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*Published in:*  
Journal of Animal Ecology

*DOI:*  
[10.1111/1365-2656.12554](https://doi.org/10.1111/1365-2656.12554)

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*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2016

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Samplonius, J. M., Kappers, E. F., Brands, S., & Both, C. (2016). Phenological mismatch and ontogenetic diet shifts interactively affect offspring condition in a passerine. *Journal of Animal Ecology*, 85(5), 1255-1264. <https://doi.org/10.1111/1365-2656.12554>

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# Phenological mismatch and ontogenetic diet shifts interactively affect offspring condition in a passerine

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## Summary

1. Climate change may cause phenological asynchrony between trophic levels, which can lead to mismatched reproduction in animals. Although indirect effects of mismatch on fitness are well described, direct effects on parental prey choice are not. Moreover, direct effects of prey variation on offspring condition throughout their early development are understudied.
2. Here, we used camera trap data collected over 2 years to study the effects of trophic mismatch and nestling age on prey choice in pied flycatchers (*Ficedula hypoleuca*). Furthermore, we studied the effect of mismatch and variation in nestling diet on offspring condition.
3. Both experimentally induced and natural mismatches with the caterpillar peak negatively affected absolute and relative numbers of caterpillars and offspring condition (mass, tarsus and wing length) and positively affected absolute and relative numbers of flying insects in the nestling diet. Feeding more flying insects was negatively correlated with nestling day 12 mass.
4. Both descriptive and experimental data showed preferential feeding of spiders when nestlings were < 7 days old. Receiving more spiders during this phase was positively correlated with tarsus growth.
5. These results highlight the need for a more inclusive framework to study phenological mismatch in nature. The general focus on only one prey type, the rarity of studies that measure environmental abundance of prey, and the lack of timing experiments in dietary studies currently hamper understanding of the actual trophic interactions that affect fitness under climate change.

**Key-words:** asynchrony, climate, feeding constraint, foraging, nestling diet, ontogenetic shift, phenology, prey switching, timing, trophic levels

## Introduction

Most trophic interactions have a seasonal component, because different potential prey species fluctuate in abundance over the year, as do predator requirements. The timing of life-history decisions in many animals is therefore matched with the timing of peak abundances of important resources. The match–mismatch hypothesis (MMH) postulates that those individuals that best match their phenology with resource phenology have the highest fitness (Cushing 1990). However, seasonal declines in fitness are more general in nature, independent of whether individuals reproduce on an increasing or declining slope of food abundance (Daan *et al.* 1988; Dunn *et al.* 2011). Therefore, these declines are not necessarily attributable

to a mismatch with food resources, but may also covary with other gradients such as winter competition being harder for late individuals (Arcese & Smith 1985), predation risk affecting prey phenology (Vonesh 2005), habitat suitability declining for later settling individuals (Tejedo 1992) and/or parental quality being correlated with earlier breeding (Verhulst & Nilsson 2008).

Given the range of factors that may affect seasonal timing and fitness simultaneously, it is hard to prove the MMH in nature (Leggett & Deblois 1994), and evidence for the MMH to play a major role in population dynamics appears weak (Dunn & Møller 2014). Despite criticism on the generality of the MMH, phenological mismatch between trophic levels is a frequently reported effect of climate change on ecosystems (Visser *et al.* 1998; Edwards & Richardson 2004; Visser & Both 2005; Thackeray *et al.* 2010). The general pattern in terrestrial ecosystems is that plants advanced more than invertebrates, which advanced

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their phenology more than vertebrates (Thackeray *et al.* 2010). If trophic synchrony is important, we thus expect that species at higher trophic levels suffer in warm years, or alternatively must switch to alternative prey.

Birds' breeding seasons are ultimately timed to match the abundance of their prey (Perrins 1970). In generalist species living in habitats with broad food peaks, mismatches may be relatively unimportant (Both *et al.* 2010; Dunn *et al.* 2011), but the opposite may hold for specialists depending on seasonal food peaks. Arctic breeding waders experience advancing insect peaks (Tulp *et al.* 2009), and golden plover *Pluvialis apricaria* chicks rely on a short burst of tipulids in spring for their growth, which may become mismatched when warming proceeds (Pearce-Higgins, Yalden & Whittingham 2005). Many insectivorous passerines in temperate forests have advanced their reproductive timing (Visser *et al.* 2003; Both *et al.* 2004), which is sometimes sufficient to match the timing of their main prey (e.g. Charmantier *et al.* 2008; Vedder, Bouwhuis & Sheldon 2013) and may in some cases be adaptive (Lof *et al.* 2012). However, phenological adjustment may also be insufficient (Visser, Holleman & Gienapp 2006; Both *et al.* 2009), leading to reduced fecundity, hampered offspring growth, lower fledging success (Reed, Jenouvrier & Visser 2013b) and potentially population declines (Both *et al.* 2006, 2010; but see Reed *et al.* 2013a). Surprisingly, diets are rarely reported in studies that link mismatch with demographic parameters (but see García-Navas & Sanz 2011), and we found no experimental studies on the effect of mismatch on prey choice. Importantly, a timing experiment would separate reproductive timing from its potential underlying causes like parental and/or habitat quality (Verhulst & Nilsson 2008), both of which may affect prey choice. Since most correlational studies do not control for these quality measures, a key premise of the MMH – that mismatch causes dietary limitations – requires further exploration.

