (mean fledgling mass and tarsus, $n = 275$ nests, measured at an age between 10 and 12 days) and number of fledglings per nest ($n = 365$ nests). Fledgling mass (with tarsus length as covariate in the model) was used as a measure of reproductive success, as previous studies found that fledgling mass is positively related to survival in pied flycatchers (Potti *et al.* 2002) and to post-fledgling survival (Naef-Daenzer, Widmer & Nuber 2001) and recruitment (Tinbergen & Boerlijst 1990) in great tits.

TEMPERATURE DATA

Temperature data were obtained from the freely available data sets of the European Climate Assessment & Data set (<http://eca.knmi.nl>, Klein Tank *et al.* 2002) and from the Russian Weather Service (<http://meteo.infospace.ru>). We used temperature data between 1980 and 2008 from the closest weather stations available to each study site (c. 20–200 km away). For each study area, the average of the mean daily temperature was calculated for a period of 50 days before and until 30 days after the average median hatching date of all available breeding seasons of the respective area. This was done to account for different phenologies of the areas and is likely to capture the most relevant period for the development of vegetation and insect prey species (Visser, Holleman & Gienapp 2006). As we also used data from several very late nests, temperatures of this late period were therefore included as well. For each area, a regression line for mean annual spring temperature across years (1980–2008) was then calculated to identify the relative degree of spring warming experienced in each area (using the slope of the linear least squares regression, 'slope T '). The deviation from the regression line for the particular years was used to identify relatively cold or warm years (' $T_{(dev)}$ ').

STATISTICAL ANALYSIS

To be able to compare seasonal changes in nestling diets between areas, date relative to the median hatching date of a population in a certain season (date of sampling minus median hatch date) was used. The presented effect of date itself therefore does not say whether a season was early or late. This date parameter is referred to in the

following methods and results sections whenever ‘relative date’ is mentioned. All analyses were carried out in R 2.11.1 (R Development Core Team 2010).

Reproductive success

To investigate the relationship between proportion of caterpillars in the diet and reproductive success, two linear mixed models (function *lmer*, package *lme4*) with normal error structure were applied. The first full model included mean fledgling mass (per nest, centred per season) of a subset of 275 nests as dependent variable. Proportions of caterpillars were log-transformed ($\log(\text{Cat})$) to achieve near-linearity. As fixed effects, we included $\log(\text{Cat})$, mean tarsus length of the focal nestlings as structural measure (in mm) and relative date. In addition, the two-way interactions of $\log(\text{Cat})$ and tarsus with relative date were included. The best random structure was selected by comparing AICs of full models with different random structures and choosing the model and random structure with the lowest AIC value (Zuur *et al.* 2009). In this case, the best random term contained season (i.e. year by area combination) as random intercept and proportion of caterpillars (\log -transformed) as random slope. By including proportions of caterpillars also as a random slope, we allow the relationship between caterpillars and fledgling mass (the response) to vary with season (Zuur *et al.* 2009), so that different slopes are modelled for every season. Furthermore, we ran a second, similar model, this time using data from 365 nests, where the number of fledglings per nest had been collected as a measure of breeding success. In this model, the fixed effects were date, habitat, clutch size and proportions of caterpillars (\log -transformed) and their two-way interactions; the best random structure contained season as random intercept. For both latter models, the ‘best’-fitting final model was determined using likelihood ratio tests.

Effects of temperature on nestling diets

To investigate the effect of temperature on diet, a general linear mixed model using function *lmer* (package *lme4*) with binomial error structure was applied. For each nest, the number of caterpillars vs. the number of other prey types was used as dependent variable (in the form of a two-column matrix), which is the normal procedure in R to model proportions (Crawley 2007). The procedure also retains information on sample size in the model that is used to weight the data accordingly. The full model included date, habitat, $\text{slope}T$ and $T_{(\text{dev})}$ and their three-way interactions. The best random structure was again determined by comparing AICs of full models with different random structures (Zuur *et al.* 2009). A complex cross-classified random structure gave the best fit according to AIC, but could, however, still not account for most of the variation present in the data. Quasi-likelihood estimation therefore had to be used in addition, to account for the overdispersion by adjusting the standard errors and *P*-values. As this method is not implemented correctly in *lmer*, function *glmmPQL* (*Mass* package) with penalized quasi-likelihood estimation was used. However, *glmmPQL* does not allow for cross-classified random effects. As a compromise, function *glmmPQL* with a simple random structure of ‘season’ (year by area combination) as random intercept was used as this kept overdispersion relatively low (2.3). Backward elimination of non-significant terms was used to determine the final model. Because of the described problems and the type of model estimation (quasi-likelihood), estimates and borderline significant *P*-values of this model should be viewed with caution.

