Resource abundance can buffer trophic mismatch in a caterpillar-passerine food-chain

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Phenological mismatch occurs where variation in the magnitude of the response to environmental cues among species disrupts previously synchronised interspecific interactions, posing a risk to ecosystems as the climate changes. Understanding how ecological and environmental factors modulate the fitness effects of mismatch is essential for forecasting its impacts. Here, we analyse trophic mismatch in a classic woodland caterpillar-passerine system, using fifteen years of data from long-term monitoring sites across England. The timing of peak caterpillar abundance and the abundance of caterpillars varies considerably among sites and years. Applying a Bayesian mixed modelling approach to thousands of nest-level observations, we show that temporal mismatch between chick demand and caterpillar abundance significantly reduces fledging success in Blue and Great Tit but has minimal effect on Pied Flycatcher. We demonstrate that fledging success is greater in years with higher caterpillar biomass, often offsetting the negative impacts of mismatch, but with buffering effects that plateau under extreme caterpillar abundance. Variation in resource availability therefore represents an important but underappreciated buffering mechanism, shaping the fitness consequences of phenological asynchrony in a warming climate.

Phenological asynchrony | Trophic mismatch | Phenological mismatch | Buffering | Demography | Climate change | Resilience | Food web

Introduction

As the climate warms, variation in the magnitude of phenological shifts among different species could lead to a decoupling of important and temporally synchronised biotic interactions (Roslin *et al.* 2021; Thackeray *et al.* 2016). In trophic interactions, where a species depends on a temporally ephemeral resource peak, fitness and population recruitment can be negatively affected if phenology is mismatched at the individual or mean population level (Cushing 1967, 1969, 1990). In recent decades, research has increasingly focused on quantifying the impacts of mismatch in food-chains, with concern that climate change could lead to mismatch occurring widely across communities and potentially destabilising entire ecosystems (IPCC 2022). However, despite evidence for negative effects of mismatch at the individual-level (Reed *et al.* 2013b; Thomas *et al.* 2001), we still lack evidence that this translates into demographic and population-level impacts (Samplonius *et al.* 2021). From a conservation perspective, this discrepancy is key gap in our knowledge—phenological asynchrony is most likely to significantly undermine ecosystem resilience to climate change where it impacts population size.

One reason why we lack evidence for the effects of mismatch at the population-level may be that species and trophic interactions are more buffered against these effects than has been acknowledged (Weir 2023). Buffers that confer some resilience to mismatch operate across a range of scales, encompassing behavioural, physiological, and environmental factors that can act to: (i) decrease the amount of temporal asynchrony experienced; (ii) decrease the negative effects of asynchrony (i.e. mismatch) where it does occur; or, (iii) generate portfolio effects (Schindler *et al.* 2015) that ameliorate the average impacts of mismatch at the aggregate (e.g., population) level (Weir & Phillimore 2024). For example, where a consumer utilises a number of different resource taxa, this enables dietary switching among resource species with different phenologies, either to reduce the amount of temporal asynchrony or select resources where the costs of mismatch are lowest (e.g. in caterpillars: Weir, 2024). In single-brooded passerine birds, changes in laying and incubation behaviours can plastically alter egg-hatch timing so that hatching is improved in relation to environmental conditions, such as temperature and food supply (Simmonds *et al.* 2017). Even heterogeneity in environmental conditions occurring over a small spatial scale can give rise to portfolio effects that average out the local mismatches experienced by individual consumers (Burger *et al.* 2012; Shutt *et al.* 2022; Weir & Phillimore

2024)—for example, differences in the spring bud-burst timing among individual trees within a woodland.

In pioneering work on the match-mismatch hypothesis in marine systems, Cushing (1982) observed that the consequences of mismatch were likely to be more severe in years of low resource abundance than in high-abundance years, because a higher resource peak provides a general increase in resource availability for any given amount of temporal asynchrony. In Cushing's *plankton→herring* system, this pattern resulted in more variable recruitment to the population in years of low resource abundance. Subsequent work has suggested that resource abundance can improve reproductive performance in a range of temporally synchronised consumer-resource interactions (Durant *et al.* 2005, 2007). The maximum abundance of an ephemeral resource (the 'peak height') therefore has the potential both to buffer mismatch at the individual level and to generate portfolio effects through spatial and temporal variation that can smooth the population-level impacts of mismatch across larger spatial scales (Weir & Phillimore 2024).

The tri-trophic *tree→caterpillar→bird* food-chain of temperate woodlands has become an archetypal model system for studying the consequences of trophic mismatch (van Asch & Visser 2007; Burgess *et al.* 2018; Cole *et al.* 2015; Samplonius *et al.* 2021). In this system, caterpillars synchronise their emergence in spring to coincide with the first flush of foliage on deciduous trees, before leaves mature and accumulate anti-herbivory defences, such as noxious secondary chemicals or structural defences (Feeny 1970, 1968). The process of leaf maturation creates a narrow time window during which poorly defended foliage is available, and a corresponding peak of caterpillar abundance occurs during early spring (Macphie *et al.* 2022; Shutt *et al.* 2019). In turn, many single-brooded woodland passerine birds time their egg laying such that their offspring's maximum food demand coincides with the peak of caterpillar availability in their environment (Both *et al.* 2009; Visser *et al.* 2006). Although temperature is a crucial phenological cue for each level in this system, birds are less responsive to warming than both trees and caterpillars (Burgess *et al.* 2018). Ongoing climate change could therefore increase trophic mismatch in this system, with cascading negative effects throughout the food-web. However, while birds finding themselves mismatched relative to the caterpillar resource peak can suffer negative effects on performance (García-Navas & Sanz 2011; Pakanen *et al.* 2016; Reed *et al.* 2013b, a; Simmonds *et al.* 2017; Visser *et al.* 1998, 2006; Youngflesh *et al.* 2023), evidence of consequences for productivity and population size remains elusive (Reed *et al.* 2013b, a; Samplonius *et al.* 2021; Wesołowski & Rowiński 2014). Seasonal declines in breeding bird fitness and demography are often linked to seasonal declines in insect abundance (Burger *et al.* 2012; Evans *et al.* 2024; Harriman *et al.* 2017; Iler *et al.* 2021), but the extent to which these seasonal patterns interact with phenological synchrony remains poorly understood. For example, mismatch may only exert meaningful negative effects in years where baseline resource abundance is low. High insect abundance may therefore be an important buffering mechanism which can offset some or all of the negative impacts of mismatch (Figure S1). Here, we assess the effects of resource abundance and phenological mismatch on the breeding performance of three classic woodland passerine birds, using fifteen years of data monitoring both arboreal caterpillar abundance and bird breeding timing and success, at fourteen sites across England. As climate warming increases the likelihood and magnitude of phenological asynchrony in a wide range of trophic systems, we consider the extent to which fluctuations in resource abundance can offer hitherto unappreciated resilience to mismatch.

Methods

We collected data over a total of 15 years (2008-23) from 14 study sites across six counties in England (Devon, West Sussex, Gloucestershire, Hertfordshire, Nottinghamshire and Lancashire; Figure 1a). At each site we monitored the breeding timing and performance of three single-brooded woodland birds (Blue Tit *Cyanistes caeruleus*, Great Tit *Parus major*, and Pied Flycatcher *Ficedula hypoleuca*) nesting in artificial nest boxes. In parallel—at the same sites—we monitored the timing and abundance of arboreal caterpillars by collecting frass fall from traps set beneath oak trees.