Apart from dietary constraints imposed by the degree of phenological matching, offspring diets vary throughout ontogeny. These ontogenetic dietary shifts have been demonstrated in a variety of taxa (Betts 1955; Winemiller 1989; Adams 1996; Fialho, Rocha & Vrcibradic 2000) and are mediated by feeding constraints and/or nutritional adaptations. One such constraint is body size, as younger individuals may only be able to ingest small prey items compared with older ones (Slagsvold & Wiebe 2007). In addition, particular prey types may be a nutritional adaptation to early offspring developmental stages. For example, many studies have found that insectivorous birds feed younger nestlings a higher proportion of spiders than older nestlings (Betts 1955; Royama 1970; Cowie & Hinsley 1988; Radford 2008), and one study showed that spider-rich diets positively affected offspring growth (García-Navas, Ferrer & Sanz 2013). In short, offspring developmental stage may alter dietary needs, apart from constraints imposed by the availability of prey items.

The general focus on just one group of abundant prey (e.g. caterpillars) may be simplistic when studying effects of climate change on trophic interactions, especially if essential nutritional requirements (e.g. spiders) throughout ontogeny are not considered. Moreover, caterpillars may be a predominant food source for many passerines (Betts 1955; Royama 1970; Sanz 1998; Cholewa & Wesolowski 2011) due to their positive effect on nestling development (Wilkin, King & Sheldon 2009; Burger *et al.* 2012), but little is known about the importance of alternative prey types for offspring development. Therefore, while previous studies of predator mismatch with one prey type have yielded important insights, the effects of phenological mismatch on variation in parental prey choice throughout offspring ontogeny are understudied, especially in an experimental way. Ultimately, this variation needs to be explored to understand the dietary components that affect offspring condition under climate change.

The aims of this study are threefold: (i) to investigate descriptively and experimentally how offspring ontogeny and mismatch affect parental prey choice, (ii) to study the effect of mismatch and variation in offspring diet throughout ontogeny on offspring condition and (iii) to propose a best practice framework to study the MMH in nature.

## Materials and methods

### STUDY SITE AND SPECIES

The pied flycatcher is an insectivorous migrant passerine that breeds in secondary cavities across Europe's temperate forests. It winters in West Africa and shows strong migratory connectivity between its breeding and wintering location (Ouweland *et al.* 2016). Flycatchers in our populations are socially monogamous, although 4% of males are polygynous (Both 2013), and provide biparental care. Pied flycatcher prey choice was studied during parental care in 2012 and 2013 at four study sites with varying degrees of coniferous and deciduous trees in National Park Dwingelderveld (52°49'5"N, 6°25'41"E) in The Netherlands. Approximately 75 pairs of pied flycatchers breed in these areas annually in the 300 wooden nest boxes provided (size W × D × H: 9 × 12 × 23 cm). These boxes are also occupied by about 100 pairs of other bird species, including mostly great and blue tits. Dominant tree species were pedunculate oak *Quercus robur*, Scots pine *Pinus sylvestris* and silver birch *Betula pendula*. All nest boxes were checked at least once per week, but flycatcher boxes several times per week, so first egg laying date could be accurately determined. From the 12th day of incubation, the nest was checked daily, to ensure the day the first eggs hatched, which is hatching day (with chick age = 0).

### EXPERIMENTAL DELAY

To study the effects of trophic mismatch on prey choice, hatch date was experimentally delayed in 2013 by 7 days in half of the broods, and the other half served as controls. Delay and control nests were assigned in box pairs that were in close spatial proximity with the same laying date and habitat characteristics. To

achieve a delayed hatch date, we replaced newly laid eggs with dummies every morning and stored them in plastic cups lined with cotton in the ground below the nest box in both the control and the delay group. When no new egg was laid in a nest and the female had initiated incubation, the dummies were removed and the original clutch was returned to the female in the control group. Delay clutches were stored for an additional week before returning them. Treatment was successful in 19 out of 23 nests in the control group and 17 out of 23 in the delay group. Note that control clutches were delayed by one day, as we only returned eggs on the day when no new egg had been laid, which was the day after clutch completion.

We are aware that no timing experiment exists that does not impact other aspects of breeding (Verhulst & Nilsson 2008). In our case, increased female incubation effort and male courtship feeding may have affected parental condition. Although this type of manipulation did not affect female body mass during incubation (Siikamäki 1998), we cannot exclude that other aspects were negatively affected. Moreover, despite male courtship feeding rates being lower than male chick rearing feeding rates (0.9–3.2 vs. 12.0–15.7 male feedings per 30 min, respectively (Lifjeld & Slagsvold 1986; Lifjeld 1988)), delayed males may have expended more energy during courtship feeding. Nevertheless, 3 years of delay experiments in our populations did not affect parental return rates when controlling for offspring hatch date (Burger, Ouwehand & Both 2014), so the additional energy expenditure does not appear to affect survival. In short, no ecological experiment is without fault, and the reader should be aware of the aforementioned limitations in interpreting our results.

#### PARENTAL PROVISIONING DATA

To investigate the nestling diet, camera nest boxes were installed onto the original nest box during the second week of incubation and nest and eggs were transferred to them. These camera boxes had the same dimensions as a regular nest box, except with a space behind them to hold a DSLR camera with the lens pointing towards the nest entrance. Cameras, infrared triggers at the nest entrance, and LEDs were installed at chick age four, six, nine and 12 days after hatching. Nikon D3100 cameras with a Nikon 40 mm f/2.8 G DX Micro-NIKKOR lens were used, and all components of the set-up were at first switched off. If the birds accepted the set-up, all components were switched on, and we observed acceptance from >50 m. If birds did not accept the set-up at any point, it was removed and a new attempt was made at the next intended chick age. A frontal picture was taken every time one of the parents passed the infrared trigger on entering the nest box to provision offspring. Sample sizes differ among age groups in 2013, because parents were less likely to accept the camera set-up at young chick ages ( $n = 23, 33, 32, 28$  for chick age four, six, nine and twelve, respectively). In 2012, this was more symmetrical ( $n = 22, 23, 20, 19$ , respectively). Twelve sessions were done at other chick ages: in 2012 d7 (1), d10 (2), d11 (1), d13 (3); in 2013 d5 (2), d8 (2), d11 (1) adding up to a total of 212 camera sessions. A camera session lasted about 2.5 h, but we analysed on average  $104 \pm 44$  min, as we discarded the unusable first part of the camera session, where birds were still exploring the camera set-up (evident from repeated photographs of the same bird with the same prey within seconds of each other). The start of the photograph analysis was the point at which birds stopped this exploration and showed regular provisioning

behaviour (evident from longer breaks between photographs and different prey types).

