The relevance of food peak architecture in trophic interactions

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Abstract

Phenological shifts and associated changes in the temporal match between trophic levels have been a major focus of the study of ecological consequences of climate change. Previously, the food peak has been thought to respond as an entity to warming temperatures. However, food peak architecture, that is, timings and abundances of prey species and the level of synchrony between them, determines the timing and shape of the food peak. We demonstrate this with a case example of three passerine prey species and their predator. We explored temporal trends in the timing, height, width, and peakedness of prey availabilities and explained their variation with food peak architecture and ambient temperatures of prebreeding and breeding seasons. We found a temporal match between the predator's breeding schedule and food availability. Temporal trends in the timing of the food peak or in the synchrony between the prey species were not found. However, the food peak has become wider and more peaked over time. With more peaked food availabilities, predator's breeding success will depend more on the temporal match between its breeding schedule and the food peak, ultimately affecting the timing of breeding in the predator population. The height and width of the food peak depended on the abundances and breeding season lengths of individual prey species and their reciprocal synchronies. Peakednesses of separate prey species' availability distributions alone explained the peakedness of the food peak. Timing and quantity of food production were associated with temperatures of various time periods with variable relevance in different prey species. Alternating abundances of early and late breeding prey species caused high annual fluctuation in the timing of the food peak. Interestingly, the food peak may become later even when prey species' schedules are advanced. Climate warming can thus produce unexpected changes in the food availabilities, intervening in trophic interactions.

Keywords: Accipiter nisus, climate change, *Cyanistes caeruleus*, *Parus major*, phenology, *Poecile montanus*, synchrony, trophic match/mismatch

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Introduction

Ecological consequences of climate change include phenological shifts and associated changes in the temporal match between trophic levels (e.g., Visser *et al.*, 1998; Durant *et al.*, 2007; Both *et al.*, 2009; Dunn & Møller, 2014; Johansson *et al.*, 2014) in addition to range shifts (e.g., Parmesan & Yohe, 2003) and changes in migratory behavior (Knudsen *et al.*, 2011). The temporal match/mismatch of a predator and its prey is an important consideration, as the food availability during the critical reproductive period (e.g., the time of the highest food needs of the young) can substantially affect predator fecundity (Durant *et al.*, 2007). On the other hand, the prey might benefit from timing its most vulnerable life stage in a period of low predation pressure (Both *et al.*, 2009). Thus, the temporal match/mismatch can affect the population dynamics of both the predator and the prey.

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A premise for the relevance of the temporal match/mismatch is that the prey availability is peaked (Durant *et al.*, 2007; Dunn *et al.*, 2011), in many cases caused by a reproductive surge of the prey population. Outside this period, the prey are fewer in numbers or more difficult to catch. For a predator, a certain type of prey can be considered as 'optimal food': abundantly available, easily catchable, of the right size, and rich in energy and nutrients. For example, insect caterpillars are considered the optimal food for feeding the nestlings of parids (Paridae; Naef-Daenzer & Keller, 1999) although they commonly use other types of food (e.g., seeds; del Hoyo *et al.*, 2007) as well. Sometimes it is presumed that the predator's diet consists largely of only one prey species. For example, Cresswell & McCleery (2003) suppose that great tits *Parus major* feed their nestlings with larvae of winter moth *Oeropthera brumata* (but see Nour *et al.*, 1998). However, the majority of predators are not strict specialists, but utilize many prey species.

We suggest that the phenologies and abundances of each prey species together determine the timing and

shape of the food peak (Fig. 1). High level of synchrony between the abundance peaks of prey species will lead to a high, peaked total food peak, whereas an intermediate level of synchrony will cause a flatter food availability distribution even if the abundances of individual prey species would be similar (Fig. 1a, b). With low levels of synchrony, multimodal food peaks will occur. It may be that one (or more) prey species play a larger role in determining the timing and shape of the food peak than the others (Fig. 1c)—such species can be considered as principal prey (like the winter moth for the great tit in Cresswell & McCleery, 2003).

In previous studies, the effect of warming spring temperatures on food availability has been considered as a bulk effect: the food peak has been thought to react as a single entity (e.g., Visser *et al.*, 1998; Both *et al.*, 2009; Vatka *et al.*, 2014), and often only the change in the timing, not in shape, of the food peak is considered (but see Visser *et al.*, 2006). We stress that the architecture of the food peak—that is, the number of species and changes in the phenology and abundance of each prey species—can play an important role in timing and shape of the food availability distribution. This novel viewpoint will improve our understanding about multitrophic interactions and populations' responses to environmental changes.

We demonstrate this idea with a case example using real data from three passerine prey species: the willow tit (*Poecile montanus*), the blue tit (*Cyanistes caeruleus*), and the great tit. They, among other species, are depredated by the sparrowhawk (*Accipiter nisus*). In Finland, the blue tit and the great tit are the two most susceptible prey species to the sparrowhawk and also willow tits seem to be preyed upon more frequently than expected of their abundance (Appendix 1 in Møller *et al.*, 2012). In particular, newly fledged young can be considered as optimal prey as they are temporarily abundant, defenseless, and easy to find due to loud begging calls (Newton, 1986). Small passerines are small enough for the male sparrowhawk to catch, and thus, they are an important food resource during the period when the female sits on the nest, brooding the young (the first 2 weeks after hatching; the male sparrowhawk is smaller than the female; Newton, 1986). The sparrowhawk has advanced its breeding on average by 0.18 days per year since the 1970s in Finland (Lehikoinen *et al.*, 2010).