Bird breeding data

For all sites, nest boxes were surveyed (at least) weekly throughout the breeding season (April to July) to determine: the total number of eggs laid; nest success (nests where at least one offspring fledged); and, nest productivity (total number of offspring fledged, inferred from the number of young alive at the last survey pre-fledging). The earliest and latest First Egg Date (FED) for each nest was estimated using all the visit data and assuming eggs were laid at daily intervals with an incubation period of 14 days. We used the midpoint between the earliest and latest estimate of First Egg Date (FED) and excluded observations where the interval exceeded ten days. In order to focus on the effects of resource availability on performance, we excluded nest data with recorded outcomes linked to any form of

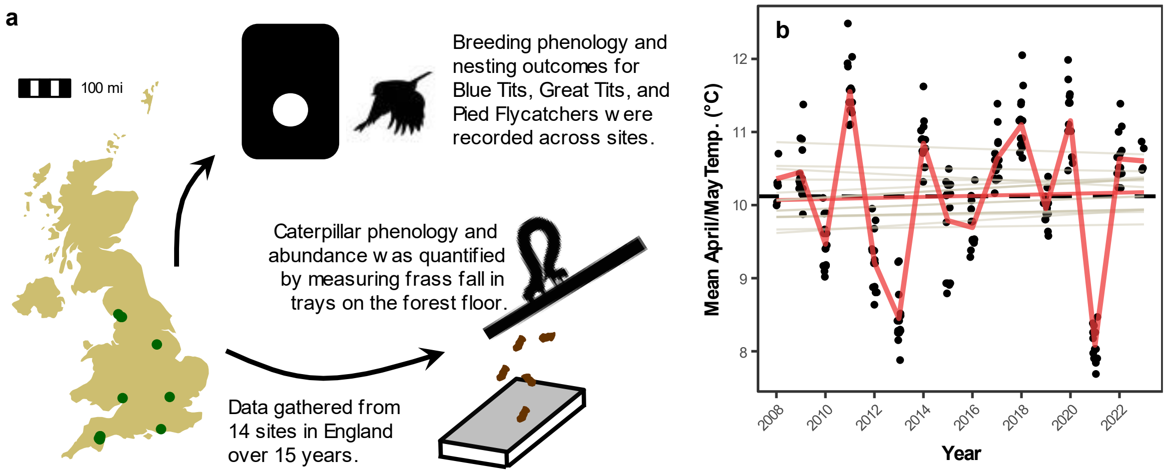

Figure 1. (a) We recorded arboreal caterpillar abundance and phenology using frass-fall data from 14 sites (•) across a 15-year period (2008-2023) in England. Concurrently, we monitored the breeding phenology and success of three woodland passerine species (Blue Tit *Cyanistes caeruleus*, Great Tit *Parus major*, and Pied Flycatcher *Ficedula hypoleuca*) using nest boxes at each site. (b) Site-level mean April/May temperature across the study period showed no significant linear trend, although there is significant annual variation around an overall average of 10.12°C across the study period (- - -). Overall linear trend and annual averages indicated by solid read lines (—), alongside site-specific linear trends in light grey (—). Points (•) show year by site averages.

predation event, or where clutches were incomplete and not incubated.

Arboreal caterpillar data

We assessed the timing and abundance of arboreal caterpillars using ‘frass’ trays set beneath oak trees to collect fallen caterpillar droppings (see Smith et al. 2011 and Burgess et al. 2018 for details of the method). We operated four trays per site, with the contents collected every 3–8 days (mean interval 5.5 days) starting from late April through to early June. The trays were (predominantly) 350×220 mm with corrugated bases and drainage holes. To minimize any impact of rainfall on the collected frass, the trays were loosely lined with permeable lightweight horticultural fleece. At every collection, the used fleeces were removed from the trays, carefully folded and replaced with new ones. The folded fleeces were dried at room temperature and the contents brushed into a sorting tray. These were then passed through a 1.2 mm mesh sieve and the frass sorted and collected by hand under a low-power binocular microscope (magnification ×7–×10) The frass was weighed to the nearest mg using a laboratory balance (Kern 440-21N).

The mass of frass for each trap collection was converted to mg per day per m^2 and attributed to the midpoint day between consecutive collections. The mass of frass was then converted to caterpillar biomass (mg) per m^2 using the average calibration equation given by Tinbergen et al. (2024), with the local mean daily temperature derived from the Meteorological Office HadUK-Grid dataset (see below, *Temperature data*). The biomass was often very sharply peaked seasonally so a log-transformation was used to allow the fitting of a simple quadratic model to determine the date (April days) and height of peak caterpillar biomass, per tray for each site and year combination.

Temperature data

We downloaded data on daily interpolated maximum and minimum temperature for the 5 × 5 km squares encompassing each site for April and May each year 2008-2023 from CEDA (Met Office, 2019) using the *R* packages ‘raster’ and ‘ncdf4’ (Hijmans et al., 2015; Pierce, 2019). We then extracted maximum and minimum daily temperature values for each site and year, and calculated mean daily temperature as the mean of the daily maximum and minimum.

To explore potential directional changes in mean April/May temperature over the duration of our study at the focal sites, which might result in increasing phenological mismatch among trophic levels, we fitted a simple Bayesian linear mixed effects model (LMM) with both a linear and categorical effect of temperature, and with random slopes and intercepts among sites for the linear trend (Table S1a). For these analyses, 2008 was treated as Year 0.

Estimating mismatch

For each site by year combination, we used Bayesian LMMs to estimate the peak date and height of the caterpillar biomass (Table S1b), using the fitted data from the quadratic model applied to each tray-level observation (see above, *Arboreal caterpillar data*). Modelling as a LMM allowed us to control for frass trap identity, trap location among-years, and trap size variation. These site by year estimates of caterpillar peak date and height (i.e. biomass, or the peak abundance of the caterpillar food resource) were matched to individual nest data for our three target bird taxa. We estimated the date of maximum offspring demand as:

Peak Chick Demand = FED + Clutch Size + 14 + 10

Where **FED** is the first egg lay date per nest, and **Clutch Size** is the recorded incubated clutch size per nest. Where clutch size was not recorded for a give nest, we calculated the numerical average clutch size per species (in each site by year combination) as an estimate. Combining FED and clutch size gives us an estimate of when offspring demand will peak across all offspring within the nest. **14** is the average incubation period across all three species, and **10** is the chick age of maximum food demand (Ferguson-Lees *et al.* 2011).

Mismatch was then calculated for each nest as the difference between Peak Chick Demand and the modelled peak caterpillar abundance date for the appropriate site by year combination. Where there is perfect temporal match between peak chick food demand and peak caterpillar abundance, mismatch equals zero. Mismatch values are negative when the peak of food demand occurs before the caterpillar abundance peak, and are positive when the caterpillar abundance peak occurs before the peak of food demand.

Temperature effects on mismatch

Divergent phenological responses to temperature cues drive asynchrony and trophic mismatch in the *caterpillar→bird* interaction (Macphie *et al.* 2023; Phillimore *et al.* 2016). To quantify the effects of temperature on mismatch, we modelled the relationship using Bayesian LMMs for each species (Table S1c). To test whether mismatch was greater warmer years, we included a fixed linear effect of mean April/May temperature. This effect was allowed to vary with random slopes and intercepts among sites, meaning that the relationship can vary at different sites. We also fitted a random effect of nest box ('Box') to control for nest-specific effects on the relationship. Random intercepts among years accounted for year-specific contingent effects on the quantity of mismatch that were unrelated to temperature. To test for differences in the temperature effect on mismatch among species, we extracted the posterior distribution of estimates for the slope of the relationship in each species and calculated the pairwise differences (with 95% credible intervals).

Performance effects of mismatch and resource abundance

To determine the effects of mismatch and caterpillar abundance on the breeding performance of the three bird species, we modelled the fledging success and productivity of each nest (Table S1d). We define 'success' as a nest having successfully fledged any offspring, and productivity as the number of offspring fledged by successful nests (inferred from the number of young alive at the last survey pre-fledging). We modelled success and productivity separately, because productivity across our study period was heavily skewed and zero-inflated. This approach also offers insights into the underlying mechanisms driving the overall performance response in each species.