#### OFFSPRING CONDITION DATA

At day 7 after hatching, chicks were ringed and weighed and parents were caught and measured; especially parental tarsus was important as this is a heritable trait in pied flycatchers (Alatalo & Lundberg 1986), and was used as a covariate in statistical models that predict offspring tarsus. At day 12, chicks were again weighed and measured (tarsus and eighth primary feather). Eighth primary feather (F8) was found to be a good proxy for wing length in small passerines (Jenni & Winkler 1989), and was measured with a ruler between the eighth (F8) and ninth (F9) primary feather to the nearest half a millimetre. Since we study the direct effect of prey variation on offspring condition, we were especially interested in the components that were affected within breeding seasons (mass, tarsus, F8).

#### CATERPILLAR PEAK DATA

In both years, seasonal variation in caterpillar abundance was monitored by collecting caterpillar frass in 0.5 by 0.5 m cheese cloths (Tinbergen 1960; Van Balen 1973) installed in each nest box area under a total of six individual pedunculate oaks that were spread out across the study area. We focused on oaks, because they have higher caterpillar abundances than other trees and the species of caterpillars brought in by pied flycatchers mainly occur on oaks. Frass nets were emptied at an interval between 3 and 5 days, and samples were dried for 48 h in a drying oven at 60 °C. In the laboratory, samples were sieved and visually cleaned from debris other than caterpillar droppings. Subsequently, the sample was weighed using a scale with 0.001 grams accuracy. Since we found little variation in peak frass fall between oaks (53–55.5 April in 2012, 62.5–66.5 April in 2013), the peak frass fall date for each year was determined by averaging the peak dates of all trees. This date was subtracted from the date for each camera session to retrieve relative date to the caterpillar peak. Since caterpillars are the dominant prey item in the pied flycatcher diet in our population (53.7%), the phenology of other prey items was not used in this analysis.

#### HABITAT DATA

The proportion of deciduous trees around each nest box was determined, because deciduous trees contain higher caterpillar densities, and hence, we hypothesized that this will affect nestling diet (Van Balen 1973; Veen *et al.* 2010). Local habitat around each nest box was determined by measuring the basal area of the seven trees nearest to the focal nest box approximately at breast height (wherever the trunk was smooth and symmetrical) and noting the tree species. We consider these seven trees a good representation of the local habitat type. We took the basal area of the trees, as this is a proxy for the foliage volume. The habitat variable used in this study was the proportion of deciduous basal area around the nest box and was calculated as the sum of all deciduous basal areas divided by the sum of the total basal area of all trees.

#### STATISTICAL ANALYSIS

Prey items were divided into four categories that are associated with different hunting strategies and nutritional profiles:

caterpillars (occasionally including Hymenoptera larvae), flying insects (including Diptera, Lepidoptera, Hymenoptera and 'winged'), spiders (including Opiliones) and beetles (including only Coleoptera). Each of these categories was treated as a separate binomial response variable. Unknown prey items were excluded from this analysis and ranged from 11.1% to 11.8% of the total between years and treatments. However, for some prey items we only knew that they were winged, not a caterpillar, or unwinged, which meant that they could contribute to some prey categories but were missing values in others (e.g. 'not caterpillar' was a 0 for caterpillars but 'NA' for beetles, spiders and flying insects). For the descriptive part of this study, the data of 2012 and only the control group of 2013 were analysed.

In the descriptive analysis, diet composition was analysed as the probability of a certain prey type occurring in the nestling diet. Generalized linear mixed effect models (GLMM) provided by the lme4 package (Bates *et al.* 2015) in R 3.2.1 (R Development Core Team 2015) were fitted to the data. The explanatory variables in this analysis were 'date relative to the caterpillar peak', its quadratic term (since the shape of the caterpillar peak is quadratic), 'nestling age' (4–12 days), 'habitat' expressed in proportion of deciduous trees, 'year', the 'interaction between nestling age and match (squared)' and the 'interaction between habitat and match (squared)'. These interactions were included to study whether the effect of mismatch on prey choice would be stronger or weaker across nestling ages or habitat types. All predictor variables were scaled by subtracting the mean and dividing by the standard deviation. To account for repeated observations of the same nest box during a session, a nested block random effect was included with 'camera session' nested in 'nest box'.

We compared different models from the simplest model with no explanatory variables except the nested random effect to the most complex model with all terms in it, arriving at a set of 25 models per prey category for the observational data (Table S1a, Supporting information). Models that did not converge were not used in the analysis. Model selection (Burnham & Anderson 2002) with the AICcmodavg package (Mazerolle 2015) was used to determine the best model, and parameter estimates of the best model were obtained through the summary function in R.

The prey items of the delay experiment in 2013 were analysed separately as a function of the most complex model, which included the predictors 'treatment' (control or delay), 'nestling age' (4–12 days) and the interaction between the two. Backward elimination was applied until a model with only significant terms was retained. To account for repeated observations and habitat variation, two random block effects were included: 'camera session nested in nest box' and 'box pair'. These box pairs were two nest boxes that were in close spatial proximity with the same first egg date, which were subsequently randomly assigned 'control' or 'delay'. Because this design controls for habitat variation, we did not include a habitat variable like in the observational data.