The climate change-driven temporal changes in the timing of breeding have been unequal in the study populations of the three passerine prey species in Oulu, Finland: willow tits and great tits have advanced their breeding but blue tits have not (Vatka *et al.*, 2011, 2014). In addition, the prey species differ in the way their fledgling production (size and number of fledged young) responds to the temporal match with their main food resource, the insect caterpillars (Vatka *et al.*, 2014). Fledgling production of a prey population may be constrained by temperatures in different stages of the (pre-)breeding season, for example, by affecting the number of breeding pairs, clutch size, and/or nestling mortality rate. It is possible that the timing and abundance of the food produced by the individual prey populations do not respond similarly to changing climate, changing the synchrony level between the prey species and affecting the timing and shape of the total food peak (Fig. 1).

In this study, we demonstrate the importance of food peak architecture with a simplified example involving three tit populations and their sparrowhawk predator. We will explore temporal trends in the timing and shape of the prey abundance peak regarding both the total food peak and its components, individual prey species, and link variation in the timing and shape of food availability distributions to annual temperature fluctuations of various parts of the (pre)breeding cycle. We will study how food peak attributes are affected by its architecture by testing the hypothesis that synchrony between the prey species affects the food peak shape (height, width, peakedness) and by identifying the most abundant prey species. In addition, we will investigate if the temporal match between the predator's breeding schedule and the food availability produced by the parids has changed. However, this work does
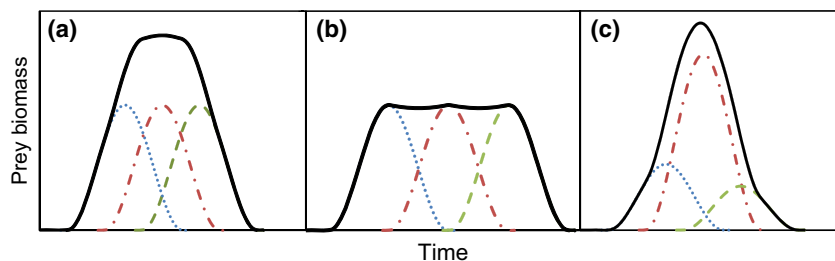

Fig. 1 Hypothetical temporal distributions of three prey species (dotted, dash-dotted, and dashed lines) and their total amount (solid line). Different amounts of synchrony among the prey species constitute dissimilar heights of the total prey peak (a, b). Subplot (c) describes a situation where one of the prey species has more influence on the total prey availability than the others.

not intend to describe the whole food availability for the sparrowhawk (that involves many other even more prominent prey species) or the actual temporal match/mismatch.

Material and methods

Data collection, study area

Data on the prey species were gathered in 2000–2014 from the Oulu study area in northern Finland (65°5′N, 25°33′E; ca. 27 km^2), consisting of commercial coniferous, deciduous, and mixed forests of varying ages (Orell & Ojanen, 1983a,b; Rytkönen & Orell, 2001). The area contains clusters of nest boxes for great tits (ca. 300–400 boxes) and blue tits (ca. 100 boxes) (Vatka et al., 2014). Willow tit nests, excavated in standing rotten trees, were located each spring (Orell & Ojanen, 1983a).

The nests of willow tits, blue tits, and great tits were routinely visited to determine the 1st egg day (the day of laying the first egg), the clutch size, the hatching day, and the number of fledged young (for more details about the field methods, see Orell & Ojanen, 1983a,b,c). The young were weighed to the nearest 0.1 g when ringed at the age of 13–15 days. Nestling mass measured at this age is a good estimate for the mass of fledging young (Orell, 1983). The fledging day was estimated as the hatching day + 18 days (the average length of the nestling period, see Orell & Ojanen, 1983b,c; del Hoyo et al., 2007).

Definition of food availability

The observed availability of easy food for the sparrowhawk was defined as the daily biomass of parid fledglings (grams per square kilometer) that have left the nest a maximum of 5 days earlier. The fledglings have the highest risk of being predated by the sparrowhawk during the first 5 days after leaving the nest (Perrins & Geer, 1980). Nest-specific information about the mass and number of fledged young was utilized from 1227 nests of willow tits, 436 of blue tits, and 1549 of great tits in total from 15 years (for annual sample sizes, see Table S1). The fledgling masses (using measures on ringing day) for nests with the same fledging day, and further, for sliding 5-day periods were summed up. The fledgling availabilities were estimated for each prey species separately, and their sum calculated, hereafter referred as the sum peak.