Species-level Bayesian GLMMs (Table S1d) of success (logistic response) and productivity (Poisson response) were run, including both a linear effect of mismatch ('Mismatch', describing the slope of the performance relationship where mismatch equals zero) and a quadratic effect of mismatch ('Mismatch^2'). The quadratic effect fits the characteristic peaked performance curve, where performance declines under both early and late hatching, relative to a perfect match. We fitted caterpillar abundance ('Peak Height') to assess the potential for this to buffer the negative impacts of mismatch on breeding performance, and a 'Peak Height by Mismatch' interaction to test whether this potential buffering effect varied across different levels of mismatch. Peak Height was log$_e$-transformed for fitting as a simple linear effect within the model. For a visual representation of each model parameter, see Figure S2.

To control for underlying differences among sites ('Site'), years ('Year'), and nest boxes ('Box'), these were fitted as random intercepts. Next success and productivity are inherently dependent on clutch size, and we therefore fit clutch size as a random intercept to control for this effect.

Model specifications

Modelling was carried out in *R* v4.5.1 (R Core Team 2025), using the Bayesian statistical package 'MCMCglmm' (Hadfield 2010). Models were run for 3 million iterations (see Table S1), with thinning every 100 iterations and a burn-in of 1 million iterations, respectively. We used default priors for the fixed effects (mean = 0, with a large variance) in all models, and inverse Wishart priors on models fitted with a Gaussian response. In Poisson and logistic models, variance was fixed at 1 and we used parameter expanded priors (scaled $F_{1,1}$ distribution, with scale = 1000) for the random effects.

Results

Temperature varies among years but shows no linear trend

The mean April/May temperature from 2008-2023 across all sites was 10.12 °C, ranging from 7.68°C (Middlewood, Lancashire, 2021) to 12.48 °C (Sherrardspark Wood, Hertfordshire, 2011)(Figure 1b). Over this fifteen-year period, there was no significant overall directional change in mean April/May temperatures across sites (slope = 0.007 °C/year, CIs: -0.11, 0.12). There is evidence for a modest amount of variation in the intercept of this linear relationship among sites (8% of σ^2_{Total} CIs: 2, 18), suggesting underlying geographical differences in baseline spring temperature (Table S2). However, variance in slopes among sites is minimal (see Table S2) suggesting the temporal rate of change is not significantly different. Among-year effects *outside* of any linear trend drive most variation in the intercept of that relationship (84% of σ^2_{Total} CIs: 68, 95).

Mismatch is greater in warmer years

Relative to expected peak offspring demand, all three species are asynchronous and late on average. Mean asynchrony across all site-by-year combinations is greatest in Pied Flycatcher at 16.4 days (SD = 7.7), while Great Tit (6.9 days, SD = 10.4) and Blue Tit (5.5 days, SD = 8.9) display lower, and more similar, average asynchrony (Figure 2).

Across all species, the extent of mismatch between maximum chick demand and peak caterpillar availability is significantly higher in years with higher spring (mean April/May) temperatures (Figure 2; Table S3). Increases in mismatch with warmer temperatures are greatest in Great Tit at 6.4 days/°C (CIs: 4.0, 9.0), followed by Blue Tit at 5.0 days/°C (CIs: 3.4, 6.8), and Pied Flycatcher at 4.7 days/°C (CIs: 2.3, 7.7)(Table S3). These differences are not statistically significant in pairwise comparisons (Table S4).

April/May temperature explained 12.5% (Blue Tit, CIs: 3.0, 23.4), 20.2% (Great Tit, CIs: 6.1, 35.1), and 21.5% (Pied Flycatcher, CIs: 5.1, 39.9) of the total variance in the temperature-mismatch relationship. However, although there was also a strong effect of year (from 7.4% of $\sigma^2_{Intercept}$ in Blue Tit to 17.4% in Pied Flycatcher), baseline differences in the intercept of the relationship among sites accounted for the largest proportion of the modelled variance (from 16.6% in Pied Flycatcher $\sigma^2_{Intercept}$ to 87.0% in Blue Tit). In every case, the baseline effects of site exceed the main effects of temperature (Table S3).

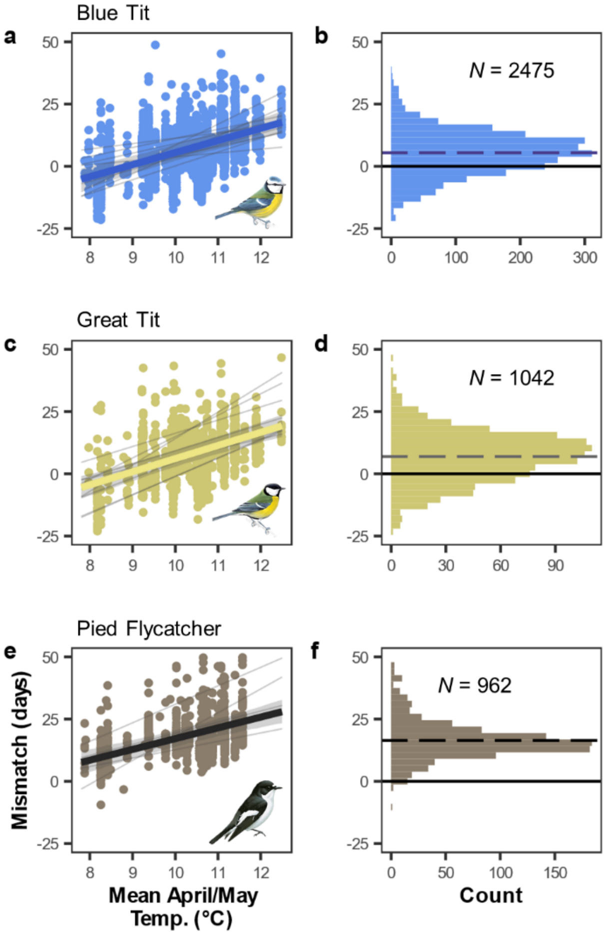

Figure 2. The effects of temperature on caterpillar-passerine mismatch (a, c, e), showing brood-level mismatch data (●) across all site-by-year combinations, as well as overall (—) and site-specific trends (—). Histograms show the frequency of different levels of mismatch across all data (b, d, f). Two sites were removed from site-specific estimates due to small sample size and poorly estimated trends. Bird drawings reproduced with permission from Mike Langman, RSPB.

Resource abundance increases breeding performance and can buffer mismatch

Overall, the fixed effects in the model (mismatch, peak height, and their interaction) generally explain more variation in breeding performance in Blue and Great Tit than in Pied Flycatcher (Table S5). For both tit species, the fixed effects are most important in explaining breeding productivity (Blue Tits = 56.7%, Great Tits = 57.8%), and explain less variation in success (Blue Tits = 13.6%, Great Tit = 6.5%).

Mismatch negatively impacts breeding performance across all species to some extent, accounting for large portions of the fixed effects variance across all species (Table 1). These effects are particularly marked in the cases of productivity in Blue and Great Tit. The quadratic (curved) effect of mismatch is significant (or marginally non-significant) in both the success and productivity models of Blue and Great Tit, indicating a curve which peaks at some level of phenological match/mismatch (Figures 3 and 4). Since the data are centred on zero, the slope of mismatch itself ought to equal zero by default under an assumption of maximum fitness with perfect phenological synchrony (i.e., the flat top of the performance peak). However, in the Blue Tit productivity model, the significant negative slope of mismatch indicates a peak in performance *before* zero mismatch (Figures 3 and 4)—i.e., caterpillar abundance peaks before estimated peak offspring demand, potentially indicating inaccuracy in our estimate of peak demand for this species. Although the confidence intervals are broad and overlapping, both the variance explained by the quadratic mismatch term and the parameter estimates themselves are consistently lower in Great Tit than in Blue Tit, across both success and productivity, suggesting mismatch may be less important in this species as a determinant of performance (Figure 4; Table 1).

Where mismatch is zero, caterpillar peak height significantly increases productivity in Blue Tit (slope = 0.05, CIs: 0.03, 0.08) and Great Tit (slope = 0.08, CIs: 0.04, 0.12), and also approaches a significant increase in success in both species (Blue Tit slope = 0.02, CIs: -0.01, 0.40, Great Tit slope = 0.2, CIs: -0.1, 0.6) (Figure 4; Table S6-8). Because peak height is $\log_e$-transformed (see *Methods: Performance effects of mismatch and resource abundance*), slopes describe the increase in number of chicks fledged (productivity) or log-odds of fledging any chicks (success) per *e*-fold (i.e. ~2.7x) increase in peak caterpillar abundance. Peak height is a major contributor to the variance explained in both the Blue and Great Tit productivity models (Table 1).