Results

Study areas differed largely in their median hatch dates: the earliest area was HogeVeluwe (the Netherlands) with an average (median) hatch date of 22 May, and the latest area was Harjavalta (Finland) with an average (median) hatch date of 14 June, a difference of 23 days. Across all areas (nine areas, 570 nests), average proportions of caterpillars were lower in coniferous/birch habitat (mean = 23.7%) than in oak habitat (mean = 37.5%). Other abundant dietary groups included adult Lepidoptera, Coleoptera, Diptera and Arachnida, which differed between study sites (see Table S1, Supporting information). Rates of spring temperature change over 28 years (1980–2008) were between -0.006 and 0.077 °C per year for the different areas, with most warming in the Netherlands, Wales and Sweden, and little to no warming in Finland and Russia (Table 1).

REPRODUCTIVE SUCCESS

Average fledgling mass was 13.6 g (± 1.13 SD, range: 8.4–16.3 g), and average number of fledglings per nest was 5.6 (± 1.51 SD, range: 0–8). It should be understood that this analysis includes only the more successful nests, because these still had chicks alive when diet was measured late in the nestling phase.

We found that fledgling mass was positively correlated with the proportion of caterpillars in the diet (Fig. 1, Table 2, final model contained $\log(\text{Caterpillars})$ and tarsus length). The relationship followed a logarithmic curve with broods that received more caterpillars having a significantly higher mean fledgling mass. When using fledgling mass without centring it for area, estimates and *P*-values were very similar to the original (centred) model. Hatching date was not significant in a model with diet, suggesting that the commonly observed decline in nestling condition with date is because of

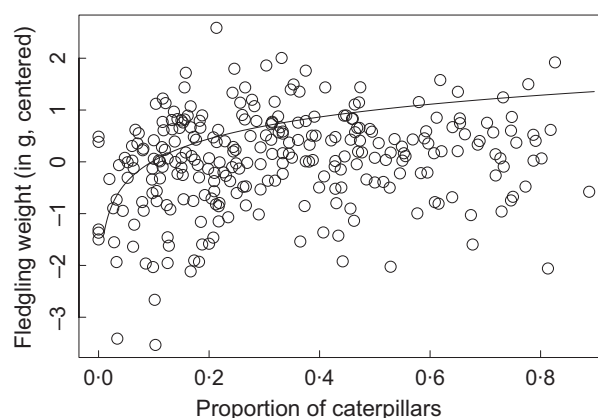


Fig. 1. Proportions of caterpillars per nest in relation to mean fledgling mass (in g, centred per season and habitat) from 275 nests. Predicted curve from a general linear model containing fledgling mass as dependent and $\log(\text{caterpillars})$ and tarsus length as fixed effects is shown.

Table 2. Results of the linear mixed model using (centred brood means) fledgling mass as the dependent variable, and its relationship with (log-transformed) proportions of caterpillars in the nestling diet (log(Cat)) and tarsus as covariate, for 275 nests, grouped for 12 seasons (year–area combination). ‘Date’ is relative date

Fixed effects	Estimates	SE	<i>t</i> -Value	<i>P</i> -value
(Intercept)	−11.342	1.515	−7.485	
Log(Cat)	0.314	0.113	2.788	0.006
Tarsus	0.684	0.086	7.971	< 0.001
Random effect	SD			
Season (intercept)	0.490			
Log(Cat) (slope)	0.290			
Residual	0.792			
Rejected terms				
Date				
Log(Cat) × date				
Tarsus × date				

a decline in caterpillar abundance over the season (see also Siikamäki 1998).