In addition to the observed food availability, the expected biomasses of fledglings that would occur if all the eggs in completed clutches produced average sized fledglings were predicted. As the average mass of a fledgling 11.0, 10.4, and 16.0 g were used for the willow tit, the blue tit, and the great tit, respectively. Here, the expected fledging date was calculated as 1st egg date + clutch size + 14 (incubation period) + 18 (nestling period). The expected fledgling availability reflects a situation that would occur if the timing of the food availability was solely determined by the realized timing and quantity of egg laying of the prey populations in their current sizes,

capturing synchrony of the onset of breeding and primary investment in reproduction (clutch size). Thus, it disregards the effect of unequal nesting success rates (caused by timing-related effects, including temporal match/mismatch with the lower trophic level, the insect caterpillars, see Vatka et al., 2014).

Describing the timing and shape of the food peak

For each study year, the data form a matrix with two columns: the first presents the day and the second the mass of fledglings available that day. To describe the shape of the food peak, the data matrix was transformed into a vector of 'unit days'. Here, the 'unit' was defined to be gram per km^2. It is important to determine the unit to be fine-scaled enough to avoid distorting rounding error—for example, for the biomass of insect larvae milligrams could be a preferable unit instead of grams. If the food availability for day '1' is two units, the vector will contain the unit day '1' twice; if the day '2' has 4 g/km^2 of fledglings, the unit day '2' is repeated four times, and so forth.

$$\begin{bmatrix} 1 & 2 \\ 2 & 4 \\ 3 & 3 \end{bmatrix} \rightarrow \begin{bmatrix} 1 & 1 & 2 & 2 & 2 & 2 & 3 & 3 & 3 \end{bmatrix}$$

So, a vector similar to a frequency distribution was generated, which mode (Mo) describes the timing of the food peak (mode instead of mean or median was used as the food peaks can be multimodal). The amount of year-to-year variation in the timing of the food peak was determined as the variance of annual modes. Measures of the shape of the food availability distribution were defined as follows: peak height as the maximum frequency value (i.e., the highest fledgling mass per day for a given year), variance of the frequency distribution vector ($\sigma^2 = \frac{1}{n}\sum_{i=1}^{n}(x_i - \mu)^2$) to represent the width, and kurtosis ($\gamma_2 = \mu_4/\mu_2^2 - 3$) to describe the peakedness or flatness as well as the uni-/multimodality (for unimodal distributions $\gamma_2 > 3$) of the food peak. Variance (σ^2) and kurtosis (γ_2) are both affected by the breeding season length, that is, the temporal spread in the emergence of parid nestings and thus the fledging dates. These parameters were calculated for each prey species as well as for the sum peak, for both the observed and expected fledgling availabilities. The prey species with the highest peak was determined as the most abundant prey of that year.

Temporal trends and model diagnostics

To study temporal trends in the timing and shape of the food peak, linear models were used to regress the statistics (Mo, peak height, σ^2, and γ_2) against the year using function 'lm' (library 'stats') in program R (R Development Core Team, 2011). This was carried out for the sum food peak and for each prey species separately, for both the observed and expected fledgling availabilities. In addition, we determined the pairwise degrees of synchrony between the prey species as the absolute value of the difference of modes of two prey species (variables are named 'asynchrony (prey A, prey B)' as 0 denotes perfect synchrony and larger values lower level of

synchrony), and tested for temporal changes. We fitted only linear trends, as the number of years ($N = 15$) is not sufficient for testing curvilinear changes although they would be equally sensible.

For each regression model fitted, the influence of individual data points was tested with Cook's distance diagnostics. Data points with Cook's distance values higher than 1 were determined to have high influence on the model parameter estimates. The model was re-fitted by down-weighting the highly influential data points with $w = 0.5$ (or with $w = 0.4$ if still highly influential; for other data points $w = 1$). Such weighting was used when testing temporal trends in the kurtosis of the expected willow tit peak (for observation from 2012) and the observed asynchrony (blue tit, great tit) (for observation from 2000).

For further model diagnostics, temporal autocorrelation (ρ) was inspected for lags of 1–8 years with Durbin-Watson test (d) using function 'durbinWatsonTest' in library 'car' (Fox & Weisberg, 2011). Strong ($|\rho| \geq 0.6$) and significant ($P \leq 0.05$) autocorrelations indicate the violation of the model assumption of independent residuals, reducing the reliability of parameter estimates. This was the case for the observed annual modes of the blue tit ($\rho_{lag=1} = -0.631$, $d = 3.213$, $P = 0.012$), the expected annual modes of the willow tit ($\rho_{lag=1} = -0.618$, $P = 0.030$), and the observed peak height of the willow tit ($\rho_{lag=3} = -0.674$, $d = 3.140$, $P = 0.006$). The models were not corrected for negative autocorrelations because no plausible ecological explanations for them were found.