Table 1. Relative contribution of phenological mismatch and caterpillar abundance to explaining variance in passerine performance, estimated as success and productivity. Each parameter shown was modelled as a fixed effect, and variances are estimated as a percentage of total variance explained by all fixed effects. Though mean estimates are often substantial, credible intervals are generally wide with lower bounds that approach zero.

		SUCCESS		**PRODUCTIVITY**	
	Parameter	**Var.**	**CIs**	**Var.**	**CIs**
BLUE TIT	Mismatch	15.9	0.0, 44.3	53.0	25.7, 68.4
	Mismatch^2	43.9	6.6, 87.6	10.8	0.8, 34.1
	Peak Height (log)	13.6	0.0, 45.1	9.7	0.0, 38.4
	Mismatch by Height	17.4	0.0, 45.2	24.5	0.0, 36.8
GREAT TIT	Mismatch	31.6	0.0, 52.1	24.9	0.0, 51.3
	Mismatch^2	10.1	0.0, 61.4	8.5	0.0, 42.4
	Peak Height (log)	7.2	0.0, 64.1	34.5	0.7, 85.9
	Mismatch by Height	42.5	0.0, 61.0	22.9	0.0, 48.8
PIED FLYCATCHER	Mismatch	27.7	0.0, 86.2	33.9	0.0, 87.9
	Mismatch^2	7.0	0.0, 42.9	10.8	0.0, 37.9
	Peak Height (log)	5.3	0.0, 23.9	5.1	0.0, 29.2
	Mismatch by Height	51.6	0.0, 84.8	30.3	0.0, 82.0

Generating slope estimates of caterpillar peak height across all levels of mismatch, the effect is significantly positive for Blue Tit success from +3 to +12 days of mismatch, and productivity from -7 to +60 days mismatched (Figure 3d and 3j). In Great Tit, productivity increases significantly with increasing caterpillar peak height when nests are from -12 to +29 days mismatched, but it has no effect on Great Tit success (Figure 3k). The buffering effect of resource abundance may therefore only offset mismatch under certain circumstances, or this may be due to limited data outside of a central range of mismatch values and therefore poorly estimated slopes at those levels (see Figure 3 for distribution of raw data).

The interaction between mismatch and peak height explains substantial amounts of variation in the data for all Blue and Great Tit models (Table 1), however, although the effect approaches significance for Blue Tit productivity, the lower credible interval on the estimates is close to zero in all cases. This suggests that the magnitude of the effect of resource abundance on fledging performance is generally consistent across all levels of mismatch, across all species (though it tends towards increasing with increasing lateness for Blue Tit productivity, see Figure 3).

It is noteworthy that most of the increase in breeding performance attributable to increased resource abundance occurs over a small range of commonly occurring values of annual caterpillar peak height (Figure 5). Because the values of peak height are $\log_e$-transformed, the significant linear relationship implies a logarithmic relationship and, though the maximum observed peak height during this study was 81287 mg caterpillar biomass / m^2, 90% of all peak heights fall below 8608 mg of caterpillar biomass / m^2.

Pied Flycatchers differed in that they showed no clear peaked relationship between breeding performance and mismatch (either success or productivity). Although there is no significant linear or quadratic effect of mismatch, peak height approaches significance, as does a (negative) mismatch-by-height interaction (Table S8)—though both account for a small fraction of overall variance explained by the model (Table 1). The latter suggests that in years of

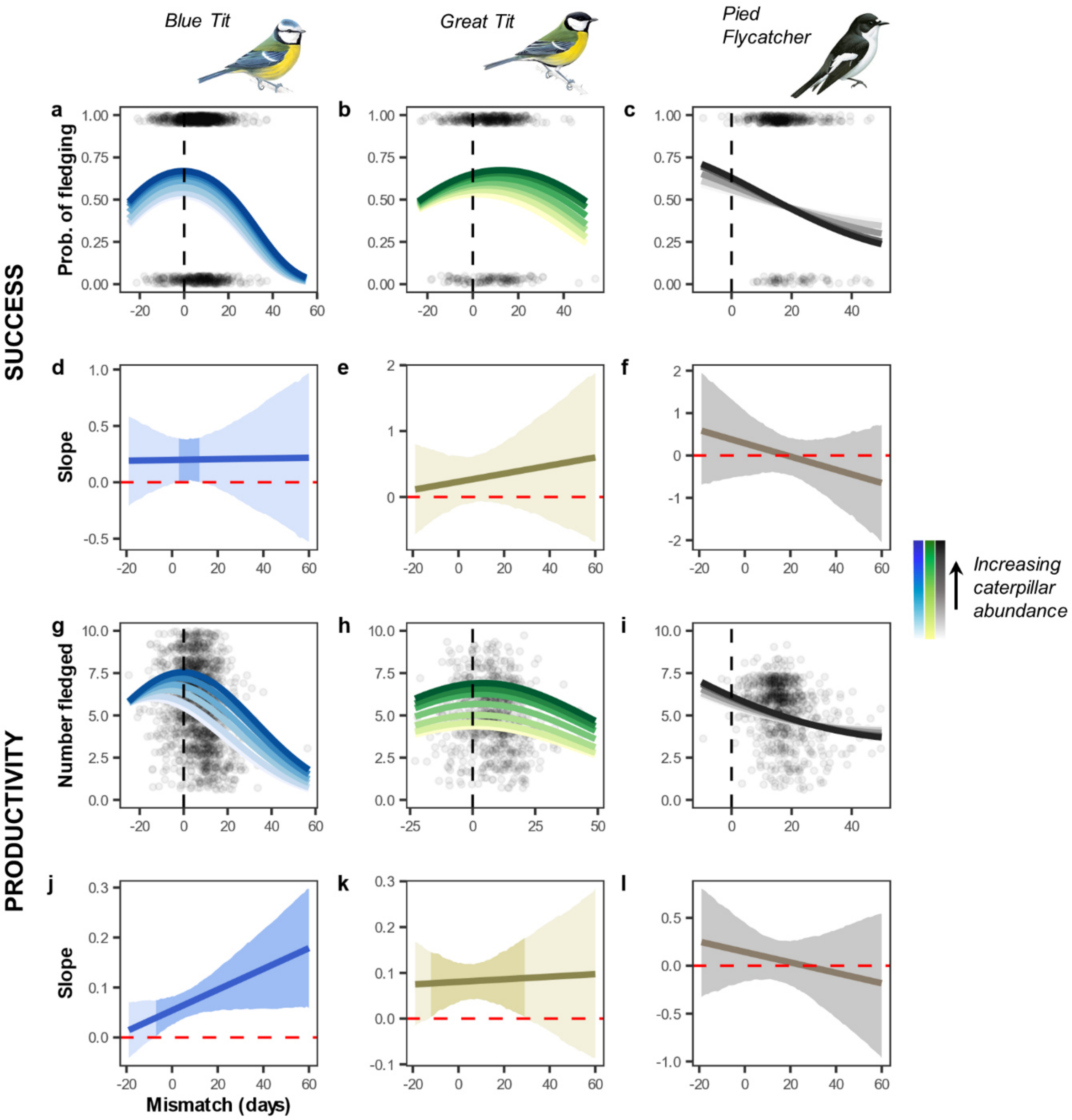

Figure 3. The effects of mismatch and caterpillar abundance on passerine breeding performance, estimated as nest success and productivity. Top panels (a, b, c, and g, h, i) show the peaked effect of mismatch on performance, where the darker lines estimate that effect at increasing levels of caterpillar abundance (see inset key). Caterpillar abundance quantified as the estimated height of the annual peak at each site/year combination. Maximum peak height used in the estimates varies across species (Blue Tits: 22000 mg/m^2; Great Tits: 13000 mg/m^2; Pied Flycatchers: 3500 mg/m^2) and is based on observed levels in our data. Lower panels (d, e, f, and j, k, l) show the estimated mean slope (with 95% credible intervals) of caterpillar abundance across a slice at each level of mismatch (see Figure S2). Credible intervals are shaded darker in lower panels where the slope is significantly different from zero, indicating that increasing caterpillar abundance increases performance at that level of mismatch. Bird drawings reproduced with permission from Mike Langman, RSPB.

high resource abundance, early-breeding Pied Flycatchers may perform better, but that they are relatively resilient to mismatch with caterpillars, even in low caterpillar abundance years.