Nestling condition (day 7 mass, day 12 mass, day 12 tarsus, day 12 F8, all expressed as means per nest box) were computed and analysed as a function of mismatch and feeding rates using linear mixed effect models (LME) in R. For this analysis, all descriptive and experimental data of 2012 and 2013 were analysed together to increase statistical power, which was accounted for by using year as a block random effect. In a first set of 13 candidate models, predictors that are often used in literature as a proxy for caterpillar abundance were contrasted to select the best 'caterpillar' model: hatch day relative to conspecifics, hatch day

relative to the caterpillar peak, feeding rates of caterpillars and habitat features (Table S2a). In a second set of candidate models, feeding rates of the remaining three prey categories (flying insects, spiders and beetles) were added to the best model of the first set (Table S3a). These feeding rates were computed by pooling the prey items of days 4 and 6 (young feeding rates) separately from those of days 9 and 12 (old feeding rates) and dividing them by the number of chicks and the number of hours in which the prey items were scored. This separation between age groups was done to specifically pinpoint when during nestling development certain prey types are either beneficial or detrimental for offspring condition. Feeding rates of the different prey items were separately analysed with the same candidate models as for the proportional data, and they were checked for collinearity with the usdm package in R (Naimi 2015).

All graphs in this article were made with the ggplot2 package in R (Wickham 2009). All estimates and standard errors are reported as the effect size per standard deviation from the mean.

## Results

### GENERAL DESCRIPTION OF ECOLOGICAL AND CLIMATIC DATA

The temperature during the pied flycatcher breeding season (25 April to 18 June, Fig. S1a) of 2012 (13.5 °C) was similar to the 24-year mean from 1990 to 2013 (13.4 °C), whereas 2013 was a relatively cold spring (12.0 °C). The caterpillar peak (Fig. S1b) was estimated at 24 May in 2012 and at 4 June in 2013. Since the average caterpillar peak from 2007 to 2013 was estimated at 17 May, both years had a late peak. Moreover, the caterpillar peaks in 2012 and 2013 were low (3.6 and 2.1 g m<sup>-2</sup> day<sup>-1</sup> caterpillar biomass, respectively) relative to other years (mean peak biomass 2007–2013: 11.0 g m<sup>-2</sup> day<sup>-1</sup>) with 2013 being the lowest on record since we started measuring in 2007. Average chick hatching dates in flycatchers (Fig. S1c) that received camera boxes were 23.5 May in 2012, 28.5 May for the control group in 2013 (1 day delayed) and 3.5 June in the 2013 delay group (7 days delayed). Flycatchers in 2012 and the delay group of 2013 had the same degree of asynchrony with the caterpillar peak (mean asynchrony at nestling day 7: 6.5 days), whereas the control group of 2013 had a mean asynchrony of 0.5 days. The respective percentage of caterpillars, flying insects, spiders and beetles in the nestling diet were 53.6%, 15.7%, 18.6% and 5.9% in 2012 and 53.9%, 18.2%, 9.0% and 9.9% in 2013 adding up to 93.8% of the total prey items in 2012 and 91.0% in 2013. The next most numerous prey type was Isopoda (3.0%), but this was too rare to include in the analysis. The total number of identified prey items for the analysis was 5637 in 2012 and 7972 in 2013 adding up to a total of 13609.

### NESTLING DIET ANALYSIS

In the analysis of the observational data, mismatch with the caterpillar peak was correlated with lower proportions

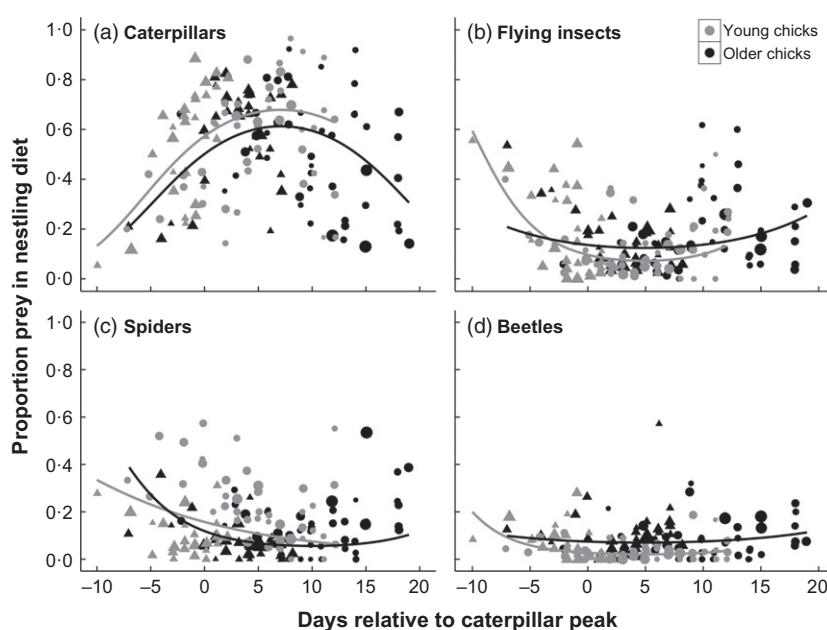
of caterpillars (Fig. 1a,  $P < 0.001$ ), and higher proportions of flying insects (Fig. 1b,  $P < 0.001$ ), spiders (Fig. 1c,  $P < 0.01$ ) and beetles (Fig. 1d,  $P < 0.01$ ) in the nestling diet. Around 6 days after our estimated caterpillar peak, caterpillar proportions reached their maximum (Fig. 1). Furthermore, in more deciduous habitats, pied flycatchers were able to sustain relatively higher proportions of caterpillars when mismatched than in coniferous habitats (interaction habitat\*match<sup>2</sup>:  $P < 0.01$ ), but this interaction was not found for other prey types. In contrast, match<sup>2</sup> interacted with nestling age in all prey types except caterpillars so that young nestlings received a relatively more constant proportion of spiders independent of mismatch (interaction age\*match<sup>2</sup>:  $P < 0.01$ ), whereas the

opposite held for flying insects ( $P < 0.001$ ) and beetles ( $P < 0.01$ , for estimates and SEs: Table S1 + S4).

