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Climate change and unequal phenological changes across four trophic levels: constraints or adaptations?

Christiaan Both[1]*, Margriet van Asch[2], Rob G. Bijlsma[1], Arnold B. van den Burg[3] and Marcel E. Visser[2]

[1]*Animal Ecology Group, Center for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands;* [2]*Netherlands Institute of Ecology (NIOO-KNAW), PO Box 40, 6666 ZG Heteren, The Netherlands; and* [3]*Bargerveen Foundation/Department of Animal Ecology, Radboud University, PO Box 9010, 6500 GL Nijmegen, The Netherlands*

Summary

1. Climate change has been shown to affect the phenology of many organisms, but interestingly these shifts are often unequal across trophic levels, causing a mismatch between the phenology of organisms and their food.

2. We consider two alternative hypotheses: consumers are constrained to adjust sufficiently to the lower trophic level, or prey species react more strongly than their predators to reduce predation. We discuss both hypotheses with our analyses of changes in phenology across four trophic levels: tree budburst, peak biomass of herbivorous caterpillars, breeding phenology of four insectivorous bird species and an avian predator.

3. In our long-term study, we show that between 1988 and 2005, budburst advanced (not significantly) with 0·17 d yr^{-1}, while between 1985 and 2005 both caterpillars (0·75 d year^{-1}) and the hatching date of the passerine species (range for four species: 0·36–0·50 d year^{-1}) have advanced, whereas raptor hatching dates showed no trend.

4. The caterpillar peak date was closely correlated with budburst date, as were the passerine hatching dates with the peak caterpillar biomass date. In all these cases, however, the slopes were significantly less than unity, showing that the response of the consumers is weaker than that of their food. This was also true for the avian predator, for which hatching dates were not correlated with the peak availability of fledgling passerines. As a result, the match between food demand and availability deteriorated over time for both the passerines and the avian predators.

5. These results could equally well be explained by consumers' insufficient responses as a consequence of constraints in adapting to climate change, or by them trying to escape predation from a higher trophic level, or both. Selection on phenology could thus be both from matches of phenology with higher and lower levels, and quantifying these can shed new light on why some organisms do adjust their phenology to climate change, while others do not.

Key-words: *Accipiter nisus*, breeding date, budburst, *Cyanistes caeruleus*, *Ficedula hypoleuca*, *Parus ater*, *Parus major*, phenology, *Quercus robus*, timing

Introduction

Most species have clearly defined periods in the year in which they reproduce, and this reproductive phenology is linked to the phenology of other organisms needed for successful reproduction. In reaction to climate change, many organisms have advanced their reproductive phenology (Post *et al.* 2001; Walther *et al.* 2002; Parmesan & Yohe 2003; Root *et al.* 2003), but these advances were often not in step with phenologies at lower trophic levels (Stenseth *et al.* 2002; Visser, Both & Lambrechts 2004). Examples are insectivorous birds that have advanced their breeding phenology less than the phenology of their offspring food supply (Visser *et al.* 1998; Both & Visser 2005; Pearce-Higgins, Yalden & Whittingham 2005), and in freshwater systems the phenology of blooms of zooplankton and phytoplankton have changed at different rates (Winder & Schindler 2004). Hence, the mere presence of a shift in phenology in response to climate change does not tell

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*Correspondence author. E-mail: c.both@rug.nl

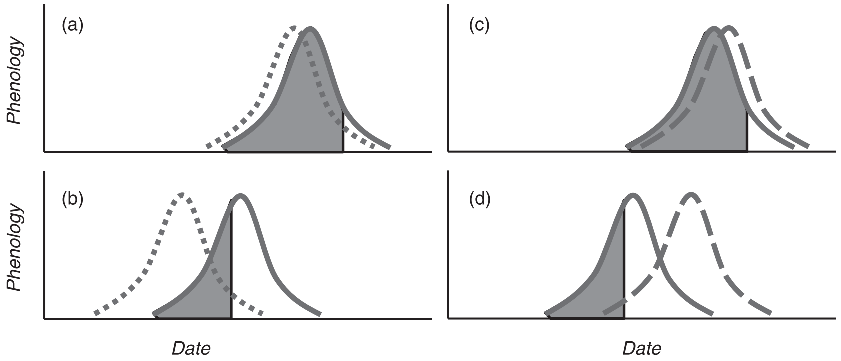

Fig. 1. Schematic phenological changes at different trophic levels and the consequences for selection of phenology (hatched areas show the frequency of relatively successful breeders). (A and B) nestling food phenology (dotted line) and passerine breeding phenology (solid line). (A) is the situation when the birds are in synchrony with their food, and selection for early breeding is weak. (B) food phenology has advanced more than the bird breeding phenology, and as a consequence only early birds are breeding successfully. (C and D) phenology of fledging in the passerine (solid line) and phenology of food demand in its predator (striped line). (C) synchrony between passerine and predator phenology results in weak selection. (D) increased asynchrony due to advance of passerine phenology, but not in predator phenology, results in stronger selection for early breeding, because now early birds escape predation more often than later breeders. Note that absolute predation pressure in D is probably less than in C, but selection is the relative success of the whole cohort.

us whether this shift has been sufficient to match shifts at other levels of the food chain (Visser & Both 2005). These different rates of phenological responses have been explained mostly by constraints on phenological plasticity (Both & Visser 2001; Visser *et al.* 2004), or the costs associated with responses during other periods of the annual cycle (Coppack & Both 2002; Gienapp & Visser 2006). The limitation of this approach is that it only considers how the phenology of the higher trophic level is affected by the phenological changes of their food (*bottom-up*), without taking into account that the consumers are also prey for other species at higher trophic levels, that is, their predators (but see Philippart *et al.* 2003). In this contribution, we want to work out how phenological changes are affected by the phenology of both food sources and predators, and this sheds new light on what we have previously called 'insufficient' adjustment (Visser & Both 2005).

An alternative approach to examining whether shifts in phenology have been sufficient to meet the requirements of ongoing climate change has been to consider changes in selection pressures for phenological traits (Møller & Merila 2004; Visser *et al.* 2004). The rationale is that if the response in phenology of a consumer is less than the phenological response of its food, early breeding individuals have higher fitness than late breeding individuals, and hence selection for early breeding should increase (Visser *et al.* 1998, 2004). This approach links phenotypic variation in phenology to fitness consequences, and most results from this approach have been consistent with changes in synchrony between the predator and its prey: a decrease in synchrony over time was associated with increased selection for early breeding (Visser *et al.* 1998, see Fig. 1a,b; Both & Visser 2001), while an increase in synchrony was associated with decreased selection for early breeding (Cresswell & McCleery 2003). This qualitative match between the two approaches suggests that selection for breeding phenology changes because of an altered synchrony between food and consumer phenology.