Discussion

We find that higher annual peaks of caterpillar abundance significantly increase Blue Tit success, Blue Tit productivity, and Great Tit productivity, even when nests are asynchronous with peak timing. High annual resource abundance therefore has the potential to act as a buffer for these consumers on the negative fitness and population-level consequences of trophic mismatch.

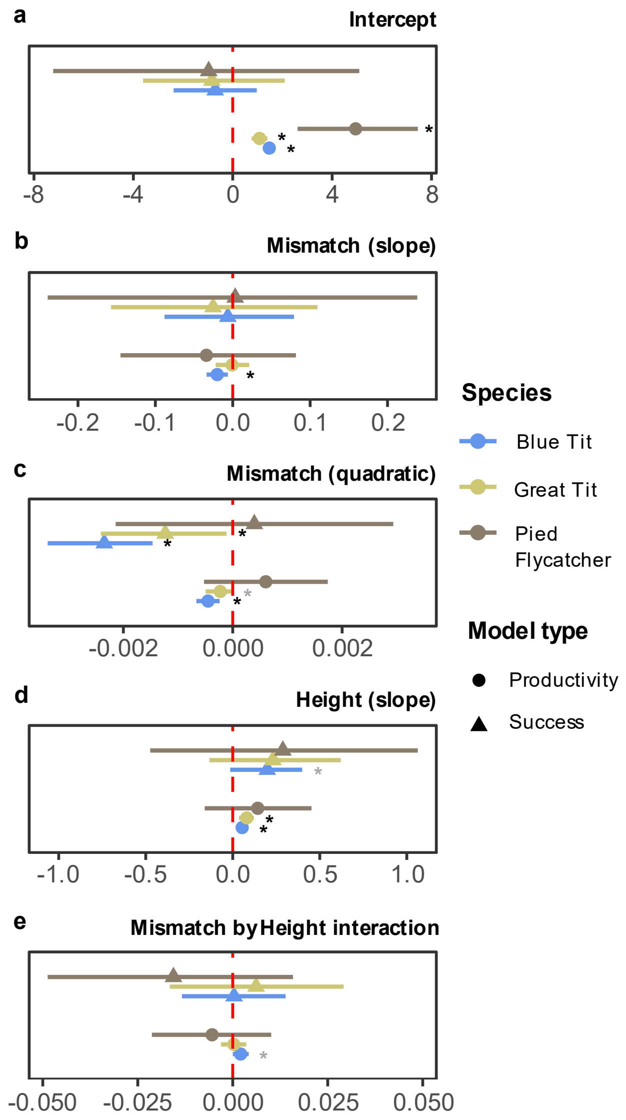

Figure 4. Estimated model coefficients for fixed effects, with significance indicated at the 0.05 (*) and 0.10 (*) levels. See for interpretation Figure S2.

Although we find no clear directional changes in spring temperature from 2008 to 2023 across the fourteen sites in England for which we have paired caterpillar abundance and bird breeding performance data, there are sizeable baseline temperature differences among sites and years. As spring temperature increases, estimated mismatch between peak chick food demand and peak caterpillar abundance increases significantly—commensurate with each trophic level having different phenological sensitivity to temperature. While trophic mismatch has significant negative effects on both the success and productivity of Blue and Great Tit nests, the capacity of resource abundance to act as a buffer could be important in contributing to the resilience of these species—both in the face of natural year-to-year variation in spring temperature, and future warming due to climate change.

Resource abundance as a buffer on mismatch

Although resource abundance can buffer mismatch, the distribution of estimated caterpillar peak heights for each site-by-year combination is highly skewed. This means that most of the increase in both breeding success and productivity occurs over a narrow range of values of caterpillar peak height (Figure 5), such that the effect begins to saturate at values of around one tenth of the maximum estimated site-by-year caterpillar abundance (max. approx. 25000 mg/m^2). Therefore, years of extreme caterpillar abundance do not result in commensurate increases to levels of breeding performance—and, as such, are likely not to be especially helpful in buffering mismatch, beyond a typical high abundance year.

While we did not observe any directional change in temperature across our study (Figure 1b), most of the variation in temperature is accounted for by among-year differences (84%), underscoring the pre-existing need for buffers within this system (Table S2). Adaptive buffering mechanisms, such as diet breadth (Burger *et al.* 2012) or plastic behavioural adjustments to egg hatching date (Cresswell & Mccleery 2003; Simmonds *et al.* 2017), likely serve to make individuals, populations, and species more resilient within an inherently variable phenological niche (Weir & Phillimore 2024). Buffering can also arise as an emergent property of heterogeneity in the landscape, generating portfolio effects (Markowitz 1952; Schindler *et al.* 2015) which smooth out the impacts of mismatch across coarser spatial scales. For example, microclimatic environmental variation can impact fine-scale plant (Kim & Oh 2025; Vitasse *et al.* 2021), insect (Checa *et al.* 2014; Greiser *et al.* 2022; Kerr *et al.* 2025; Rytteri *et al.* 2021), and bird phenology (Shutt *et al.* 2022), increasing spatial variability in timing, which can buffer mismatch at the population-level. Equally, spatial variation in the distribution and abundance of different resource taxa can introduce heterogeneity in the amount of local trophic match/mismatch, buffering the population-level effects of any asynchrony (Weir & Phillimore 2024). In coniferous woodlands, caterpillar abundance does not exhibit the distinct peak present in deciduous (especially oak-dominated) woodlands, which could act to soften the fitness costs of asynchrony for resident bird populations (Burger *et al.* 2012). At the landscape-scale—and the level of bird populations—variation in local tree species diversity, which influences the shape and timing of caterpillar abundance in spring, is very likely to be an important portfolio buffer acting on trophic mismatch. Indeed, even at a fairly coarse spatial scale, we find site effects are a major driver of both the amount of mismatch at the nest level (after controlling for temperature; Table S3), and breeding performance across all three species (after controlling for mismatch and resource abundance; Table S5). Great Tits are particularly sensitive to these site-

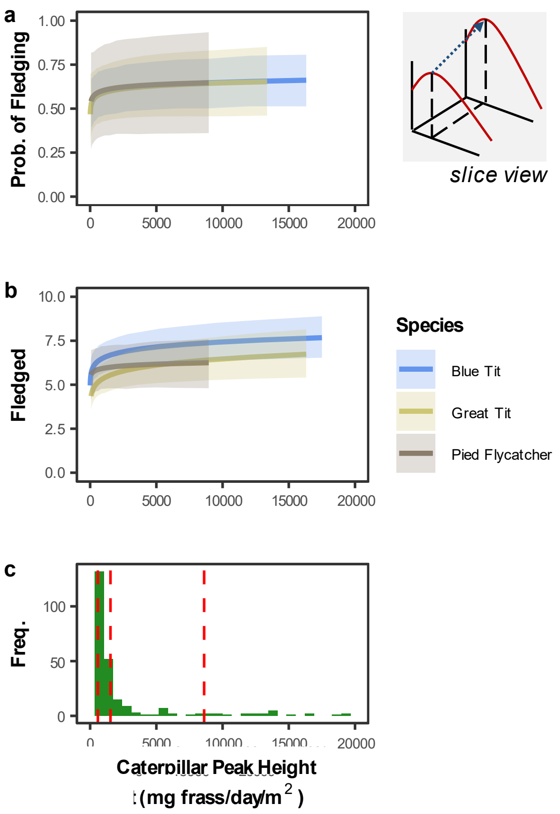

Figure 5. (a - b) The effects of caterpillar abundance on passerine breeding performance, where mismatch is zero. Performance is quantified as breeding success (probability of fledging offspring) and productivity (number fledged). (c) The height of the caterpillar peak across all site-by-year combinations is heavily skewed to low values, with occasional years of extremely high abundance. Vertical dashed lines (- - -) show distribution of recorded peak heights (*N* = 407) in our data, with 50% falling below 582 mg/m^2, 75% falling below 1536 mg/m^2, and 90% falling below 8608 mg/m^2. Passerine performance increases rapidly over a relatively low range of caterpillar peak height values, such that extreme years of caterpillar abundance do have marked effects on performance.