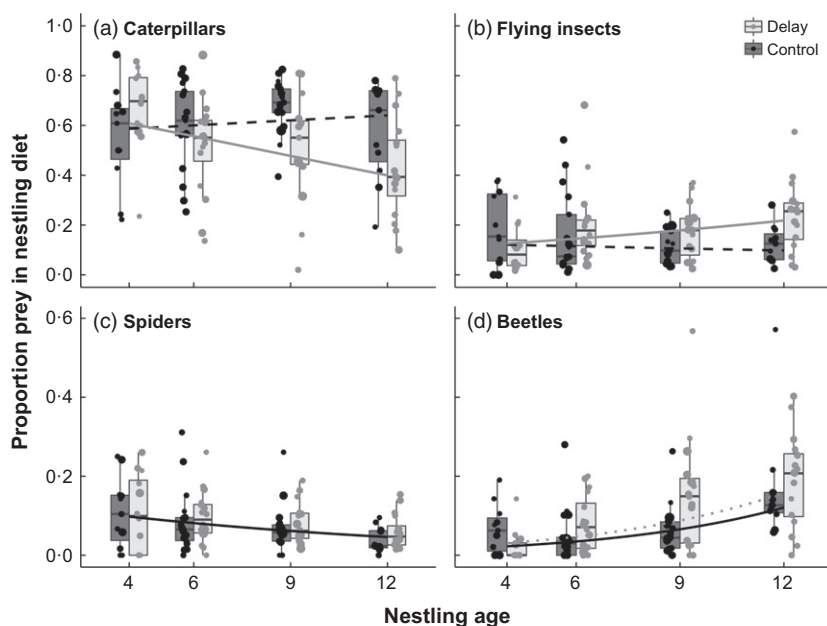
In the analysis of experimental data, a delay caused parents to provision lower proportions of caterpillars and higher proportions of flying insects in older age classes (interaction age\*delay:  $P < 0.01$  for caterpillars and  $P < 0.05$  for flying insects), but no delay effect was found for spiders and beetles (Fig. 2). These latter prey types were explained only by nestling age with higher proportions of spiders ( $P < 0.001$ ) for younger nestlings and higher proportions of beetles ( $P < 0.001$ ) for older nestlings (for estimates and SEs: Table S5).

Total feeding rates (per chick per hour) were constant over season, years and habitats and were 18% lower

**Fig. 1.** Effects of mismatch with the caterpillar peak and nestling age on the proportion of caterpillars (a), flying insects (b), spiders (c) and beetles (d) in the nestling diet of pied flycatchers based on observational data in 2012 and the control group of 2013. Data points are proportional data per session and their size is sample size dependent (average sample size per session  $N = 63.6 \pm 31.5$ ). Triangles are 2013 data, and dots are 2012 data. Lines are model fits on binomial data based on best model outputs in Table S1b. There was a significant interaction between age and match (squared) for all prey types except caterpillars.



**Fig. 2.** Effects of experimental delay and nestling age on proportions of different prey types in the pied flycatcher nestling diet in 2013. Data points are proportional data per session and their size is sample size dependent (average sample size  $\pm$ SD per session  $N = 65.5 \pm 30.1$ ). Two lines depict significant differences between treatments, single and/or continuous lines are significant for chick age, and dashed lines are non-significant for chick age. The dotted lines in (d) were marginally non-significant for treatments at the  $P < 0.10$  level. There was a significant interaction between age and treatment in caterpillar and flying insect provisioning. All outputs can be found in Table S5.



( $P < 0.001$ ) in younger compared with older nestlings (Table 1). Caterpillar feeding rates increased ( $P < 0.01$ ) when parents were better matched with the caterpillar peak, and flying insect ( $P < 0.01$ ) and spider feeding rates ( $P < 0.05$ ) subsequently decreased. However, in more deciduous habitats, spider feeding increased rather than decreased with a better caterpillar peak match (interaction  $\text{habitat} \times \text{match}^2$ :  $P < 0.01$ ). Furthermore, more deciduous habitats resulted in parents provisioning more caterpillars ( $P < 0.001$ ) and fewer flying insects ( $P < 0.001$ ) and beetles ( $P < 0.01$ ). For older nestlings, beetle provisioning rates were higher and increased monotonically over time ( $P < 0.001$ ), but for younger nestlings beetles were kept at low frequencies throughout the season (interaction  $\text{match} \times \text{nestling age}$ :  $P < 0.05$ ). Of all prey types, only spider provisioning rates tended to be higher for younger compared with older nestlings, but this was non-significant ( $P < 0.10$ , for estimates and SEs: Table 1).