We want to consider additional causes for the changed selection, because selection may change when synchrony with the underlying trophic level remains equal. Consider the situation when a consumer, in this case a passerine bird, is prey for a predator at a higher trophic level. This predator selects mainly the young, inexperienced individuals, and its food requirements are strongly linked to its breeding phenology. When predators breed in synchrony with their prey, their predation does not pose a clear directional selection pressure on their prey (Fig. 1c). If the passerine birds advance their breeding phenology, but the predators do not, the asynchrony will create an increased selection for early breeding, because the early fledglings gain enough experience to escape predation before predation pressure reaches its peak (Fig. 1d). The passerines in this example may advance their phenology in synchrony with their food, but still experience a change in selection pressure from the higher trophic level (*top-down*), and by doing this the early birds partly escape from their predators.

In this study, we consider the phenological responses across four trophic levels of a simplified food chain in northwest European deciduous forests. These forests are characterized by a highly synchronized budburst, and leaves are only palatable for most herbivores during the period when they are growing (Feeny 1970; Buse *et al.* 1999). During that period, a whole range of herbivorous insects forage on the leaves, and caterpillars (Lepidoptera) are one of the most important components of this insect community. For caterpillars, it is important to hatch at the time of budburst of their host trees; otherwise, they suffer from mortality, either due to food shortage or low-quality food. Consequently, caterpillar biomass peaks in our area last on average only 24 days (Visser, Holleman & Gienapp 2006). Many species of insectivorous birds feed their chicks with caterpillars, and for them it is important to hatch their chicks at the time that the peak in food requirements matches the caterpillar peak (Perrins 1970). For blue tits *Cyanistes caeruleus* and great tits *Parus major*, it has been shown that the match between hatching date and the peak in food availability is tight (Perrins & McCleery 1989), as we found for pied flycatchers *Ficedula hypoleuca* (Both & Visser 2005). The fourth trophic level we consider are the sparrowhawks, *Accipiter nisus*, which prey mainly on passerines, and the diet of which comprises a large proportion of fledglings, the most easily caught prey (Newton 1986; Bijlsma 1993). We expect that for sparrowhawks, it is also important to match the time of peak food requirements for their chicks with the time when most food is around (Newton 1986; Nielsen & Møller 2006). The food peak is to some extent difficult to measure, because we can only measure when chicks fledge, and do not know how many will survive for how long. Some detailed studies have, however, shown that during the first week after fledging, mortality can be up to 50% (Drent 1984; Naef-Danzer, Widmer & Nuber 2001). Moreover, young birds become progressively better at flying (Geer 1982), making them more difficult to catch, and therefore we expect that the sparrowhawks can profit only for a short period after fledging of their prey.

In previous papers, we have addressed several responses of this food chain to climate change by examining whether the consumer advances in synchrony with its food. We have shown that in warm springs, the caterpillars *Operophtera brumata* are disrupted with their oak hosts (Visser & Holleman 2001), and that great tits and pied flycatchers advanced their laying dates less than the peak date of their caterpillar prey (Visser *et al*. 1998, 2004, 2006; Both & Visser 2001, 2005). We expand in this paper on these previous results, by considering more species of passerines simultaneously, and including a fourth trophic level to undertake a novel examination of the role of top-down selection pressure by predation on constraints on phenological changes at lower trophic levels. Rather than concentrating on median values per year, we also want to investigate interannual variance in phenology, because variance may differ for species in different ecology niches (Winkler, Dunn & McCulloch 2002). Our emphasis, however, is on how changes in the phenology of higher trophic level may impose different selection pressures on their prey, as an alternative explanation for the observed changes in selection pressure.

Methods

STUDY AREAS

The fieldwork on oaks, caterpillars and passerines was carried out in the Hoge Veluwe (The Netherlands) between 1985 and 2005. This study area consists of 171 ha of mixed woodland on poor sandy soils, dominated by oak (the native *Quercus robur* and introduced *Quercus rubra*) and pine *Pinus sylvestris* with about 400 nest boxes designed for breeding passerines. The sparrowhawks were studied in a larger area of 110 km^2 bordering the Hoge Veluwe to the west, with similar vegetation. For tree, caterpillar and passerine phenology, we excluded the data from 1991, when a late night frost from 18–21 April damaged the leaves and delayed the caterpillars to a large extent, because early hatched caterpillars all were killed by the frost. At this time, many birds already had started egg laying, and therefore this year is an extreme outlier in the relationship between matching of caterpillars and passerines.

STUDY SPECIES

Tree phenology

Tree leaf phenology was scored twice a week from 1988 to 2005 for the same 102 pedunculate oak trees *Q. robur*, and we use the date at which the leaves protruded from their buds in the canopy of the tree as their budburst date (Visser & Holleman 2001). Trees were spread out over the entire area, to take into account spatial variation in budburst.

Caterpillar phenology

Caterpillars are the most important nestling food item for both the tit species (van Balen 1973) and pied flycatchers (Sanz 1998). Caterpillars feeding on deciduous trees in temperate forests grow best on young leaves, and eggs normally hatch around the time of budburst, and caterpillar growth results in a peak in abundance some weeks after the start of budburst. When caterpillars have reached a certain size and tree leaves become unpalatable, caterpillars pupate in the ground or hidden in the tree and become largely unavailable for foraging birds. We sampled the abundance of caterpillars by collecting their frass, and hence we do not know the species. Additional sampling of branches has shown that winter moth *O. brumata* and oak leaf roller *Tortrix virirdana* were the most abundant species (Visser *et al*. 2006). Variation between years in peak biomass may be partly due to changes in relative densities between species which differ in phenology, although all abundant species rely on young leaves and therefore should be timed to the budburst. From 1993 to 2004, frass nets were placed under a varying number of trees on the Hoge Veluwe but there is fixed set of seven oak trees, located at different sites within the study area (> 500 m apart), which were sampled throughout these years with two nets per tree. Furthermore, from 1985 to 1992, frass nets were used in the same area by J.M. Tinbergen, and we use these data on the phenology of the caterpillar biomass (Tinbergen & Dietz 1994; Verboven, Tinbergen & Verhulst 2001), to obtain a 20-year time series. Frass nets (a cheesecloth of 0·25 m^2 in a metal frame, with a weight hung from the centre of the net (see Fig. 3a in Tinbergen 1960)) were put up under oak trees *Q. robur*. Two of these nets are placed under a tree (about 1–1·5 m from the stem) and every 3–4 days, all caterpillar droppings are collected, dried at 60 °C for 24 h, sorted (i.e. all debris is removed), weighed and from this the caterpillar biomass is calculated (see Visser *et al*. 2006, for details). The caterpillar peak is defined as the mid-date of the sample of calculated maximal caterpillar biomass/day. As a phenological measure for the peak in food availability for the passerines this is probably a good yardstick (Visser & Both 2005). However, for comparing the match in timing of oaks and caterpillars, this measure is biased because it includes both the response of the caterpillars as well its consequences: caterpillars that were either too late or too early have not survived and therefore we will inevitably find a match between the caterpillar peak date and the budburst of their host trees.