specific effects on performance (in terms of both success and productivity), as is Pied Flycatcher nest success (Table S5). Although also important for Blue Tits, site-specific effects on performance are outweighed by substantial year-specific effects (Table S5). As well as buffering mismatch and conferring resilience, these mechanisms are likely to make any performance effects of asynchrony more difficult to detect at the population-level.

Variation in the sensitivity of our three target passerine species not only to trophic mismatch but also to among-site and among-year effects may also partly reflect differences in their degree of dietary specialisation. Blue Tits feed more exclusively on caterpillars than Great Tits and Pied Flycatchers (Cholewa & Wesołowski 2011), and are likely therefore more dependent on fluctuations in the occurrence of those caterpillars (Figure 3). A broad diet could buffer the effects of mismatch in the latter two species, as well as helping to compensate for other negative drivers of population growth, such as rainfall (Martin *et al.* 2026; Nater *et al.* 2023). In Pied Flycatchers, a broader diet combined with breeding consistently later than both Blue and Great Tits could account for their general resilience to asynchrony with the caterpillar resource peak (Figure 3).

Buffering mechanisms, such as diet breadth and habitat specialisation, seem to trade-off with one another in different taxa and under different ecological circumstances (Weir 2023). For example, although Blue Tits are more common than Great Tits in Britain (Massimino *et al.* 2023), they are clearly more sensitive to mismatch in the data presented here (Figures 3 and 4; Table 1), fledging similar number of chicks to Great Tits despite laying initially larger clutches (from our data: $\bar{x}$ = 8.7 and SD = 1.9, versus $\bar{x}$ = 7.0 and SD = 1.6). Blue Tits may therefore opt for larger clutch sizes as a trade-off with increased specialisation on caterpillars as prey, in the expectation of higher overall mortality if mismatch occurs.

Resource abundance and future climate warming

Our data show annual temperature fluctuations of 4.8°C across sites, suggesting inherent robustness within the system to variation across this naturally occurring range. Estimated increases in mean summer temperature in England range from 1.8°C to 5.3°C by the end of this century, under low to high climate warming scenarios (Met Office 2022). Assuming no adaptive shifts in the temperature-mismatch reaction norm (Figure 2), we would expect a moderate warming scenario of 3.5°C (on top of our current 2008-2023 site average baseline, 10.12°C) to induce considerable levels of trophic mismatch in this system: 27.6 days in Blue Tit (CIs: 21.6, 34.1) and 31.0 days in Great Tit (CIs: 24.6, 37.3). This would result in significant declines in Blue Tit performance and substantial, though statistically non-significant, declines in Great Tit performance (Figure 3; Table 2). Could increases in caterpillar abundance offset these effects? In Great Tits, we find that the negative effects of mismatch are so gradual, there would be no statistically significant difference in terms of performance at the climate-induced end-of-century mismatch, relative to present-day zero mismatch, at median levels of caterpillar abundance. Even at *lower* caterpillar abundance, there is likely to be little difference in performance (Table 2). In Blue Tits, moderate increases in caterpillar abundance seem enough to offset the effects of end-of-century mismatch. Blue Tit productivity is most impacted, and in this case the minimum caterpillar peak height required to produce a non-significant difference in performance

Table 2. Predicted end-of-century mismatch, based on a moderate warming scenario for England (3.5°C). Performance at the predicted level of mismatch, based on our estimated temperature-mismatch reaction norm, is shown alongside present-day performance with perfect trophic match (i.e., zero mismatch). These are estimated for the median recorded caterpillar peak height across all of our data (582 mg/m^2). It is possible that the performance impacts of climate-induced mismatch could be offset by greater resource abundance, i.e., higher caterpillar peaks. The minimum caterpillar peak height required for there to be no statistically significant difference between present-day performance with zero mismatch and predicted levels of climate-induced mismatch is shown, as well as the % of peaks in our data which exceed this value to give some idea of commonality of abundance of this level. Blue Tit performance—which is most sensitive to mismatch—can maintain pre-climate change levels with moderate increases in caterpillar peak height.

		Success (log-odds) and Productivity (no. of fledglings) at zero mismatch and with median peak height	**Predicted end-of-century mismatch (days)**	**Predicted performance at end-of-century mismatch**	**Minimum peak height necessary to equal no mismatch (mg/m^2)**	**% Recorded frass peaks exceeding minimum value**
Blue Tits	**Success**	0.57 (CIs: 0.44, 0.69)	27.6 (CIs: 21.6, 34.1)	0.33 (CIs: 0.21, 0.45)	446	62
	Productivity	6.3 (CIs: 5.4, 7.1)		3.6 (CIs: 3.1, 4.4)	3905	14
Great Tits	**Success**	0.57 (CIs: 0.41, 0.73)	31.0 (CIs: 24.6, 37.3)	0.47 (CIs: 0.31, 0.64)	10	100
	Productivity	5.0 (CIs: 4.3, 5.9)		4.2 (CIs: 3.3, 5.1)	74	98

relative to present-day zero mismatch, at median peak height (582 mg/m^2), is 3905 mg/m^2—a level of biomass only exceeded in our dataset 14% of the time.

There is clear evidence that while warmer years lead to increased levels of caterpillar-bird mismatch (Figure 2) they also produce higher caterpillar peaks (Macphie *et al.* 2023; Smith *et al.* 2011), raising the possibility of bird performance being unexpectedly resilient under future climate change. Indeed, this built-in buffering mechanism—high temperature, high mismatch, high resource abundance *versus* low temperature, low mismatch, lower resource abundance—may underlie the long-term stability of the temperature-mismatch relationship in these species, which are seemingly subject both to high dependence on caterpillar match, and simultaneously high inter-annual variation in temperature (quite apart from any long-term linear temperature trends). However, we note that in Blue Tit, caterpillar abundance would need to increase to a relatively high level to offset the amount of mismatch expected under predicted end-of-century temperature changes (Table 2). Although the simple forward projection of a present-day reaction norm over 75 years is unrealistic (e.g. van Asch *et al.* 2013), it nonetheless highlights that while buffers have some capacity to offset mismatch, they can also be overwhelmed by environmental change of sufficient magnitude.

Integrating mismatch and buffering to understand resilience

Across taxa and trophic systems, variation in resource abundance likely represents an important factor modulating the effects of trophic mismatch—and yet, despite early recognition of its importance (Cushing 1982), it remains largely unexplored. In order to robustly assess the impacts of climate change on population recruitment, persistence, and even food-web stability, it is not sufficient to simply project phenological shifts and infer mismatch. Any forecasting framework seeking to evaluate the importance of mismatch must incorporate quantitative data on the extent and nature of reliance on the target resource taxa—ecological context that is currently sorely lacking. For example, surveying 125 diverse studies that expressly attempted to investigate the importance of trophic mismatch, Samplonius *et al.* (2021) found that only 26% included *any* quantitative assessment of the extent to which the consumer taxon actually relied on the identified 'ephemeral resource'.