For the second model on a different but overlapping subset of the data (365 nests), using number of fledglings as the dependent variable, there was no significant effect of proportion of caterpillars in the diet (Table 3). There was a non-significant tendency for numbers of fledglings to be lower late in the season ($P = 0.15$). When clutch size was excluded from the model, there was still no significant effect of caterpillars on the number of fledglings.

EFFECTS OF TEMPERATURE ON NESTLING DIETS

In oak forests, we found a strong decline in caterpillars in the diet over the season in warm years, whereas in colder years, this was less apparent. In non-oak habitats, date and spring temperatures did not explain significant variation in proportion of caterpillars in the diet (Fig. 2, Table 4). This result reveals the need to consider habitat differences when examining phenological changes between trophic levels.

Table 3. Results of the linear mixed model with number of fledglings as the dependent variable, and its relationship with clutch size, relative date, habitat and proportions of caterpillars, based on 365 nests, grouped for 15 seasons

Fixed effects	Estimates	SE	<i>t</i> -Value	<i>P</i> -value
(Intercept)	1.070	0.668	1.601	
Clutch size	0.698	0.101	6.889	< 0.001
Random effect	SD			
Season (Intercept)	0.404			
Residual	1.422			
Rejected terms				
Prop. Caterpillars				
Date				
Habitat				
Two-way interactions between main effects				

Although we found a strong effect of date on the proportion of caterpillars, we found no evidence that this date effect was stronger in areas with more warming, even when accounting for habitat differences (neither slope $T \times$ date nor slope $T \times$ date \times habitat was significant). There was some indication that in oak habitats, caterpillars were less abundant in nestling diets in areas with more warming, whereas in coniferous/other habitats, caterpillar proportions were higher when there was more climate warming (significant two-way interaction between habitat and slope T , Table 4, Fig. 3), but this effect is driven by the single area that had oak habitat and no climate warming (Turku, Finland).

Discussion

Our data showed that caterpillars form a substantial part of the nestling diet of pied flycatchers, especially in oak habitats, where in warm years, their proportions drop steeply throughout the season. In contrast, pied flycatchers breeding in more coniferous or other deciduous habitats had no clear seasonal decline in caterpillars in nestling diets, and this was independent of spring temperature. We did not find that the seasonal decline of caterpillars in the diet was stronger in areas with more climate warming. Because populations in the strongly seasonal oak habitats are more likely to be mismatched, we expected the decline in caterpillar proportion to be steeper in this habitat in areas with more warming. However, we only had a single study area with oak in a region with no climate warming (Turku), which could be a reason for the lack of this effect. We found that pied flycatcher nestlings raised on a diet with a higher proportion of caterpillars fledged heavier, irrespective of date, indicating a positive effect of caterpillars on fitness.

IMPORTANCE OF TIMING

When considering the effects of climate change on differential responses in phenology, it is often implicitly assumed that timing of breeding is important, irrespective of habitat type. However, habitats can differ strongly in how food availability varies throughout the season (see e.g. Both *et al.* 2010), and therefore, the effects of timing of breeding may vary between habitats. Our data on seasonal changes in diet composition indeed showed that in forests with oaks, early breeders can profit from the caterpillar peak, whereas late breeders cannot, and this effect was exaggerated in warmer years. The other habitats clearly had fewer caterpillars during the early part of the season, but later in the season, the proportion of caterpillars was generally higher than in oak forests, especially in warmer years. Birds raising their young in coniferous/other habitats therefore seem less affected by spring temperatures, and hence, climate change may influence these trophic interactions to a lesser extent. Mixed habitats of birch and pine trees seem especially suitable: the early caterpillars on deciduous trees were replaced by species emerging on pine later in the season (Eeva, Lehikoinen & Pohjalainen 1997).