Passerine phenology

We used data from four species of hole-nesting passerines that breed commonly in our nest boxes. Three species are closely related tit species, which are year-round residents in the area. They range in size from 9 g in coal tits *Parus ater*, 11 g in blue tits and 18 g in great tits. The species differ in their habitat preferences, with coal tits preferring more the coniferous areas, blue tits the deciduous areas, while great tits are common in both (Perrins 1979). The tits produce second broods in variable proportions after having successfully raised a first brood, with coal tits having most frequent second broods, and blue tits least frequent. Pied flycatchers are long-distance migrants, wintering in West Africa (Lundberg & Alatalo 1992) and arriving in our study area mainly during the second half of April. Flycatchers produce a single brood, and leave the area from July onwards, and the whole population has left by the end of August (van Balen 1979).

Data on laying and hatching dates of blue tits, coal tits, great tits and pied flycatchers were collected by weekly checks of the nest boxes. Although data have been collected since 1955, we present in this paper data from 1985 to 2005, because caterpillar data were available for this period. Pied flycatchers and great tits were the most numerous species with on average 89·7 (range 70–122) and 104·1 (range 48–152) breeding pairs per year, and breeding outside nest boxes in the area is rare. Blue tits and coal tits were less numerous in the nest boxes, with on average 38·5 (range 22–74) and 9·1 (range 4–18) breeding pairs per year, but both species also breed frequently in natural nest holes. In many cases, especially for great tits and pied flycatchers, more frequent checks were performed around the expected hatching date, to measure this more accurately. In other instances, the hatching dates were estimated by experienced observers from the development of the chicks or calculated from the known laying dates, clutch sizes and incubation periods. Laying dates are calculated back assuming that one egg per day is laid. All analyses of laying and hatching dates were restricted to first clutches, excluding repeat clutches of known females, and all clutches that were started 30 days after the first clutch start in that year. Laying dates are given as April-days (1 April is April-day 1, 24 May is April-day 54). The date of maximal food requirements for these species is when chicks are 8 days old, so we expect that the birds should match this date with the date of the caterpillar peak. For each species/year combination, we calculated the median date of maximal food requirements. For pied flycatchers and great tits, we also calculated the interval between the 25th and 75th percentiles, as a measure of how synchronous breeding was in a given year. Due to smaller sample sizes, we do not regard this measure as reliable for the other two species.

Predator phenology

We systematically located all sparrowhawk nests in the study area adjacent to Hoge Veluwe between 1974 and 1991. From that time onwards, search effort was restricted to a smaller area (18% of the former study plot), but enlarged again to the original area since 1996, employing the same standardized field methods (Bijlsma 1997). We excluded 3 years of data when fewer than five nests were available (1993–95) and the time series stopped in 2004. We calculated hatching date of the first chick directly (hatching date known exactly), or via sex-specific ageing of nestlings (using maximum wing chord; cf. Bijlsma 1997 for growth curves). The date of maximal food requirements is when chicks are 12 days old (Vedder *et al.* 2005).

Sparrowhawks prey mainly on passerine birds, and a large proportion of the nestling food in the study area consisted of small passerines weighing up to 100 g (Newton & Marquiss 1982; Bijlsma 1993). Main prey species were house sparrow (*Passer domesticus*, 22·3%), great tit (13·3%) and chaffinch (*Fringilla coelebs*, 8·5%); pied flycatcher, coal tit, blue tit respectively comprised 1·4, 1·3 and 3·2% of the summer diet (9233 prey items, 1974–2005; Rob G. Bijlsma, unpublished data). As date of the food peak for sparrowhawks, we calculated at what date the mass of all fledglings from the nest boxes peaked. For this we assumed that flycatchers fledged 14 days after hatching (Lundberg & Alatalo 1992), and for the tit species this was assumed to be 21 days. As fledgling mass, we took the averages for each species: blue tit: 11 g, coal tit: 9 g, great tit: 17 g and pied flycatcher: 14 g. The daily fledgling mass is thus the number of fledglings per species, times their mass, and this summed over all four species.

STATISTICAL ANALYSES

For all the phenological traits analysed, we give means and their standard deviations, and test whether the variances are equal across two trophic levels by a simple F-test for equality of variances (ratio of the variance of the trait with the higher variance over the trait with the smaller variance, (Sokal & Rohlf 1995)).

We analysed all time trends using simple linear regressions with year as explanatory variable, without taking temporal autocorrelation into account. This assumes that subsequent years are independent, which is partly not the case because the same individuals are sampled subsequently, and their response in one year may have consequences for the next year. This is especially true for leaf budburst, because the same individual trees were samples every year. There was no temporal autocorrelation in budburst between years ($r = 0{\cdot}075$, $n = 15$, $P = 0{\cdot}79$). For caterpillars, this is not a problem because they are annual species, and passerines and sparrowhawks are between these extremes. Our interest is mostly on how the phenology of one trophic level responds to the phenology of a subsequent trophic level, and we test whether responses are similar by analysing whether there is a correlation in phenology of the two levels, and whether the slope of this correlation differs from 1 (using linear regression models). This way, we test whether an advance of 1 day at one level results in an advance that is similar or not. Furthermore we tested for 1 year lagged responses of the underlying trophic level, but these were never statistically significant if the current year phenological state was included (all P-values > 0·23).

Results

MEANS AND VARIANCES

Over all the study years, budburst was on average at 30 April (SD 4·82), caterpillar peak date at 21 May (SD 6·80), and the date of peak needs for blue tit 23 May (SD 4·57), coal tit 14 May (SD 5·50), great tit 21 May (SD 4·22) and pied flycatcher 4 June (SD 4·23). The peak date of fledgling mass of the passerines was on average 6 June (SD 5·00) and the date of sparrowhawk peak needs was 20 June (SD 3·07). When comparing the between-year variances across trophic levels, budburst tends to have less variance than the caterpillar peak ($F_{16,19} = 1{\cdot}99$, $P = 0{\cdot}085$), whereas the caterpillar peak has clearly a larger variance than the passerines (comparisons with blue tit $F_{20,19} = 2{\cdot}22$, $P = 0{\cdot}043$, coal tit: $F_{20,19} = 1{\cdot}53$, $P = 0{\cdot}18$, great tit: $F_{20,19} = 2{\cdot}60$, $P = 0{\cdot}020$, pied flycatcher: $F_{19,19} = 2{\cdot}58$, $P = 0{\cdot}023$). Also the peak date in passerine fledging mass showed more between-year variance than the date of peak requirements of sparrowhawks ($F_{16,19} = 2{\cdot}65$, $P = 0{\cdot}027$). Our results of means and variance show in general that between-year phenological variance is smaller for predators than for their prey.