Here, in a classic model species, we demonstrate that fluctuations in the abundance of a trophic resource can substantially alter the outcomes expected from any given level of mismatch, within a synchronised system. In woodland food-web studies that increasingly use vegetation green-up as a proxy for timing and synchrony (e.g., Cole *et al.* 2015; Morley *et al.* 2025), potentially pivotal resource fluctuations happening on the ground could go unnoticed. Our results are an important step towards developing a predictive model of mismatch under climate change that incorporates not only relative phenological shifts in a resource-consumer system, but also the modulating role of resource abundance. An integrated approach of this kind is vital to shed light on the true ecological threat posed by phenological mismatch.

Author Contributions

JCW led conceptual development of the study, carried out the analyses, and wrote the manuscript. KWS, LS, and MDB contributed extensively to conceptual development, edited successive drafts of the manuscript, and collected raw bird and caterpillar data. KWS also compiled frass data and converted to caterpillar biomass. KB, JRC, CRF, IF, LT, and BW collected raw bird and caterpillar data.

Data Availability

Code and data necessary to reproduce the results in this paper are archived at: https://github.com/jamiecweir/Henry_Walter_Bates.

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SUPPLEMENTARY MATERIAL *for*

Resource abundance can buffer trophic mismatch in a caterpillar-passerine food-chain

Jamie C. Weir, Ken W. Smith, Linda Smith, Kevin Briggs, John R. Clark, Chris R. du Feu, Ian Flack, Lewis Thomson, Barbara Wilton, Malcolm D. Burgess. (2026). *EcoEvoRxiv.*

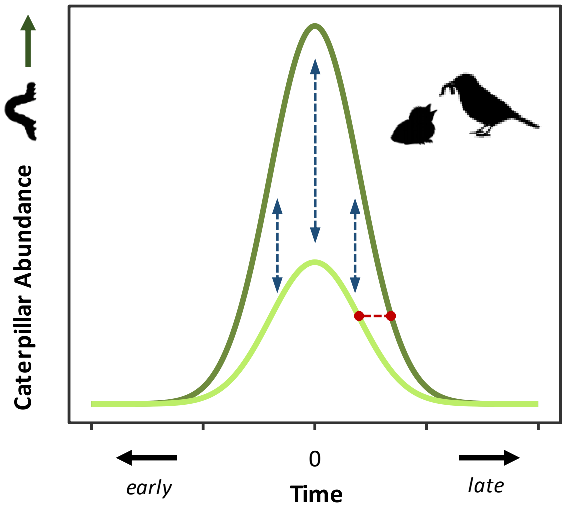

Figure S1. High annual peak caterpillar abundance can buffer trophic mismatch in nesting woodland birds. For any given time-point—whether chicks hatch in perfect synchrony with the peak of caterpillar abundance (Time = 0), or if they are asynchronous (hatching late or early)—the food available for parent birds to provision their chicks is consistently greater (**<-->**) when the annual caterpillar abundance peak is high (**dark green**) relative to when it is low (**light green**). High caterpillar abundance therefore has the potential to buffer some of the negative effects of mismatch. Indeed, the food available to parent birds (which is related to breeding performance) can be *equivalent* when chicks hatch **more synchronously but in a low peak abundance year** and when they **hatch less synchronously but in a high peak abundance year**. This is illustrated by taking horizontal slices (a fixed level of caterpillar abundance) through the two curves at any point (e.g., **•--•**).

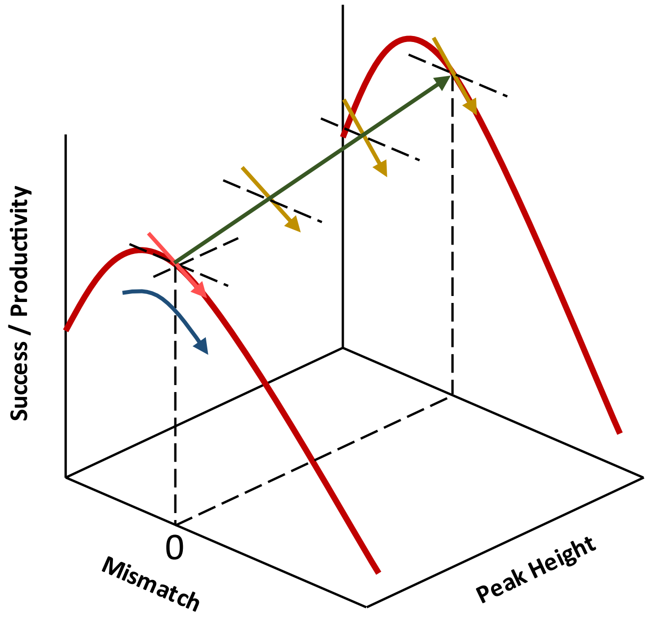

Figure S2. Interpreting the modelled relationship between performance (nest success and productivity), phenological mismatch, and resource abundance (peak height). The peaked performance curve, indicative of a **MATCH-MISMATCH RELATIONSHIP**, is represented by a linear effect of MISMATCH (the slope of performance where mismatch = 0) and a **QUADRATIC EFFECT** to describe the curved relationship (rate of change of performance with increasing mismatch). The slope of **PEAK HEIGHT** describes the change in performance with increasing caterpillar abundance (quantified as mg/m^2 of biomass estimated from frass-fall). The **MISMATCH BY PEAK HEIGHT INTERACTION** tests for any change in the effect of mismatch at different levels of peak height—allowing the overall shape of the performance peak to vary as peak height increases.

Table S1. Model structures and term interpretations. Interaction between terms indicated (as per *R* syntax) with “:”. All models were run for 3 million iterations, with a 1 million iteration burn-in. For a visual representation of model terms in (d) see Figure S2.

		Response/s and Error Distribution	**Model Structure**	**Term Interpretations**
(a)	**Temperature Change**	Mean April/May temperature (°C) Gaussian response	*FIXED*	
			Year (starting from zero)……	Linear change in Temp. across time
			RANDOM	
			Site (intercept)……………………	Baseline among-site differences
			Site (slope)………………………	Slope differences among sites
			Year (categorical)………………	Non-linear among-site differences
(b)	**Frass Peaks**	Peak Date (April days) (year by site by trap) Gaussian response *and* Peak Height (mg/m^2) (year by site by trap) Gaussian response	*FIXED*	
			Year (categorical)	
			Site	
			Year : Site…………………………	Interaction effect, allowing the effect of Year to vary among Sites
			RANDOM	
			Pan Trap Identity……………….	Control for differences among individual Pan Traps at a site
(c)	**Temperature Effects on Mismatch**	Mismatch (days) Gaussian response	*FIXED*	
			Mean April/May Temperature	
			RANDOM	
			Site (intercept)……………………	Baseline among-site differences
			Site (slope)………………………	Slope differences among sites
			Year…………………………………	Baseline among-year differences
(d)	**Mismatch and Resource Abundance Effects on Fledging Success**	SUCCESS (Did any chicks fledge?) (0/1) Logistic response *and* PRODUCTIVITY (Where chicks fledged, how many?) (count) Poisson response	*FIXED*	
			Mismatch (days)	
			log(Peak height [mg/m^2])……	Peak height of caterpillar biomass, log-transformed to allow fitting as a linear term
			$Mismatch^2$…………………………..	Quadratic effect of mismatch
			Mismatch : log(Peak height)…	Interaction effect, allowing the effect of Mismatch to vary at different Peak Heights
			RANDOM	
			Year (intercept)………………….	Baseline among-year differences
			Site (intercept)…………………..	Baseline among-site differences
			Box (intercept)…………………..	Baseline among-box differences
			Clutch Size (intercept)……….	Control for fledging success depending on number of offspring initially in brood

Table S2. Model estimates of temperature change across 14 sites in England, 2008-2023. For model structure and interpretation, see Table S1.