Inspecting effects of ambient temperature on the timing and shape of the food peak

The relationships were studied between variables describing the timing and shape of food availability (Mo, height, σ^2, γ_2) and ambient temperatures of different parts of prey species' prebreeding and breeding seasons. The food peak attributes may respond to temperature changes even if temporal trends are not yet to be found. In addition, in different prey species temperatures of different parts of the (pre)breeding seasons can have the strongest effects on fledgling production. To discover these periods, average temperatures for time periods of varying lengths (from 10 to 212 days at 1-day intervals) in January–July were calculated and Pearson's correlation coefficients with the variables derived. Periods with the strongest correlations were selected (only strong correlations with $|r_P| > 0.6$ are interpreted), and effects of temperature changes on variables determined with linear regression models. However, even the strongest correlations cannot be taken as strict evidence for causal relationships of temperature effects without knowledge of sensible causal mechanisms. Thus, potential mechanisms through which the temperatures could affect the timing and the abundance of parid prey were investigated in an additional analysis, presented in Appendix S1.

Temporal trends in temperature were inspected with linear models using year as an explanatory variable. For the effect of temperature change on sum peak's height a data point from 2006 was down-weighted with $w = 0.4$, and on great tit's kurtosis with $w = 0.5$. Data of daily mean ambient temperatures are available from the Finnish Meteorological Institute, Oulunsalo observatory, 20 km S of the study area.

Explaining the shape of the food peak with its architecture

The shape (height, variance, and kurtosis) of the sum peak was analyzed with linear models, using corresponding shape measures for each prey species and degrees of synchrony between the prey species as explanatory variables. There were no strong correlations between the explanatory variables ($|r_P| < 0.6$). Model sets containing all combinations of the explanatory variables were built (function 'dredge' in library 'MuMIn'; Bartón, 2011), and the best model(s) were selected according to AICc values (ΔAICc ≤ 2). If more than one model was selected, model averaging was performed with function 'model.avg' in library 'MuMIn', by the natural averaging method (Burnham & Anderson, 2002). The statistical significance (P-values) of parameter estimates from models with multiple explanatory variables need to be interpreted with caution, as these models may be over-fitted due to a low number of observations ($N_{years} = 15$).

Temporal match/mismatch between the food peak and breeding of the predator

The data on the timing of breeding included 203 sparrowhawk nests from Yli-Ii area, located ca. 40 km northward from the Oulu study area, in 2000–2012. The hatching dates were derived either by direct information on the breeding timetable (onset of laying and hatching) or from the age of the oldest chick at the date of ringing. The chick age, measured in numbers of days since hatching, was estimated by comparing the length of the chick's wing with a known growth curve (own unpublished data), or when this information was lacking by the general size and behavior of the young (fleeing ability etc.). A comparison of annual average timing of breeding in Yli-Ii and Oulu areas (data from 1993–1999, $N_{Yli-Ii} = 117$ and $N_{Oulu} = 42$ nests) revealed that sparrowhawks in Oulu area breed consistently on average 4.5 days earlier. This difference was accounted for when comparing the phenologies of the sparrowhawk and its prey by estimating annual median sparrowhawk hatching days in Oulu area by subtracting 4.5 days from Yli-Ii annual median hatching days.

The temporal match/mismatch between the total food availability peak and the sparrowhawk's breeding was inspected by setting the time windows when 75% of the parid fledglings are available against the median timing of the nestling period of the sparrowhawk for each year. In a good match, the food availability peak occurs during the first half of the nestling period.

Results

Temporal trends in the timing and shape of the food peak

The timing of the observed parid fledgling availability (i.e., the peak of 'easy food') shows no linear temporal

trends in 2000–2014, neither when regarding the mode values of the sum peak nor any of the three prey species (Fig. 2a, Table 1). However, when considering the expected fledgling availability (i.e., the food peaks that would occur if all the eggs laid produced fledglings), the sum peak has become significantly later (Fig. 2b, Table 1).

The observed peak height of the total parid fledgling availability distribution shows no temporal trends, nor do the peak heights of the great tit or the blue tit fledgling availabilities. Instead, the observed and expected willow tit peaks have become lower during 2000–2014 (Fig. 2c, d Table 1). The height of the expected great tit peak has increased, indicating that nowadays the great tit population produces more eggs than before. Willow tits and great tits have by turns been the most abundant prey (Fig. 2c).

The variances representing the width of the observed and expected sum peaks, great tit fledgling availability distribution and the expected willow tit fledgling availability distribution have increased (Table 1, Fig. S1a, b). However, the increase in variance for the great tit that also affects the sum peak may be an artifact arising from a low search effort for late great tit nests (i.e., re-nesting attempts and second clutches) in the early years of the study (2000–2005). Although only a handful of late nests per year are potentially missing, the early years can hence have inaccurately small variance values. If the fledgling production of the first clutches (that have been searched for with similar efforts throughout the study) is considered, variances of the observed great tit peaks show no temporal trend ($b = 0.091$, SE = 0.473, $P = 0.850$). Yet, the results for the willow tit have not been contorted by such an artifact, implying that the breeding season of the prey species has indeed become longer.

The observed sum peak and the observed blue tit fledgling availability peak have become more peaked over the study period, indicated by increased kurtosis values (Table 1, Fig. S1c). Concerning the expected food availabilities, corresponding increases in peakedness are found in the blue tit and the great tit (Table 1, Fig S1d).