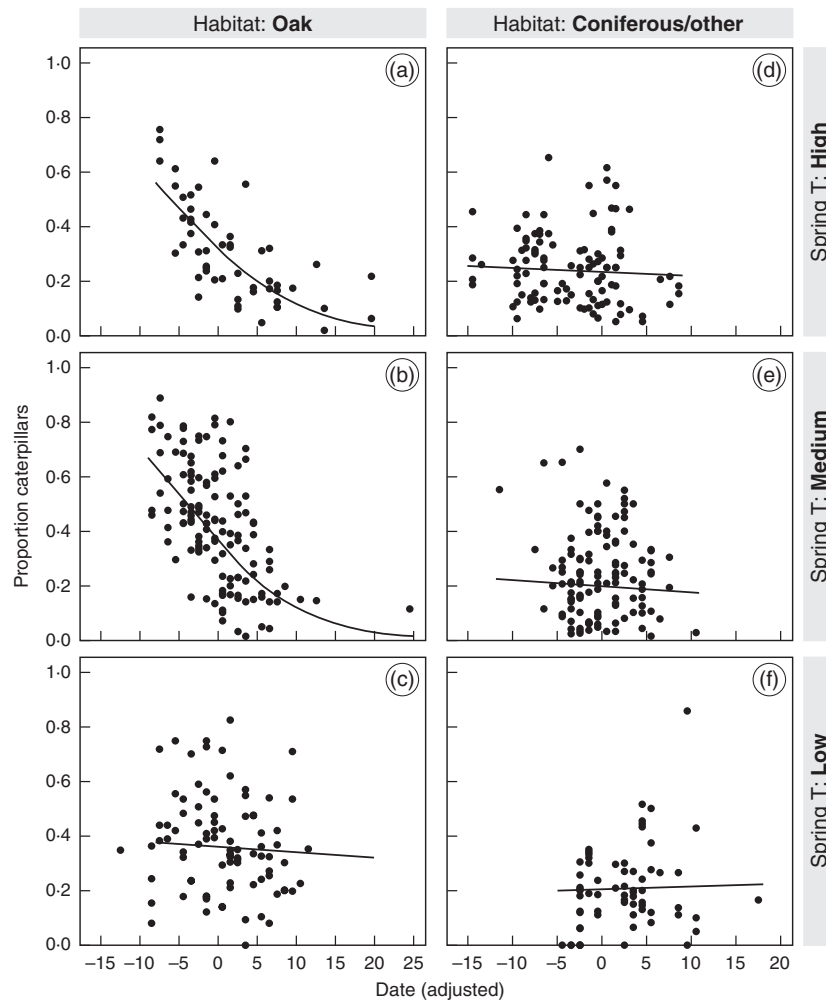


Fig. 2. The effect of mean spring temperature and habitat type on seasonal patterns of nestling diets (proportions of caterpillars) from 553 nests across nine areas. Effects are shown for high, medium and low spring temperatures ($T_{(dev)}$). Panels a–c show the effect for oak habitat and panels d–f for coniferous/other habitat. Raw data are shown and predicted curves as calculated from separate GLMs for the six categories (with proportion of caterpillars as dependent, relative date as fixed effect and binomial error structure) are plotted.

Pine trees also show much lower yearly fluctuations in timing and abundance of *Lepidoptera* larvae (Veistola, Eeva & Lehikoinen 1995). Indeed, birds breeding in similar habitats in northern Scandinavia seem not to time their breeding to coincide the nestling period with the maximum availability of caterpillars, but instead react more to the local conditions around the time of arrival or egg laying (Slagsvold 1976; Eeva, Veistola & Lehikoinen 2000).

Because there was a positive correlation between chick growth and proportion of caterpillars fed, irrespective of date, we hypothesize that as springs get warmer, habitat selection in pied flycatchers should change from a general preference for oak habitats to less seasonal habitats and/or habitats that have a later food peak. Earlier studies have shown a clear preference of pied flycatchers for deciduous forests (Lundberg & Alatalo 1992; Siikamäki 1995), but in the Netherlands, pied flycatcher populations have strongly declined in rich deciduous forests during the last decades, whereas no clear decline has been observed in mixed or coniferous habitats (Visser, Both & Lambrechts 2004; Both *et al.*

2006). The habitat with the highest food density has therefore been generally abandoned, if only because few birds manage to breed at the appropriate time. Evidence for directional dispersal (Kawecki & Holt 2002) into coniferous and mixed habitats is still lacking for pied flycatchers (see also Eeva *et al.* 2008 and references within), but the severe population declines in some oak forests suggest that this might already be occurring (Both *et al.* 2006).