#### OFFSPRING CONDITION ANALYSIS

Synchrony with the caterpillar peak significantly predicted higher nestling day 7 mass ( $P < 0.01$ ), tarsus length ( $P < 0.05$ ) and wing length ( $P < 0.01$ ), but not day 12 mass (Fig. 3, Table 2). Moreover, relative hatch date in relation to the caterpillar peak was a better predictor of nestling condition than habitat type, relative hatch date to conspecifics, or feeding rates of caterpillars (Table S2). Interestingly, higher feeding rates of spiders to young nestlings carried over to later nestling phases to positively affect day 12 tarsus length (Fig. 4a, Table 2,  $P < 0.05$ ). Moreover, the feeding rate of flying insects to older nestlings was negatively correlated with nestling day 12 mass (Fig. 4b, Table 2,  $P < 0.01$ ). No collinearity between predictor variables was detected with a maximum VIF of 1.46.

#### Discussion

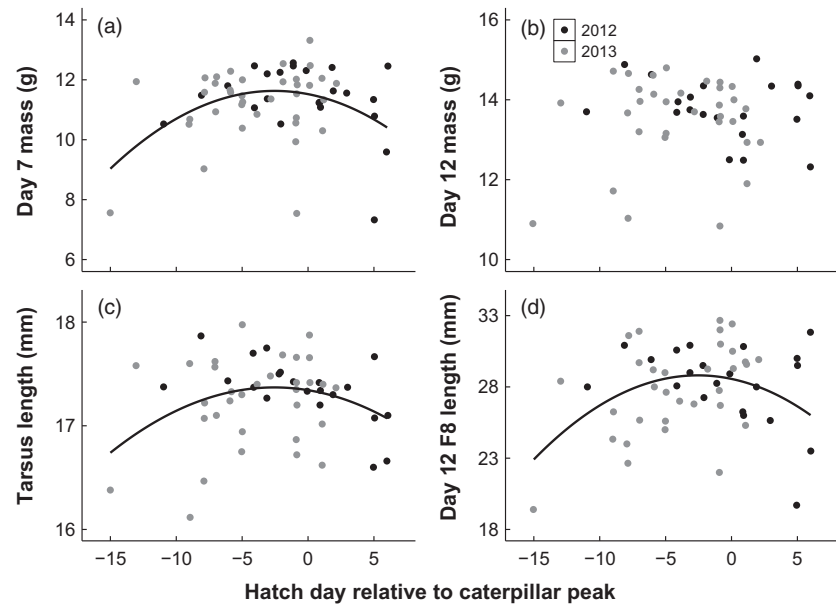
We showed descriptively and experimentally that asynchronous timing with the caterpillar peak is associated with lower proportions and numbers of caterpillars in the nestling diet, higher proportions and numbers of flying insects and lowered offspring condition. Total feeding rates per chick only varied with nestling age, so these consequences are attributed to variation in prey types. Consistent with previous literature (Both *et al.* 2009), the most productive hatch date was 8–9 days before caterpillar provisioning peaked in the nestling diet. Furthermore, we showed that alternative prey types affect offspring condition: more spiders at a young age positively affected tarsus growth, and more flying insects for older nestlings negatively affected their fledging mass. Habitat characteristics also affected offspring diets with relatively more beetles, more flying insects and fewer caterpillars in coniferous habitats.

Our results support earlier evidence that pied flycatcher fitness in temperate forests is affected by the synchrony with the caterpillar peak, as three out of four offspring

**Table 1.** Feeding rates (number of prey per nestling per hour) of pied flycatcher nestlings across mismatch with the caterpillar peak (match), nestling age ('younger' 4–6 or 'older' 9–12 days old nestlings), habitat (proportion deciduous trees) and year. Model outputs are from the best models in Table S2c. All predictors were scaled by subtracting the mean and dividing by the standard deviation

	Caterpillars			Flying insects			Spiders			Beetles			Total feeding rate		
	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P	Estimate	SE	P
(Intercept)	4.227	0.224	***	0.753	0.130	***	0.945	0.117	***	0.513	0.106	***	6.408	0.386	***
Match <sup>2</sup>	-0.345	0.103	**	0.142	0.054	**	0.104	0.045	*	-	-	-	-	-	-
Match	-	-	-	0.176	0.072	*	-	-	-	0.284	0.080	***	-	-	-
Age young	-0.593	0.235	*	-	-	-	0.187	0.109	.	-0.378	0.114	**	-1.156	0.319	***
Habitat	0.636	0.157	***	-0.353	0.072	***	0.040	0.069	ns	-0.144	0.053	**	-	-	-
Habitat*Match <sup>2</sup>	-	-	-	-	-	-	-0.155	0.050	**	-	-	-	-	-	-
Age young*Match	-	-	-	-	-	-	-	-	-	-0.291	0.113	*	-	-	-
Year 2013	-	-	-	0.276	0.146	.	-0.620	0.112	***	0.252	0.106	*	0.260	0.447	ns

Significance codes P: <0.001 '\*\*\*', <0.01 '\*\*', <0.05 '\*', <0.1 '.';



**Fig. 3.** Effect of match with the caterpillar peak on day 7 mass (a), day 12 mass (b), day 12 tarsus (c) and 8th primary feather length (d). Lines are model fits based on best model outputs in Table 2. Hatching 8–9 days before the peak in caterpillar provisioning (Fig. 1) was correlated with highest offspring condition.

components were affected by mismatch. The lack of a mismatch effect on day 12 mass is probably due to compensatory growth. Pied flycatchers usually reach their maximum mass before day 12, and therefore, underdeveloped chicks will have had time to catch up. Caterpillar peak phenology fluctuated by 31 days between 2007 and 2013 (Fig. S1b) compared with 5.4 days in pied flycatcher laying dates (Samplonius & Both 2014), a pattern that is in line with previous results of lower trophic levels having more pronounced shifts in timing than higher ones (Both *et al.* 2009; Thackeray *et al.* 2010). Interestingly, due to the cold spring of 2013 with a late caterpillar peak, we could show a clear seasonal increase in caterpillar provisioning and offspring condition when flycatchers had to forage prior to the caterpillar peak. This is exceptional, because their nestling period generally coincides with the declining slope of the caterpillar peak (Both *et al.* 2009). This suggests that breeding early can be disadvantageous for individual pied flycatchers in an exceptionally cold spring. Evidence for selection against being early is rare, possibly because individuals being too early may die without being observed or otherwise delay egg laying or

incubation until circumstances improve. Recently, selection on early born female recruits was also found to depend on temperature at arrival in their first breeding season, with dampened selection during cold springs (Visser *et al.* 2015).