Synchronies between the prey species did not show any temporal trends [asynchrony (willow tit, blue tit): $b = 0.107$, SE = 0.152, $P = 0.492$; asynchrony (willow tit, great tit): $b = 0.071$, SE = 0.134, $P = 0.603$; asynchrony (great tit, blue tit): $b = 0.107$, SE = 0.128, $P = 0.421$] although there was substantial year-to-year variation. For example, the willow tit and the great tit peaks occurred from 5 to 12 days apart.
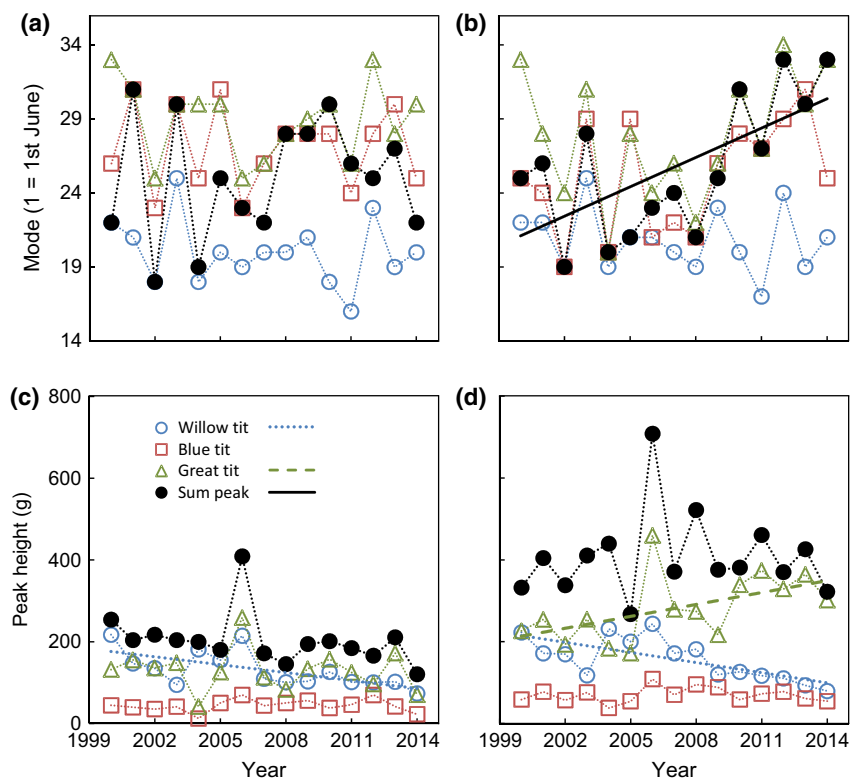

Fig. 2 Temporal variation in the timing of the (a) observed and (b) expected parid fledgling availabilities that would occur if all the eggs in completed clutches produced average sized fledglings, and in the height of the (c) observed and (d) expected availability peaks in Oulu, Finland. For the parameter estimates of the regression lines, see Table 1.

Table 1 Temporal trends in the timing and shape of the parid fledgling availabilities of the sum peak and of each individual prey species, for both the observed prey availabilities and the expected availability distributions that would occur if all the eggs in completed clutches produced average sized fledglings. Mode describes the timing of the highest prey availability peak. Peak height is the highest annual value of fledgling mass per a day. Variance describes the amount of temporal spread in the annual fledgling availability distribution and kurtosis its peakedness. Statistically significant trends ($P < 0.05$) are indicated with bold lettering

Variable (unit)	Observed				Expected			
	Sum peak	Willow tit	Blue tit	Great tit	Sum peak	Willow tit	Blue tit	Great tit
Mode (days)								
b	0.139	−0.121	−0.014*	−0.050	**0.661**	−0.096*	0.364	0.261
SE	0.246	0.135	0.170	0.159	**0.217**	0.130	0.212	0.251
P	0.580	0.383	0.934	0.758	**0.009**	0.472	0.110	0.318
Peak height (g/km²)								
b	−5.232	**−6.451***	0.427	−1.541	0.986	**−8.251**	0.295	**9.690**
SE	3.748	**2.072**	0.927	3.088	6.404	**2.289**	1.127	**4.227**
P	0.186	**0.008**	0.653	0.626	0.880	**0.003**	0.798	**0.039**
Variance								
b	**3.915**	0.927	1.262	**5.828**	**2.896**	**1.607**	1.407	**2.101**
SE	**1.375**	0.430	0.906	**2.075**	**0.871**	**0.549**	0.888	**0.876**
P	**0.014**	0.050	0.187	**0.015**	**0.005**	**0.012**	0.137	**0.032**
Kurtosis								
b	**0.475**	0.191	**0.545**	0.554	0.360	0.204†	**0.293**	**0.774**
SE	**0.217**	0.279	**0.203**	0.461	0.203	0.210	**0.125**	**0.336**
P	**0.048**	0.506	**0.019**	0.251	0.099	0.350	**0.036**	**0.038**

*Strong autocorrelation interferes parameter interpretation, see Methods.
†A lower weight was given to one of the years due to a model diagnostic issue, see Methods.