Colder springs in oak habitats did not result in overall higher proportions of caterpillars in nestling diets, as might have been expected if a larger fraction of the population had timed its breeding adequately relative to the caterpillar peak. Instead, these years showed only medium proportions of caterpillars in nestling diets throughout the season, likely due to less synchronous occurrence of caterpillars. Between-year differences in the shape of the caterpillar peak have been described previously (Keller & van Noordwijk 1994; Eeva, Veistola & Lehikoinen 2000) and have been shown to depend on spring temperatures (van Asch & Visser 2007; Smith *et al.* 2011).

Table 4. Results of the linear mixed model of the proportion of caterpillars (loglinear model) in the nestling diet in relation to relative date, temperature (slope T and $T_{(dev)}$, centred), habitat type and their (three-way) interactions, for 553 observations, grouped for 22 seasons (year–area combination). All parameters and interactions of the final model are shown

Fixed effects	Estimates	SE	<i>t</i> -Value	<i>P</i> -value
(Intercept)	-1.63	0.17	9.37	
Date	-0.01	0.03	-0.46	0.647
Habitat	0.44	0.06	6.79	0.000
Slope T	8.82	5.16	1.71	0.104
$T_{(dev)}$	0.11	0.24	0.44	0.665
Date \times habitat	-0.03	0.01	-2.53	0.012
Date \times Slope T	-0.51	0.29	-1.78	0.076
Habitat \times Slope T	-3.79	1.48	-2.57	0.011
Date $\times T_{(dev)}$	0.06	0.03	2.17	0.031
Habitat $\times T_{(dev)}$	-0.08	0.09	-0.81	0.418
Slope $T \times T_{(dev)}$	-5.10	7.22	-0.71	0.489
Date \times habitat $\times T_{(dev)}$	-0.04	0.01	-3.95	0.000
Random effect	SD			
Season	0.47			
Residual	2.38			

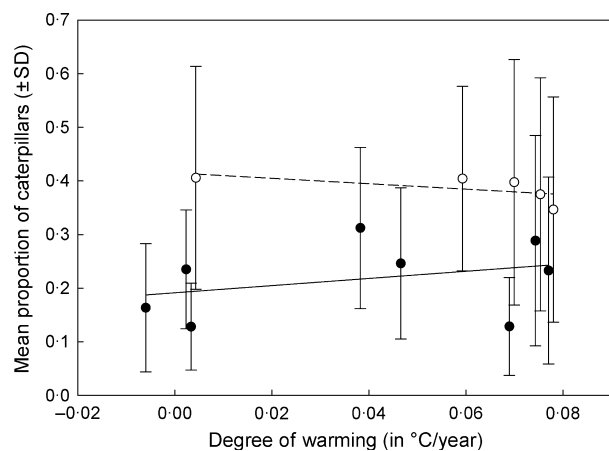


Fig. 3. The effect of the degree of warming (in °C per year, between 1980 and 2008) on average proportions of caterpillars in nestling diets for two habitat types. Data points represent values per study area (\pm SD). Open circles and dashed regression line show data for oak habitat, and filled circles and solid regression line show data for coniferous/other habitat. For graphical reasons, values for oak habitat were shifted by 0.001 along the *x*-axis.

BREEDING SUCCESS

Nestlings fed on higher proportions of caterpillars grew better, irrespective of date or habitat. A similar relationship has been found for great tits (Tremblay *et al.* 2005; Wilkin, King & Sheldon 2009) and blue tits *Cyanistes caeruleus* (Tremblay *et al.* 2003; Garcia-Navas & Sanz 2011). The asymptotic relationship suggests that a certain amount of caterpillars is important for nestling growth in these populations, but very high proportions do not improve fledgling mass further. A deficiency of certain (micro-) nutritional components, which are scarce in caterpillars (Arnold *et al.* 2010), may arise in broods receiving almost exclusively caterpillars (e.g. for

taurine: Ramsay & Houston 2003; for calcium: Bureš & Weidinger 2003). The high level of unexplained variation in the data could be due to the often rather small sample size for dietary sampling, the exclusion of overall feeding frequencies and focusing on a short period at the end of the nestling period. Factors like parental quality or genetic components may also play a role in determining fledgling mass (Merilä, Kruuk & Sheldon 2001). Recruitment rate might have been a better measure of breeding success, but was not available here for most data sets. The number of fledglings was at best weakly affected by the dietary proportions of caterpillars (Table 3).