TEMPORAL TRENDS IN PHENOLOGY

Tree budburst advanced by 0·17 (SD 0·23) days per year since 1988, which was not statistically significant (Fig. 2a, linear

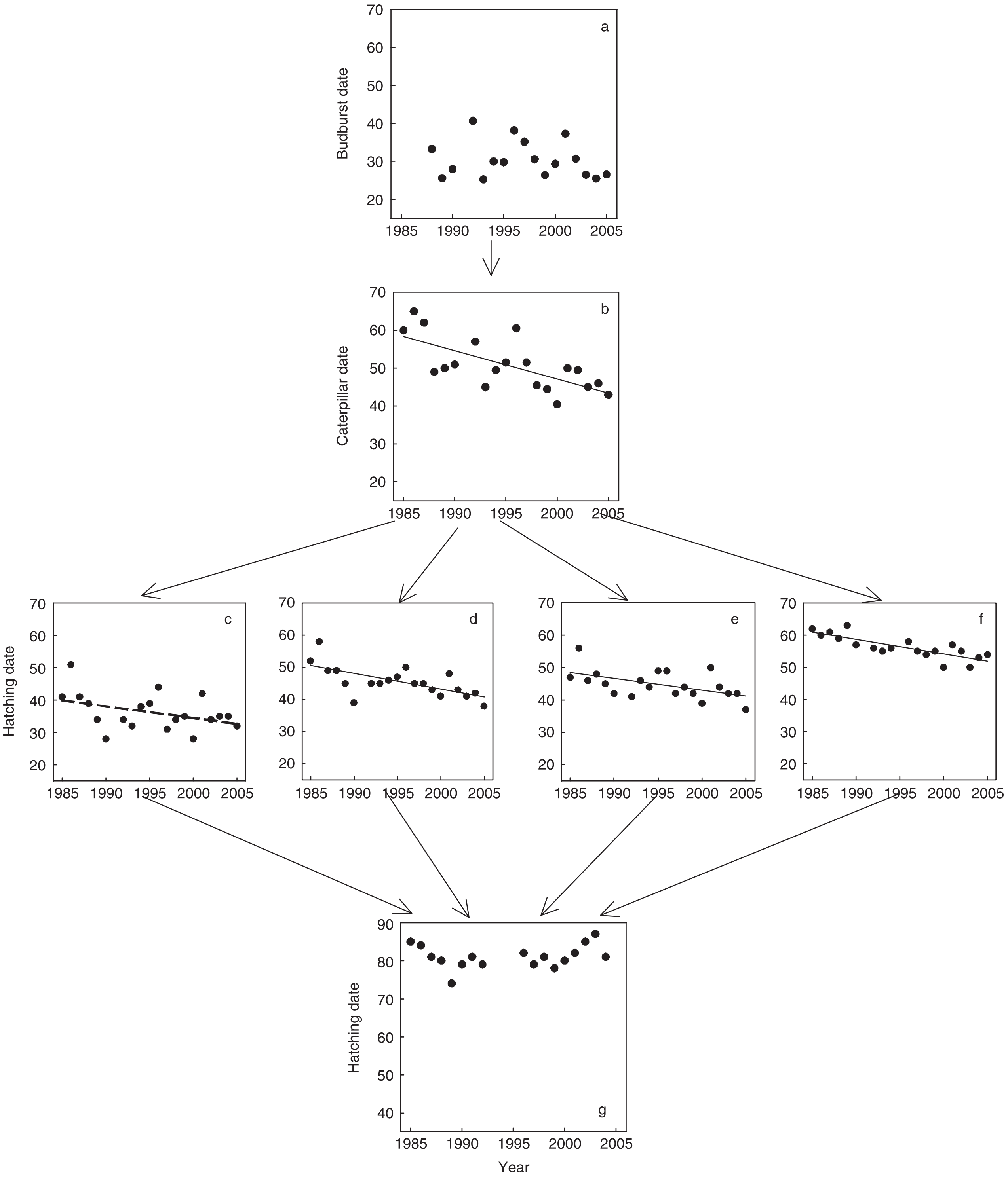

Fig. 2. Trends in annual budburst (a), caterpillar peak date (b), hatching dates of coal tits (c), blue tits (d), great tits (e), and pied flycatchers (f) and hatching dates of sparrowhawks (g) in the period 1985–2005 on the Veluwe area, The Netherlands.

regression: $F_{1,15} = 0{\cdot}54$, $P = 0{\cdot}47$). In contrast, the caterpillar peak advanced significantly by 0·75 (0·18) days per year between 1985 and 2005 (Fig. 2b, $F_{1,18} = 16{\cdot}42$, $P = 0{\cdot}0007$). The difference between the advance in budburst and caterpillar peak was partly due to the longer time series of the caterpillar peak, and the years 1985–87 were cold with late caterpillar peaks (see Fig. 2b). Restriction of the data to 1988–2005 for the caterpillar peak gave a trend of 0·42 (0·22) days per year advancement ($F_{1,15} = 3{\cdot}74$, $P = 0{\cdot}07$).

Annual mean hatching dates advanced for all four passerine species during 1985–2005 (Fig. 2c–f). The advance was for blue tits 0·48 (SE 0·13, $F_{1,19} = 13{\cdot}59$, $P = 0{\cdot}002$) days per