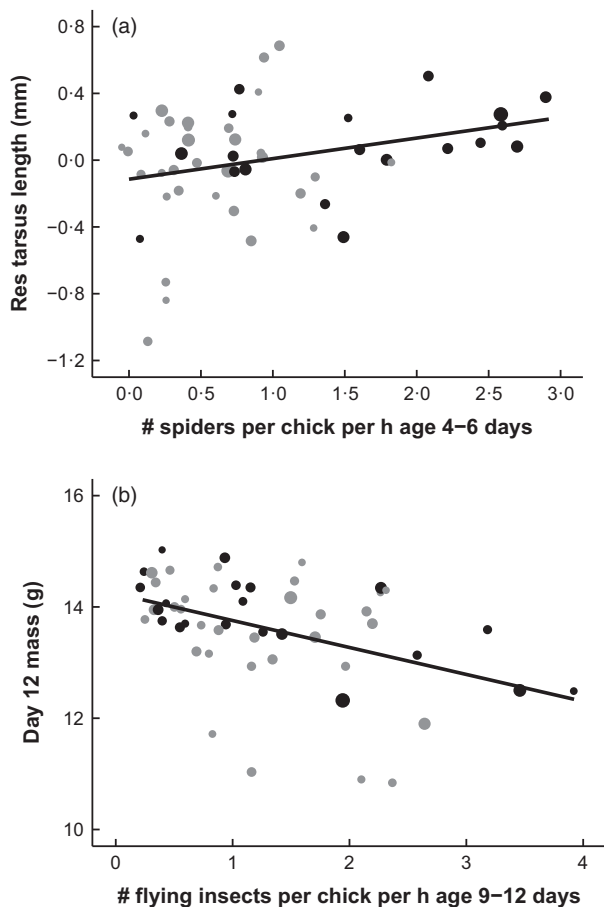
It has rarely been shown how individuals that are mismatched with their major food cope with dietary limitations. Surprisingly, models that included caterpillar feeding rates were not competitive compared with models that included mismatch, suggesting that the latter captured more important variation in diet than the caterpillar feeding rates did. Pied flycatchers appear to compensate for asynchrony with the caterpillar peak by prey switching mostly to flying insects, which had an apparent negative effect on nestling body mass. However, interpreting these results should be done with caution, because alternatively lower nestling mass may have forced parents to change their foraging behaviour, and the large fraction of flying insects could be the effect of hungry offspring rather than the cause. This is in line with the idea that nestling hunger changes the parent's decision rule for prey choice to maximize energy over time at the expense of quality over time,

**Table 2.** Effects of mismatch with the caterpillar peak and variation in nestling diets on nestling condition. Model results are the best model outputs from Table S3b. 'Match<sup>2</sup>' is hatch day relative to the caterpillar peak, 'Old flying' is the feeding rate of flying insects to older nestlings (9–12 days), and 'Young spiders' is the feeding rate of spiders to younger nestlings (4–6 days). Mass is in grams, tarsus length and eighth primary feather (F8) in millimetres. All predictors were scaled by subtracting the mean and dividing by the standard deviation

	Day 7 mass			Day 12 mass			Day 12 tarsus			Day 12 F8 (wing length)		
	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>	Estimate	SE	<i>P</i>
(Intercept)	11.63	0.173	***	13.62	0.128	***	17.37	0.055	***	28.81	0.482	***
Match <sup>2</sup>	−0.354	0.104	**	–	–	–	−0.091	0.034	*	−0.852	0.294	**
Old flying	–	–	–	−0.433	0.121	**	–	–	–	–	–	–
Young spiders	–	–	–	–	–	–	0.095	0.043	*	–	–	–
Parent tarsus	–	–	–	–	–	–	0.148	0.044	**	–	–	–

Significance codes *P*: <0.001 '\*\*\*', <0.01 '\*\*', <0.05 '\*', <0.1 '·'.





**Fig. 4.** Effects of spider (a) and flying insect (b) feeding rates on offspring condition. Lines are model fits based on best model outputs in Table 2. The line in (a) is on residuals after controlling for mismatch with the caterpillar peak and parental tarsus. Black points are 2012; grey points are 2013.

as found in starlings *Sturnus vulgaris* (Tinbergen 1981; Wright *et al.* 1998). Moreover, experimentally manipulated nestling hunger led to feeding smaller prey in another study on pied flycatchers, which was attributed to a switch from net to gross energy maximization (Lifjeld 1988). Finally, experimental pied flycatchers in our study were unable to downregulate clutch size with season, a pattern that is regularly observed in breeding birds (Perkins 1970) and was stronger in years with an early caterpillar peak (Both & Visser 2005). Our experimental delays forced individuals to raise their nestlings later, without the potential reduction in clutch size, and therefore, the experimental date effect on prey choice could have been overestimated. Nevertheless, the prey switching observed in this study provides novel insight into the compensation mechanisms used by mismatched parents once clutch size has been established.