Nestling growth was found to be related to diet, and earlier work has shown that the seasonal decline in reproductive success in pied flycatchers was because of declining food availability or quality: food supplementation of experimentally delayed broods mostly took away the seasonal decline in fledgling mass (Siikamäki 1998). Seasonal diet changes as a response to changes in habitat-specific availability of high-quality food could therefore result in later broods fledging in lower condition, especially in the habitat with the earliest and/or narrowest caterpillar peaks. In the Netherlands, population trends were mostly negative for oak areas, and not for mixed and pure coniferous forests (Visser, Both & Lambrechts 2004; Both *et al.* 2006), which is consistent with the observed effects here of date and spring temperature on seasonal dietary changes. Furthermore, the fitness penalties of breeding late increased over the decades when spring warming increased in a habitat with oak as one of the dominant tree species (Both & Visser 2001). This suggests a link between local reproductive output (i.e. number and/or quality of fledglings) and population trends (see e.g. Virolainen 1984; Goodenough, Elliot & Hart 2009). Whether the effect of a mismatch between breeding date and the caterpillar peak also extends to increased costs for parents is presently unknown, although for the Dutch population selection for early breeding intensified as measured not only on recruit number, but also on adult female return rate (Drent *et al.* 2003). In recent years, late parents should be working harder to feed their offspring appropriately, and therefore return rates of these birds dropped relative to earlier breeders. Whether these demographic consequences could drive local populations towards extinction depends on other factors, such as density-dependent feedbacks. If indeed food availability is the determining factor, a decline in breeding density will release competition for the available food, and hence, a new equilibrium density may be achieved. Identifying the responsible factors with certainty would require an experimental approach that manipulates both food availability and hatch dates at the same time and measures both reproductive output and survival.

Conclusions

Birds have been shown to adjust their breeding time to varying spring temperatures through phenotypic plasticity (Gienapp *et al.* 2008), which has allowed them to partially track directional advances in their food peak. However, we show

that the benefit of breeding at a certain moment depends strongly on the seasonality of the breeding habitat: in oak forest habitat, pied flycatchers generally benefit strongly from breeding earlier, whereas in other habitats, this effect is less strong. The latter habitat also seems to require less plasticity in the timing of reproduction, as warm and cold years did not differ substantially in the proportions of caterpillars in nestling diets. In great tits, two populations were found to differ in their plasticity of timing of egg laying (Nussey *et al.* 2005; Charmantier *et al.* 2008), with higher variation in plasticity in the Dutch compared with the British population (Husby *et al.* 2010). In the light of the current study, this may be surprising, because the British population inhabits a more homogeneous oak habitat where greater plasticity would seem to be required to track rapid seasonal changes in caterpillars, as compared with the Dutch population breeding in oak-mixed forest. This highlights the complexity of adaptation to local conditions and a need for future studies to see whether indeed habitat seasonality is likely to play an important role in the differential evolution of such phenotypic plasticity as predicted by our study using multiple populations.

Yardsticks for detecting the mistiming of breeding in a species (Visser & Both 2005) might only be suitable in certain habitats but not in others because of differing trophic relationships. So far, such within-species habitat variation has been largely ignored (Møller, Rubolini & Lehikoinen 2008; Saino *et al.* 2011). In addition, phenotypic plasticity in the timing of breeding to match the caterpillar peak might mean that evolutionary change is not required, as long as food levels are above a certain threshold. Careful choice of ecologically relevant indicators of mistiming, in combination with the assessment of fitness consequences of asynchrony, is therefore crucial for understanding phenotypic plasticity and adaptation to climate change.

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Supporting Information

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

Appendix S1. Analysis of seasonal changes in nestling diet in relation to timing of caterpillars in the environment.

Fig. S1. Relationship between proportion of caterpillars in the nestling diet and the deviation from median hatch date (in days, panel A) or the deviation from peak date of caterpillars (in days, panel B).

Table S1 Additional information on method of diet collection, number of food items per nest, percentage caterpillars in the diet, other important prey types and percentage of unidentified items for the different areas.

Table S2 Model comparison using AIC, with proportion of caterpillars as dependent and deviations from either hatch date (model 1) or peak date (model2) as covariate.

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