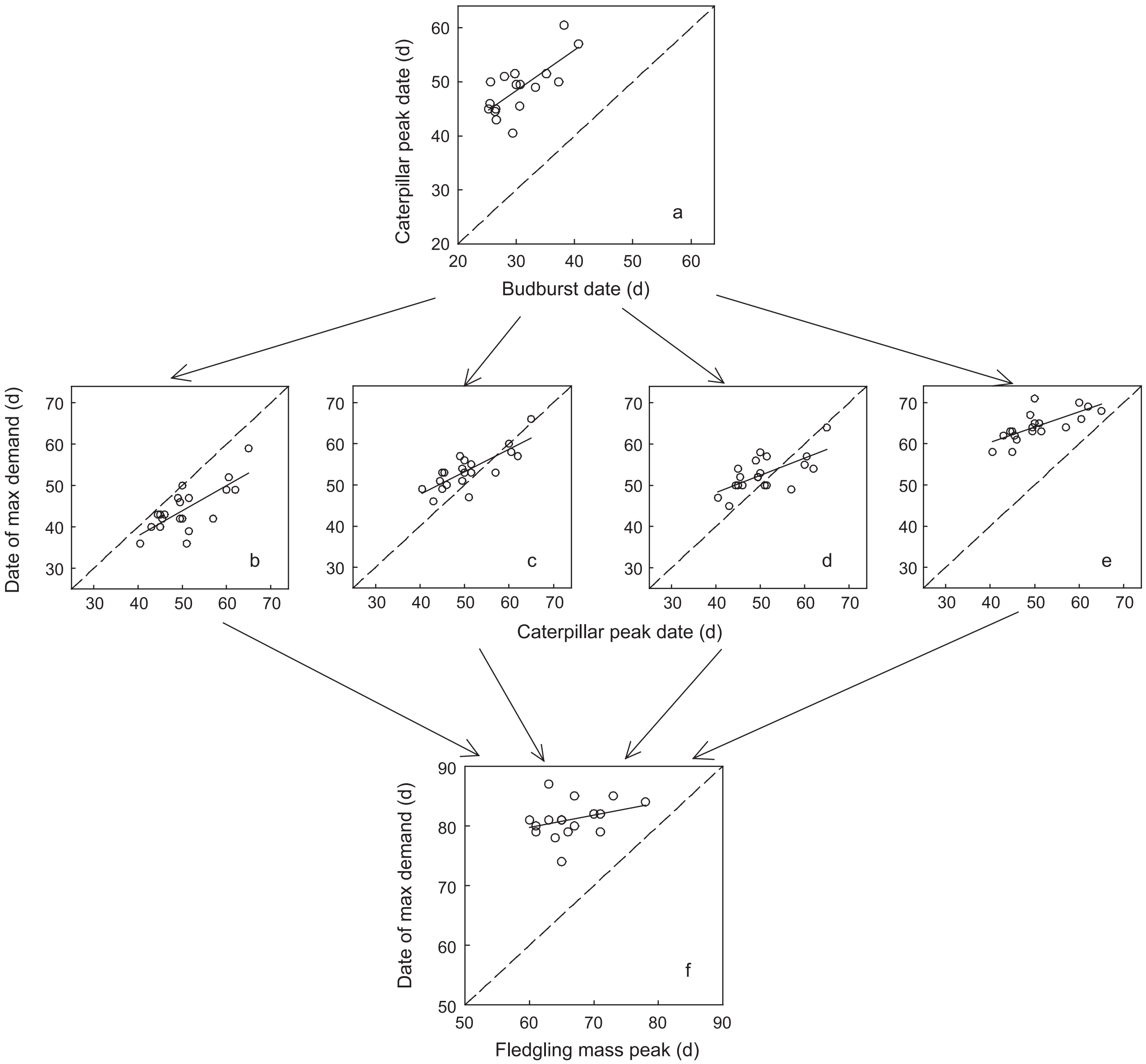

Fig. 3. Correlations between the annual timing of consumers and their food in a four-trophic-level forest system in The Netherlands. (a) caterpillars and bud oak budburst, (b) coal tit peak requirements and caterpillars, (c) blue tit peak requirements and caterpillars, (d) great tit peak requirements and caterpillars, (e) pied flycatcher peak requirements and caterpillars, (f) sparrowhawk peak requirements and passerine fledging.

year, for coal tits 0·36 (SE 0·19, $F_{1,19} = 2·88$, $P = 0·06$) days per year, for great tits 0·36 (SE 0·13, $F_{1,19} = 7·39$, $P = 0·014$) days per year, and for pied flycatchers 0·50 (SE 0·10, $F_{1,18} = 22·59$, $P = 0·0002$) days per year. Across species, we found no significant difference in advancement of hatching date over the years (interaction species*year: $F_{3,71} = 0·20$, $P = 0·89$), and the average advance for the four species was 0·42 (SE 0·07) days per year ($F_{1,74} = 35·71$, $P < 0·001$). Across tit species we found no significant difference in intercept in median hatching date, while pied flycatchers hatched on average 10·59 days later than the tit species.

We found no significant change in the hatching dates of sparrowhawks between 1985 and 2004 (slope: 0·091 (0·12), $F_{1,15} = 0·57$, $P = 0·46$).

PHENOLOGICAL CORRELATIONS ACROSS TROPHIC LEVELS

The caterpillar peak was positively correlated with the budburst (Fig. 3a), and 1 day later budburst resulted in a delay in caterpillar peak of 0·75 (SE 0·18) day ($F_{1,15} = 17·00$, $P = 0·0009$). This slope was not significantly different from unity ($t_{15} = -1·36$, $P = 0·19$).

Hatching dates of all passerine species were positively correlated with the caterpillar peak (Fig. 3b–e). The coal tit had its average time of peak requirements 6 days before the caterpillar peak, great and blue tits around the day of the caterpillar peak whereas the pied flycatcher peak requirements were 13 days later than the food peak (Fig. 4b). The slopes for