Relationships with ambient temperature

Average temperatures of varying parts of the prebreeding and breeding seasons explained timing and some of the variables describing the shape of the food availability peak (Table 2). Timing of the food peak is earlier in warm years than in cold ones. Timings of the sum peak and the blue tit fledgling availability peak are mostly affected by temperatures of prebreeding period, when willow tits and great tits seem to respond to a longer temperature period, extending to the nestling period.

Height of the willow tit fledgling availability peak is negatively correlated with early spring temperatures (from the end of February to the beginning of March), peaks being lower after warm early springs (Table 2). Early spring temperatures have negative associations with the number of breeding pairs in willow tits (Appendix S1). Blue tit peak height seem to be similarly affected with temperatures in April (which correlate negatively with the number of breeding pairs, Appendix S1), but for great tits warm temperatures during the nestling period in June–July are associated with increases in peak height, likely due to an increase in nestling survival rate (Appendix S1).

Variance of willow tit fledgling availability distribution is negatively related to prebreeding temperatures (Table 2). In warm springs, there is less variation in the

onset of breeding in the willow tit, decreasing the width of the fledgling availability peak (Appendix S1). Blue tit fledgling availabilities are less peaked in warm summers, indicated by negative parameter estimates for kurtosis. Instead, warm springs lead to more peaked distributions of great tit fledglings, which is also reflected in the peakedness of the sum peak. Great tits seem to breed in greater numbers when springs (April–May) are warm, increasing the peakedness of the fledgling production peak (Appendix S1).

No fixed temperature period correlates strongly ($r_P > 0.6$) with variances of the sum peak, blue tits or great tits, or with kurtosis of the willow tit peak. None of the best correlating temperature periods show statistically significant temporal trends of warming or cooling during the study years ($P > 0.05$ in all cases).

The effects of food peak architecture on its timing and shape

The timing of the sum peak shows pronounced year-to-year variation, mode values range from 18th to 31st July (Fig. 2a; $s^2 = 14.996$). In comparison with the individual prey species, the variation in the timing of the sum peak is significantly higher than in the willow tit fledgling availability ($s^2 = 4.667$, $F = 3.213$, $p_{1\text{-tailed}} = 0.018$) and nonsignificantly higher than in the

Table 2 Periods with the highest correlations ($|r_P > 0.6|$) between the average temperature and variables describing timing and shape of the food peak, their responses to temperature change of that period and coefficients of determination (R^2)

Variable (unit)	Temperature period	Response to temperature change (units/°C)	R^2	Breeding cycle period
Mode (days)				
Sum peak	19 March – 9 May	−3.101	0.705	Prebreeding –egg laying
Willow tit	31 March – 16 June	−1.890	0.562	Prebreeding –nestling
Blue tit	10 April – 2 May	−2.387	0.710	Prebreeding
Great tit	28 March – 24 June	−2.301	0.475	Prebreeding –nestling
Peak height (g/km²)				
Sum peak	2 March – 12 March	−7.746*	0.445	Prebreeding
Willow tit	23 Feb – 12 March	−8.734	0.567	Prebreeding
Blue tit	6 April – 22 April	−8.611	0.413	Prebreeding
Great tit	13 June – 8 July	26.994	0.543	Nestling
Variance				
Willow tit	30 March – 9 April	−2.691	0.570	Prebreeding
Kurtosis				
Sum peak	25 April – 25 May	2.627	0.393	Prebreeding –incubation
Blue tit	20 June – 5 July	−2.013	0.658	Nestling
Great tit	24 April – 26 May	4.628*	0.435	Prebreeding –incubation

*A lower weight was given to one of the years due to a model diagnostic issue, see Methods.

blue tit ($s^2 = 6.996$, $F = 2.144$, $p_{1\text{-tailed}} = 0.083$), and the great tit ($s^2 = 6.196$, $F = 2.420$, $p_{1\text{-tailed}} = 0.055$). High fluctuation in the timing of the sum peak can be explained by alternating influence of early and late breeding prey species, the willow tit, and the great tit, respectively. For example, in the year 2000 the availability of willow tit fledglings was higher than of the great tit, causing an early sum peak, whereas in 2013 the great tits were the most abundant prey, leading to a late sum peak (Fig. 3). Interestingly, although both the willow tit and the great tit were timed earlier in 2013 than in 2000, the sum peak was actually later.