The ontogenetic prey shift in spider and beetle provisioning implies that the match–mismatch hypothesis may underestimate the importance of less abundant, but essential prey during ontogeny. Beetle provisioning increased for older chicks and was kept at low levels for younger

nestlings. Since beetle provisioning was not correlated with offspring condition, this suggests a feeding constraint for this prey type. Furthermore, parents fed young nestlings higher proportions of spiders than older nestlings, and receiving more spiders during this phase positively affected tarsus growth, a result similar to a study on tits (García-Navas, Ferrer & Sanz 2013). Interestingly, spiders have been found to contain high levels of taurine compared with other woodland arthropods (Ramsay & Houston 2003), and taurine supplemented blue tits were bolder and performed better than controls in spatial learning tasks (Arnold *et al.* 2007). Furthermore, taurine supplementation was related to heavier tibia in chickens during the first 2 weeks after hatching (Martin & Patrick 1961), highlighting its role in early bone development. Combined, our results suggest that offspring ontogeny plays an important role in determining parental prey choice, which may be driven by adaptive choices or feeding constraints.

There is a growing body of literature on the importance of trophic match–mismatch and how predator and prey phenologies are differentially affected by climate change (Thackeray *et al.* 2010). Most studies assume that the focal predator depends on one major prey type, but they seldom show how prey choice relates to its abundance in the environment (but see Maziarz & Wesolowski 2010; García-Navas & Sanz 2011). It is therefore often unclear whether mismatch with the major prey results in lower total food provisioning, or that predators can switch to alternative prey. Switching to alternative prey types may have cascading effects on the food web and may not only increase mortality of these prey, but also increase competition with individuals specialized in these alternative prey types. Furthermore, the ease of fulfilling dietary requirements likely depends on the relative timing of different prey types throughout the season. There is no reason to assume *a priori* that different groups of invertebrates respond equally to climate change, as their ecologies strongly differ (Thackeray *et al.* 2010). For a system where spiders are essential for early offspring and caterpillars are used as staple food, an asynchronous occurrence of both prey may hamper reproductive success. Arboreal spiders were shown to increase over the season in a Swiss forest (Naef-Daenzer, Naef-Daenzer & Nager 2000), which could, for example, be disadvantageous for early breeding individuals. Moreover, absolute abundances likely matter as well, as birds raising their offspring during the caterpillar peak may have more time left to search for spiders if these are rare.

The importance of mismatching in understanding consequences of climate change is still under debate (Dunn & Møller 2014). However, this debate should not be muddled by study systems in which the MMH cannot play a role. Moreover, timing in itself may be correlated with a range of factors that affect fitness including parental and habitat quality. Due to these complexities, we suggest a best practice framework with steps we deem important for future studies on the MMH. First, identify whether

your study system depends on a seasonally or spatially fluctuating abundant resource to understand whether the MMH is a suitable framework. Secondly, measure variation in prey composition and not just provisioning rates, as both prey types and load sizes need to be known and important seasonal patterns in prey choice will be lost using only provisioning rates. Similarly, study the role of alternative prey types on offspring development and/or recruitment and not just one single abundant prey type. Thirdly, get an unbiased estimate of the seasonal variation in environmental abundance of main prey type(s), because the diet itself is a choice by the animal and may not just reflect frequency-dependent predation (but also, e.g., ontogenetic effects). Fourthly, despite its aforementioned limitations, perform a timing experiment, but be aware of potentially confounding factors. Our study is an attempt at resolving some of these complexities, and we encourage future research to consider these issues to ensure rigorous conclusions about the role of the MMH in explaining fitness and/or demographic consequences of climate change.

## Acknowledgements

We thank Mirjam Oosting for collecting data on the habitat characteristics around the nest boxes, Jurjen Brands for helping to assemble the camera nest boxes, Esther Chang for helpful comments on an early version of the manuscript, and Staatsbosbeheer Dwingelderveld and Natuurmonumenten for granting us permission to do nest box research in their forests. We thank Emma Vatka and two anonymous referees for constructive comments. We are grateful to the Dutch animal ethical committee Dierexperimentencommissie (DEC) for overseeing ethical treatment of animals during our experiment under DEC 6598A. The authors declare no conflict of interest.

## Data accessibility

Data available from the Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.5p65q> (Samplonius *et al.* 2016).

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Received 14 January 2016; accepted 18 May 2016  
Handling Editor: Albert Phillimore

## Supporting Information

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

**Figure S1.** Seasonal patterns in (a) mean daily temperature, (b) caterpillar frass biomass, and (c) pied flycatcher hatching dates in our study area in Drenthe in 2012.

**Table S1a.** Candidate models of the observational diet analysis. “Match” is the match with the caterpillar peak, “Habitat” is the proportion of deciduous trees.

**Table S1b.** Diet proportions in pied flycatcher nestling diets, model rankings of the best models to predict pied flycatcher nestling diet proportions.

**Table S1c.** Feeding rates in pied flycatchers nestling diets, model rankings of the best models.

**Table S2a.** First set of candidate models to predict offspring components of fitness (day 7 mass, day 12 mass, day 12 tarsus, day 12 F8).

**Table S2b.** model ranking of the best models for four fitness components in pied flycatcher nestlings.

**Table S3a.** Second set of candidate models to predict offspring components of fitness (day 7 mass, day 12 mass, day 12 tarsus, day 12 eighth primary feather).

**Table S3b.** model ranking of the second set of models for four fitness components in pied flycatcher nestlings.

**Table S4.** Estimates, standard errors, and significance codes of the best model(s) (based on AICc) fixed effects in the observational data, subdivided in four main prey items of the pied flycatcher nestling diet.

**Table S5.** Estimates, standard errors, and significance codes of the fixed effects in the 2013 experimental data, subdivided in four main prey items of the pied flycatcher nestling diet.