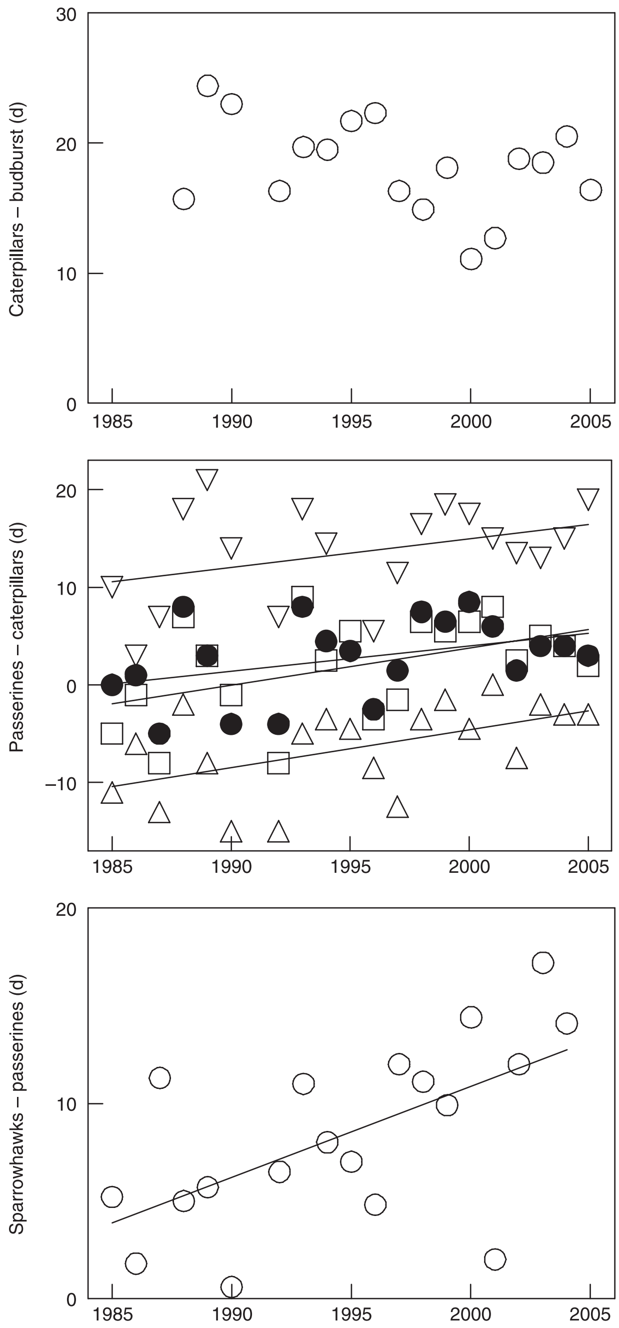

Fig. 4. Temporal trends in the match between the timing of consumers and their food in a four-trophic-level forest system in The Netherlands. (a) caterpillar peak date and budburst, (b) timing of maximum passerine nestling food demand and caterpillar peak date (downwards triangles: pied flycatchers, solid dots: great tits, squares: blue tits, upwards triangles: coal tits), (c) timing of maximum sparrowhawk nestling food demand and the peak in fledgling mass of four passerine species. The match is the difference in days between the time of maximum food demand of a consumer, and time of maximum availability of their food. Maximum passerine nestling food demand is assumed to be 8 days after hatching. Maximum sparrowhawk nestling food demand is assumed to be 45 days after the laying date.

the separate species were: blue tit 0·54 (0·10, $F_{1,18} = 18{\cdot}52$, $P = 0{\cdot}0005$); coal tit 0·61 (0·13, $F_{1,18} = 21{\cdot}15$, $P = 0{\cdot}0002$); great tit 0·42 (0·11, $F_{1,18} = 13{\cdot}71$, $P = 0{\cdot}002$); pied flycatcher 0·37 (0·09, $F_{1,17} = 18{\cdot}52$, $P = 0{\cdot}0005$). These slopes did not differ across species (interaction species×caterpillar peak $F_{3,71} = 1{\cdot}01$, $P = 0{\cdot}39$), and the average advance for the four species was 0·49 (SE 0·06) days per year ($F_{1,74} = 79{\cdot}25$, $P < 0{\cdot}001$). For each individual species, the response of hatching date to the caterpillar peak was different from unity (BT: $t_{17} = -4{\cdot}60$, $P = 0{\cdot}0003$, CT: $t_{17} = -3{\cdot}00$, $P = 0{\cdot}008$, GT: $t_{17} = -5{\cdot}27$, $P = 0{\cdot}00006$; PF: $t_{16} = -7{\cdot}00$, $P < 0{\cdot}00001$) and for all species simultaneously this was also the case ($t_{74} = -9{\cdot}35$, $P < 0{\cdot}00001$). Thus, each 1-day advance of the caterpillar peak resulted in an advance of the birds' hatching date of about half a day. The different species differed in whether they were timed best in years with early or late food peaks: coal tit peak demand dates were best timed with the caterpillar peak in early years, blue and great tits in average years and pied flycatchers in late years (Fig. 3b–e).

The date of sparrowhawk peak requirements was on average 15 days later than the peak in passerine fledgling mass, and we found no significant correlation between these variables [slope 0·21 (0·16) $F_{1,15} = 1{\cdot}72$, $P = 0{\cdot}21$].

In multiple repression models including both year and the timing of the higher trophic level, year did not explain a significant part of the variation (all $P > 0{\cdot}07$) or the interaction between year and the timing at the higher trophic level (all $P > 0{\cdot}25$) for all pairs of comparisons except for pied flycatchers, where year replaced the significance of the caterpillar peak date.

TEMPORAL CHANGES IN MATCH BETWEEN TROPHIC LEVELS

So far, we have shown that the advance over the years has been different across trophic levels, and that each 1-day advance at one trophic level is not fully matched by an equivalent advance at the higher trophic levels. Therefore, we want to explore whether the synchrony between trophic levels also has changed over time.

We found no significant change over the years in the interval between caterpillar peak date and oak budburst, although the interval tended to decline (Fig. 4a, slope: $F_{1,15} = 2{\cdot}32$, $P = 0{\cdot}15$). In contrast, in all four passerine species the interval between the date of maximal food requirements and the caterpillar peak increased over the two decades (Fig. 4b; blue tit 0·26 d yr^{-1} ($\text{SE} = 0{\cdot}15$, $F_{1,18} = 3{\cdot}14$, $P = 0{\cdot}093$); coal tit 0·39 (0·15, $F_{1,18} = 6{\cdot}80$, $P = 0{\cdot}018$); great tit 0·38 (0·17, $F_{1,18} = 4{\cdot}99$, $P = 0{\cdot}038$); pied flycatcher 0·30 (0·17, $F_{1,17} = 2{\cdot}84$, $P = 0{\cdot}11$)). For the coal tits, the match between food requirements and availability improved, from 10 days before the caterpillar peak to the maximal requirements exactly matching the caterpillar peak. For blue and great tits, there was a change from a match between maximal requirements and peak availability in 1985 to a mismatch of about 5 days in 2005. Pied flycatchers had their maximal requirements in 1985 about 10 days later than the food peak, and this mismatch increased to about 15 days in 2005. The largest change in mismatch was found in sparrowhawks, which had their peak in requirements about 10 days later than the peak date in fledging mass in 1985, and this mismatch increased to 20 days in 2004 [Fig. 4c: 0·49 (0·15) d yr^{-1}, $F_{1,18} = 9{\cdot}36$, $P = 0{\cdot}007$].

CHANGES IN HATCHING DISTRIBUTION OF PASSERINES

Apart from changes in the median hatching dates over time, and in relation to the food peak, the distribution of hatching dates may change. We tested this by comparing the difference in days between the 25th- and 75th- percentile of the distribution of hatching dates in great tits and pied flycatchers. For great tits the width of the distribution declined with the caterpillar peak, thus showing less variation in years with a late food peak [slope: –0·12 (0·05), $F_{1,18} = 6{\cdot}81$, $P = 0{\cdot}018$]. For flycatchers, the opposite trend was found: years with an early food peak showed less variation in hatching dates than years with a late food peak [slope: 0·11 (0·06), $F_{1,17} = 3{\cdot}30$, $P = 0{\cdot}09$], and slopes differed across species (species × peak date: $F_{1,35} = 9{\cdot}11$, $P = 0{\cdot}005$).