According to the best models, the height of the sum peak increases with high great tit peaks ($b = 0.830$, SE $= 0.102$, $P < 0.001$) and high willow tit peaks
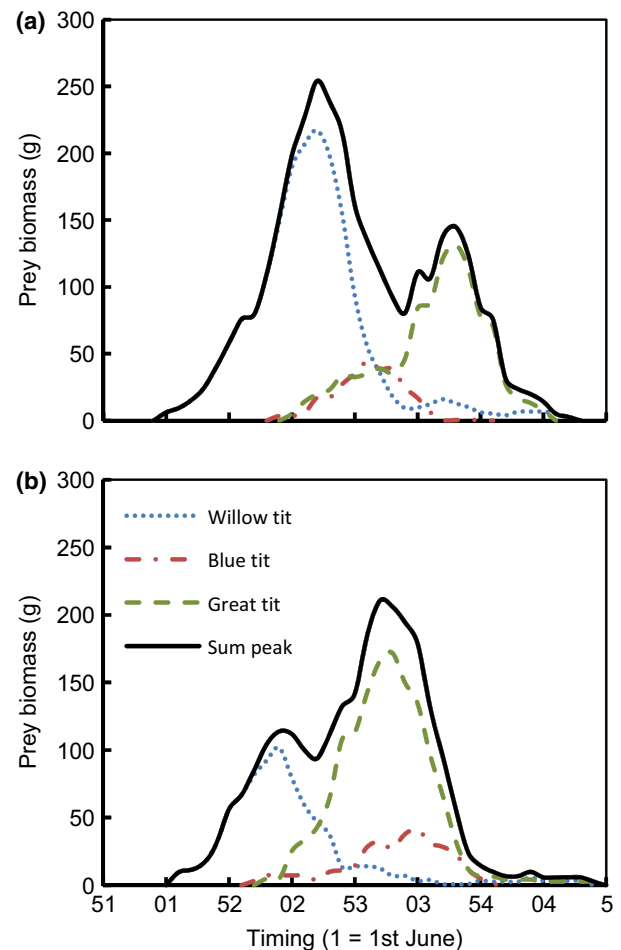
Fig. 3 Observed availabilities of newly fledged parids in Oulu, Finland in (a) 2000 and (b) 2013. The willow tit is the most abundant prey in 2000, when in 2013 the great tit has that role.

($b = 0.699$, SE $= 0.119$, $P < 0.001$), and decreases with increasing levels of asynchrony between the willow tit and the blue tit ($b = -5.494$, SE $= 1.962$, $P = 0.017$). The variance of the sum peak increases with the variance of the great tit peak ($b = 0.632$, SE $= 0.028$, $P < 0.001$) and asynchrony between the willow tit and the great tit ($b = 1.449$, SE $= 0.551$, $P = 0.022$). The peakedness of the sum peak is according to the averaged model explained with the kurtosis of the great tit peak ($b = 0.464$, SE $= 0.063$, 95% CL $= [0.327, 0.600]$, relative importance $= 1.00$) and the blue tit peak ($b = 0.275$, SE $= 0.115$, 95% CL $= [0.024, 0.526]$, relative importance $= 0.73$).

The temporal match between the food availability and sparrowhawk's breeding

The food needs of the sparrowhawk have been in temporal match with the observed food availability in the boreal habitat. Throughout the study years, the timing

of the highest annual availability of parid fledglings occurred during the first half of average timed sparrowhawks' nestling periods, with only one exception in 2010 (Fig. 4). No temporal trend in the level of trophic match/mismatch was found.

Discussion

We studied changes in the timing and shape of the food peak and determined if they are affected by food peak architecture. We did not find temporal trends in the timing of the food peak consisting of fledglings of three parid species, but the shape of the food peak has changed over the study period. Timing and quantity of fledgling production seem to be affected by temperatures of various parts of the prebreeding and breeding seasons with variable relevance in different prey populations.

In our case example, the timing of the highest food availability expected by the timing and quantity of eggs laid in the prey populations showed a postponing trend (Fig. 2b). Such a potential shift in timing of the food availability can be explained with changes in the abundances of individual prey species. When the willow tit becomes less and the great tit more abundant (Fig. 2d), the later breeding great tit constitutes the most abundant prey that determines the timing of the food peak. In the realized situation, the effect is dampened down

Fig. 4 Timing of the availability of parid fledglings in relation to the nestling period of the sparrowhawk. The median hatching date (=0) and the median fledging date of the sparrowhawk are marked with broken lines. Dots present timing of the annual modes of parid fledgling availabilities, and gray bars the time windows when 75% of the fledglings are available each year.

by the relatively low nesting success of the great tit (this study; Rytkönen & Orell, 2001). The changing abundances of early vs. late prey seem to affect the timing of the food peak more than phenological shifts of individual prey species. For their predator, factors that reduce the productivity of one prey, or improve it in another species, can thus be considered more important than climate change induced phenological shifts *per se* (which may also produce changes in productivity). Indeed, improved nesting success of the great tit could double the height of the total food peak (Fig. 2c, d).

We observed that the timing of the total food peak showed pronounced year-to-year fluctuations. Therefore, the predator might find it very difficult to predict the timing of the highest food availability, yet it seems to correlate with mean temperature of a particular spring period. This is one potential explanation for insufficient responses in adapting phenology to food phenology at higher trophic levels (Both *et al.*, 2009). Our study does not provide a thorough inspection of the synchrony of the sparrowhawk with the total food availability during the breeding season, as parids are merely a part of the prey assemblage. However, on average the hawk has timed its breeding aptly in relation to the parid fledgling availabilities.

Our study demonstrates temporal increases in the width and peakedness of a food peak. The width is related to both the length of fledgling production seasons of prey populations (σ^2 of individual prey species) and the level of synchrony between the prey species. However, the change in peakedness was not caused by increasing synchrony between the prey species, as hypothesized (Fig. 1). Instead, the kurtosis of the food peak was explained by the kurtosis values of the individual species, resulting from both synchrony within prey species and timing-related factors in the nesting success (Vatka *et al.*, 2014). The increased peakedness of the food peak is expected to increase the relevance of the trophic match/mismatch for the predator's breeding success (Durant *et al.*, 2007; Dunn *et al.*, 2011), hence altering the relative powers of ultimate factors determining the timing of breeding in the predator population.

Temperatures of different periods can affect timing and shape of the food peak through various mechanisms. Our results show that warming climate can lead to variable changes in the timing and shape of food production peaks of prey species. Willow tit peaks seem to be low after warm early springs. Warm early spring denotes temperatures fluctuating around zero degrees of Celsius and precipitation in a form of rain or sleet, whereas cold weather means frost and snow. Cold but dry weather may thus be less severe for the regulation of bird's body temperature. This could
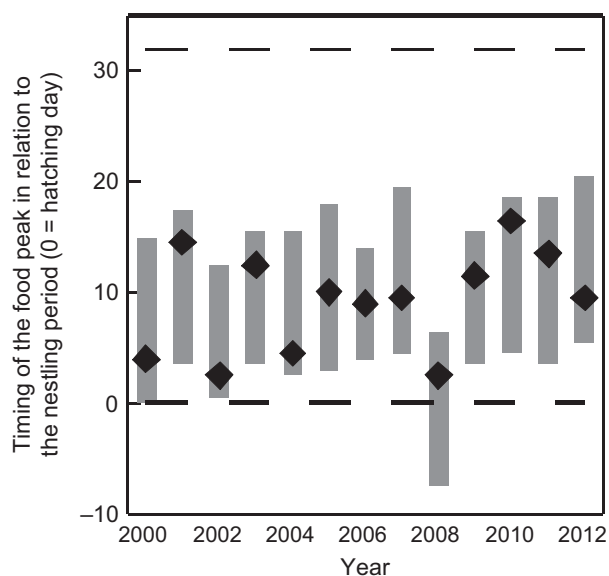
influence bird's body condition and ultimately their breeding decisions. Indeed, after warm early springs fewer pairs breed than in cold springs (Appendix S1). There seems to be fewer breeding blue tit pairs, but more breeding great tit pairs in warm springs (Appendix S1), yet causal mechanisms are not apparent. Warm summer temperatures are associated with low nestling mortality in the willow tit (Orell & Ojanen, 1983c) and the great tit (Orell & Ojanen, 1983a; Appendix S1). It is likely that in all the prey species temperatures of several parts of the prebreeding and breeding seasons affect the fledgling production, but their significances vary between species. Similarly, changes in population size can only be predicted if the full annual life cycle is considered (Ådahl et al., 2006). Resulting changes in timing, width and height of the productivity peaks of individual prey species can sum up to erratic changes in the timing and shape of the total food peak.

Timing of breeding has advanced in many bird populations (reviewed in Dunn & Winker, 2010; Dunn & Møller, 2014), including the Oulu willow and great tit populations (Vatka et al., 2011, 2014). Temporal trends of species inhabiting the same area can be parallel (e.g., Both et al., 2009) or unequal, due to different factors determining the breeding schedule (Dunn & Winker, 2010). The latter would lead to changing synchrony between prey species. In addition, the length of the breeding season, reflecting in the width of the food peak, can change. For example, Gullett et al. (2013) report a reduction of 33% in breeding season length over 17 years in the long-tailed tit Aegithalos caudatus in U.K.

We did not find temporal trends in synchrony between prey species. Nevertheless, such an effect may be possible in other cases and at other trophic levels. For example, the optimal prey to parids consists of a diverse group of insect larvae (moths Lepidoptera and sawflies Hymenoptera). Some of the species overwinter as eggs, some as pupae or in the adult stage. Thus, depending on spring temperature patterns, occurrences of larvae of species with different life cycles can become either concurrent or asynchronous, affecting the shape of the food peak experienced by the parids. However, by far the responses of the timing of larvae availabilities to warming of the springs have been considered like bulk effects, as if all the prey species would be similarly affected (e.g., Visser et al., 1998; Both et al., 2009; Vatka et al., 2014).

To understand the ecological consequences of climate change in trophic interactions, especially the temporal match/mismatch between food availability and food needs of a predator, we need to better comprehend the architecture of the total food peak and the factors affecting its components. Factors that affect the timing of the reproductive surge and the abundance of food yielded by each prey species determine their synchrony and, ultimately, the timing and shape of the total food peak experienced by the predator. They can alter the ultimate factor affecting the timing of breeding of the predator and underlie insufficient phenological adaptations at higher trophic levels.

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Supporting Information

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

Figure S1. Temporal variation in the variance and kurtosis of parid fledgling availabilities.
Table S1. Annual numbers of nests.
Appendix S1. Additional analysis on temperature effects.