Discussion

We examined shifts in phenology across four levels in a food chain in temperate forests: oak budburst, caterpillars feeding on the oaks, passerines feeding on the caterpillars and sparrowhawks preying on the passerines. We showed that during the last 20 years, these different trophic levels have shifted their phenology to different magnitudes: we found no significant advance in budburst and sparrowhawk hatching dates, while both caterpillar peak biomass and passerine hatching dates advanced considerably. Interpretation of these shifts in phenology is only sensible if we consider how one trophic level shifts relative to both the phenology of food and predators. For passerines, we showed that all four species advanced less than their caterpillar prey, resulting in a change in the match between prey abundance and predator needs. The same was true for sparrowhawks and their passerine prey: a weaker response in the sparrowhawks resulting in a decreased synchrony between peak needs and prey abundance (see also Nielsen & Møller 2006). We found no evidence for such a change in match between caterpillar and tree phenology, which is most likely because our measure of caterpillar phenology is partly the consequence of their timing with budburst. Earlier work on budburst and egg hatching of winter moths (rather than their peak mass date) has indeed shown that climate change caused a mismatch between these two trophic levels as well (Visser & Holleman 2001; van Asch *et al.* 2007; van Asch & Visser 2007). Thus, for all three interactions between the phenological responses of predators and their prey, we found evidence for a decrease in synchrony over time, probably due to climate change. This change in synchrony may be due to constraints in adapting sufficiently, but may also be an adaptation to try to escape predation from higher trophic levels, and we discuss both possibilities below.

INSUFFICIENT RESPONSES IN ADAPTING PHENOLOGY TO FOOD PHENOLOGY

If the phenological trend over time of a lower trophic level is stronger than of its predator, it has most often been regarded as an insufficient response because the predators are constrained to respond (Visser, 2005; 1128/id). An alternative but not mutually exclusive explanation is that the costs of responding do not outweigh the benefits, and hence the lack of response is beneficial given the circumstances.

Information is an important constraint in adapting phenology to some moment in the future when food needs are high. Caterpillars develop in their eggs from December onwards, and have to hatch at the moment of budburst in April. Their advantage relative to the birds is that they can readily react to temperature changes, and their anticipation to this information gives them more flexibility to tune their phenology to their food. Passerines take about 30 days between the start of laying and the moment when most food is needed for nestlings (van Noordwijk & Müller 1994), and sparrowhawks take on average about 53 days (Newton 1986; Vedder *et al.* 2005). For the tits information on when the food peak will occur seems to be a clear constraint, and high temperatures after they have started egg laying do advance the caterpillar peak, and the tits have only limited possibility to speed up their hatching (Visser *et al.* 1998; Cresswell & McCleery 2003). This problem is emphasized by the differential warming over the season: early spring temperatures just before laying have not increased in the study area, while later spring temperatures after the birds started egg laying have increased (Visser *et al.* 1998). In contrast, flycatchers arrive in the second half of April from their wintering sites and lay in the second and third week of May, well after budburst and much closer to the caterpillar peak date. We do not expect that information during egg laying represents a constraint on adjusting adequately to the advanced caterpillar peak, but do consider arrival from the breeding grounds to be an important constraint (Both & Visser 2001). At their wintering grounds, they lack information on when spring starts at their breeding sites, and therefore they use day length variation to time their migration (Gwinner 1996), and indeed we see no change in arrival date during the last decades (Both & Visser 2001; Both, Bijlsma & Visser 2005; Hüppop & Winkel 2006; but see Jonzen *et al.* 2006). For sparrowhawks, the long period between hatching and the peak in food requirements makes it difficult to synchronize with their prey, which can be the reason why we did not find a correlation between the phenology of food and predator in this case. In all bird species, the lack of information most likely is an important constraint, explaining why they respond insufficiently to the phenological advance of the underlying level in the food chain.

Food availability during laying has been shown to be another constraint preventing birds from advancing their breeding phenology, especially if this early food source has advanced to a lesser extent than the nestling food phenology. Food supplementation in passerines gave mixed results on advances in breeding phenology, being most pronounced in circumstances with low natural food availability, supporting the constraint hypothesis (Nager, Rüeger & van Noordwijk 1997). Food supplementation in sparrowhawks resulted in a 5-day advance in laying date (Newton & Marquiss 1981). The support for the constraint hypothesis should be taken with care, because birds may in fact be able to advance their phenology, but refrain to do so because the costs are too high.

There are several candidate ultimate explanations why both tits and flycatchers have not fully adjusted their laying date to the advanced caterpillar phenology, and sparrowhawks not to the advanced passerine phenology. The first reason is that earlier laying (and arrival) may be costly in survival prospects for the female, and that this outweighs the benefits of a better match with the food peak. Because temperatures in early spring have not increased, an advance in laying date for the tits means that they lay at lower temperatures, which is at least energetically expensive (Stevenson & Bryant 2000). For the flycatchers, an advance in arrival means that they encounter lower temperatures upon arrival in the breeding area, which can impose high mortality costs in insectivorous birds (Møller 1994; Brown & Brown 2000). An additional explanation for tit species that produce facultative second broods (mainly coal and great tits) is a shift in balance between the fitness value of first and second broods when the caterpillar peak advances. When they produce a second brood these tits should time their first brood before the caterpillar peak, allowing them to profit also with their second brood from the food peak (Crick, Gibbons & Magrath 1993). If the value of the second brood declines, the laying date of the first brood can in principle be delayed relative to the date of the caterpillar peak, and therefore the response to the advancing caterpillar peak is less than unity (Visser *et al.* 2003). The possibility of producing a second brood could also explain why great tits reduce the variation in hatching dates in years with a late caterpillar peak, while the opposite trend was found for the flycatchers. In early years, the best quality birds start laying as soon as possible because this allows them to produce a second brood, whereas in late years hardly any bird produces a second brood, and there is no point in starting early. Flycatchers never start a second brood, and the low variation in early years is probably a direct consequence of all birds starting laying immediately after arrival at the breeding grounds.

ADAPTIVE RESPONSES TO ESCAPE PREDATION

The stronger response in phenology of prey relative to their predators can be a way to escape predation. Caterpillars thus may react more strongly than the passerines to prevent being consumed, and passerines may advance more strongly to escape predation from sparrowhawks. This is an alternative to our insufficient response hypothesis, but can also act additionally to that. We discuss the passerines and sparrowhawks here, but a similar reasoning can be applied to caterpillars as prey and passerines as predators. If passerines are more responsive than these predators, they may escape predation to a certain extent. This counts especially for early fledgings that have least overlap with the peak food requirements of the sparrowhawks (Gotmark 2002), leading to higher relative reproductive success of early vs. late breeders (Fig. 1c–d). The observed increased selection for early breeding (Visser *et al.* 1998; Both & Visser 2001) could be explained by this alternative hypothesis. Whether this hypothesis works depends to a large extent on how important differential predation is for fitness of the prey species, and whether the response of the higher trophic level is constrained. Estimates of the proportion of tit and flycatcher fledgings that are eaten by sparrowhawks are between four percent (Bijlsma 1993) and nine percent (Gotmark 2002), suggesting that these selection pressures are of minor importance. Sparrowhawks are however not the only predators of passerine fledglings (Naef-Danzer *et al.* 2001), and these other predators together had a large impact on overall survival. If these predators also have advanced their phenology less than the prey, and predation equally depends on their phenology relative to the phenology of the passerines, they will impart an important selection pressure on the passerines to breed earlier.

The escaping-predation hypothesis and the insufficient-adjustment hypothesis are not mutually exclusive: selection promotes advanced breeding because the earliest birds are best synchronized with the food, and these birds are also favoured because of reduced fledging predation. The predation hypothesis is consistent with the increased selection for early breeding in The Netherlands, but not with the decreased selection for early breeding in the UK (Cresswell & McCleery 2003), although we do not know whether sparrowhawks in the UK have advanced their breeding phenology. The escaping predation hypothesis still requires a constrained (and hence insufficient) response at the higher trophic level, and hence cannot stand on its own at all trophic levels. The relative contribution of both hypotheses in causing phenology to advance, and selection on advanced phenology to increase, could be made when the relative contribution of both selection pressures on fitness is assessed. If the passerines would indeed escape predation, without compromising their reproductive success as a result of a greater mismatch with their own prey, we may expect their population size to increase. For the pied flycatcher this was not the case: populations in areas with the greatest mismatch declined most strongly (Both *et al.* 2006), suggesting that at least for this species the selection pressure from the timing with food was more important than from the timing with the predators.

So far, selection from food and predators was assumed to be both for early breeding phenology, but we want to point out that both selection pressures could also work in opposite directions. For this, we concentrate again on passerines and hawks. It is possible that predation depends not only on the relative overlap between mean predator and prey phenology, but also on the frequency distribution of both. For prey it has been shown to be of great importance to appear in synchrony with others to reduce overall predation rates (Emlen & Demong 1975) and hence passerines may fledge preferentially at the same time to reduce fledgling predation by sparrowhawks and other predators. Individuals that breed early thus enhance the predation rates on their offspring. Although at that time, most sparrowhawks have not reached peak requirements, the few available fledgling passerines may be easily caught. This process hampers an evolutionary response to advanced breeding and remaining in synchrony with the caterpillars (see also Reed *et al.* 2006), because genotypes with an early phenology are selected against because they differ from the rest of the population. Consideration of selection by both the lower and the higher trophic level thus gives new insights in why birds do or do not adjust to advances in other levels of the food chain.

SINGLE FOOD SOURCE VERSUS MULTIPLE FOOD SOURCES

We simplified the food chain to a large extent by assuming that each predator is consuming one major food type. This is evidently not true, and the degree of specialization declines at higher trophic levels: caterpillars can only forage on one tree, passerines can forage on caterpillars and other prey, and sparrowhawks have an even larger prey repertoire. Our food peak for sparrowhawks consists of only a limited portion of their diet (about 20%), and inclusion of more species may give a better fit between sparrowhawk and prey phenology. However, Nielsen & Møller (2006) included more prey species, and came to a very similar conclusion: sparrowhawks showed no advance in hatching, whereas their prey did. In our study area, the important prey species outside forested areas (house sparrow, starling) have their fledglings from the third week of May and if sparrowhawks were to rely mostly on those for raising offspring, they should time their reproduction considerably earlier than we observed. Furthermore, poor food forests where breeding sparrowhawks have to rely on farmland birds for food are unfavoured localities at which sparrowhawks perform less well compared to sparrowhawks in prey rich forests (van den Burg 2002), underlining the importance of the forest habitat and its bird community for successful reproduction. As forests are characterized by a short period of insect availability in spring and most passerines breed at this time, we expect that the peak in fledgling availability of our hole nesting species will mirror that of the whole insectivorous bird community. However, the food peak is certainly broader for sparrowhawks than for passerines, because young passerines are available for a longer period of time, and a long tail may occur at later dates from the species producing second broods and repeat layings. Predicting the effects of climate change on changes in phenology thus also should take into account alternative prey.

CONCLUDING REMARKS

In general, we saw that for each trophic level the phenology responded to a different degree than that of the underlying trophic level on which it depends. Caterpillars respond more strongly than the oaks (Visser & Holleman 2001), passerines less than the caterpillars, and sparrowhawks less than the passerines. We contend that some of these apparently insufficient responses are due to a lack of predictability. The general problem is that the organism reacts to the environment of decision making, which is temporally separated from the environment of selection (van Noordwijk & Müller 1994), that is, 30 days for our passerines (lay date versus peak food demand) and 53 days for sparrowhawks. For each trophic level, both the time-lag and the ability to respond differ: for caterpillars it is important to hatch at about the time of budburst, and their time-lag is therefore short. Also, their ability to respond is probably very high, because at higher temperatures they can grow faster, and keep pace with the bud burst. For passerines, the time lag is larger and the ability to respond lower, and for sparrowhawks this is even more extreme. It is probably not that just each higher trophic level will get a larger mismatch with the underlying level, because avian parasites, such as fleas or blowflies, may show a strong response and may react appropriately (or too strongly?) when temperatures increase. We hypothesize that larger animals that take more time from the environment of decision making to the environment of selection will be most vulnerable, because they will have least flexibility to respond to climate change. These differential responses across trophic levels may impact on ecosystem functioning, because predators at higher trophic levels may decline most strongly because of the asynchrony with the phenology of their prey.

Finally, our analyses suggest that a differential response at the lower trophic level may be partly a solution to prevent being eaten by the higher trophic level. In principle, caterpillars could respond more strongly than the oaks, because it is advantageous to create a mismatch with the birds and in this way, they escape being eaten. For each organism, there is selection both from the lower trophic level (synchrony with its food) as well as from the higher trophic level (synchrony with its predators), and so far we have ignored the latter, and the relative strengths of these selection pressures should be known for a full understanding of whether differential responses at different trophic levels are indeed a proper adaptive response to climate change.

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