	Estimate/ Variance	**CIs**	**Effective Sample Size**	**Variance %**	**CIs**
FIXED TERMS					
Intercept	10.07	8.97, 11.12	20000		
Year (linear)	0.007	-0.11, 0.12	20000	3	0, 17
RANDOM TERMS					
Site (intercept)	0.12	0.04, 0.23	18977	8	2, 18
Site (slopes)	0.00005	0.00, 0.0002	20000	0	0, 0.3
Site by Year CoVar	-0.001	-0.004, 0.0007	18389		
Year (factor)	1.27	0.44, 2.40	4123	84	68, 95
Residual	0.04	0.03, 0.05	20000	3	1, 5

Table S3. Model estimates and variance components of mismatch-temperature relationship in three passerine species. For model structure and interpretation, see Table S1.

		Estimate/ Variance	CIs	Effective Sample Size	Variance %	CIs
Blue Tit	*FIXED TERMS*				12.5	3.0, 23.4
	Intercept	-44.8	-63.1, -28.5	9689		
	Temp (linear)	5.0	3.4, 6.8	9715		
	RANDOM TERMS				92.9	84.8, 98.9
	Site (intercept)	124.9	15.1, 322.6	9331	87.0	76.4, 96.4
	Site (slopes)	1.4	0.1, 3.5	9502	0.5	0.2, 0.9
	Site by Temp CoVar	-11.6	-31.1, -0.6	9478		
	Year (factor)	13.9	3.7, 29.6	7444	7.4	1.1, 19.3
	Box (intercept)	1.5	0.0, 3.1	9709	0.8	0.0, 2.3
	Residual	49.7	46.5, 52.9	10000	31.2	8.8, 53.4
Great Tit	*FIXED TERMS*				20.2	6.1, 35.1
	Intercept	-58.2	-83.9, -33.3	9699		
	Temp (linear)	6.4	4.0, 9.0	9640		
	RANDOM TERMS				79.6	64.9, 93.6
	Site (intercept)	71.0	0.0, 231.9	9454	31.6	0.00, 71.6
	Site (slopes)	0.5	0.0, 1.9	8787	0.1	0.0, 0.6
	Site by Temp CoVar	-3.8	-17.4, 1.8	9284		
	Year (factor)	21.1	4.1, 48.8	9478	12.3	1.6, 30.6
	Box (intercept)	2.8	0.0, 6.7	10874	1.7	0.00, 5.5
	Residual	68.7	61.9, 75.8	10000	50.3	16.3, 80.4
Pied Flycatcher	*FIXED TERMS*				21.5	5.1, 39.9
	Intercept	-31.1	-60.7, -6.2	8560		
	Temp (linear)	4.7	2.3, 7.7	8572		
	RANDOM TERMS				78.2	60.0, 94.7
	Site (intercept)	25.3	0.0, 90.7	10000	16.6	0.0, 62.3
	Site (slopes)	0.3	0.0, 1.1	10000	0.1	0.0, 1.0
	Site by Temp CoVar	-0.9	-5.0, 1.6	9466		
	Year (factor)	16.5	2.2, 44.0	8769	17.4	2.4, 45.8
	Box (intercept)	0.3	0.0, 1.2	10000	0.2	0.0, 1.8
	Residual	40.5	36.8, 44.2	9308	59.2	24.0, 88.3

Table S4. Pairwise comparisons of the mismatch-temperature relationship in three passerine birds.

Slope Comparisons	Slope Difference	CIs
Blue Tit vs Great Tit	-1.37	-4.41, 1.61
Blue Tit vs Pied Flycatcher	0.33	-3.13, 3.50
Great Tit vs Pied Flycatcher	1.70	-2.09, 5.68

Table S5. Variance components of passerine performance (success and productivity) with increasing mismatch and caterpillar abundance. Clutch size is fitted as a random effect to control for variation in initial clutch size as a predictor of final success/productivity, and % variance is shown as a proportion of overall variance. All other variance components are estimated as a % of the remaining variance, excluding clutch size. Fixed effects variances are shown as a % of total variance explained by all fixed effects to convey relative importance. For model structure and interpretation, see Table S1. For a visual representation of fixed effects model terms, see Figure S2.

		Parameter	**Var.**	**CIs**	**Parameter**	**Var.**	**CIs**
BLUE TIT	**SUCCESS**	ALL FIXED	13.6	5.7, 22.7	Intercept		
		Nest box	5.9	0.0, 16.1	Mismatch	15.9	0.0, 44.3
		Site	9.1	0.5, 29.7	Mismatch^2	43.9	6.6, 87.6
		Year	19.9	6.7, 39.2	Peak Height (log)	13.6	0.0, 45.1
		Residual	46.5	30.5, 61.7	Mismatch by Height	17.4	0.0, 45.2
		Clutch size	59.9	36.1, 81.0			
	PRODUCTIVITY	ALL FIXED	56.7	32.1, 77.8	Intercept		
		Nest box	0.4	0.0, 3.4	Mismatch	53.0	25.7, 68.4
		Site	9.5	0.0, 31.2	Mismatch^2	10.8	0.8, 34.1
		Year	27.1	10.3, 51.1	Peak Height (log)	9.7	0.0, 38.4
		Residual	1.9	0.3, 5.3	Mismatch by Height	24.5	0.0, 36.8
		Clutch size	55.5	33.2, 76.9			
GREAT TIT	**SUCCESS**	ALL FIXED	6.5	0.3, 17.9	Intercept		
		Nest box	3.6	0.0, 19.2	Mismatch	31.6	0.0, 52.1
		Site	41.3	15.1, 73.0	Mismatch^2	10.1	0.0, 61.4
		Year	6.6	0.0, 22.3	Peak Height (log)	7.2	0.0, 64.1
		Residual	35.5	15.7, 73.0	Mismatch by Height	42.5	0.0, 61.0
		Clutch size	65.0	35.0, 89.3			
	PRODUCTIVITY	ALL FIXED	57.8	20.1, 88.7	Intercept		
		Nest box	1.5	0.0, 11.9	Mismatch	24.9	0.0, 51.3
		Site	18.4	0.0, 60.5	Mismatch^2	8.5	0.0, 42.4
		Year	7.9	0.0, 33.7	Peak Height (log)	34.5	0.7, 85.9
		Residual	5.2	0.6, 16.0	Mismatch by Height	22.9	0.0, 48.8
		Clutch size	75.2	48.4, 93.9			
PIED FLYCATCHER	**SUCCESS**	ALL FIXED	18.7	3.0, 35.0	Intercept		
		Nest box	8.4	0.0, 31.3	Mismatch	27.7	0.0, 86.2
		Site	11.7	0.0, 64.5	Mismatch^2	7.0	0.0, 42.9
		Year	5.9	0.0, 20.8	Peak Height (log)	5.3	0.0, 23.9
		Residual	43.6	14.9, 70.1	Mismatch by Height	51.6	0.0, 84.8
		Clutch size	86.5	60.8, 99.4			
	PRODUCTIVITY	ALL FIXED	5.6	2.0, 9.3	Intercept		
		Nest box	3.2	0.0, 9.7	Mismatch	33.9	0.0, 87.9
		Site	1.9	0.0, 14.5	Mismatch^2	10.8	0.0, 37.9
		Year	1.3	0.0, 5.7	Peak Height (log)	5.1	0.0, 29.2
		Residual	85.9	73.5, 94.2	Mismatch by Height	30.3	0.0, 82.0
		Clutch size	44.4	18.3, 73.9			

Table S6. Model estimates for Blue Tit performance (success and productivity) with increasing mismatch and caterpillar abundance. Statistical significance indicated at the 0.05 (*) and 0.10 (*) levels. For model structure and interpretation, see Table S1. For a visual representation of model terms, see Figure S2.

		Estimate/ Variance	**CIs**	**Effective Sample Size**	
SUCCESS (Logistic)	*FIXED TERMS*				
	Intercept	-0.70	-2.38, 0.97	15259	
	Mismatch (linear)	0.01	-0.09, 0.08	18850	
	Mismatch^2	-0.002	-0.003, -0.001	18775	*
	Peak Height (log)	0.20	-0.01, 0.39	17942	
	Mismatch : Peak Height	0.0003	-0.013, 0.014	18843	
	RANDOM TERMS				
	Year (intercept)	0.49	0.12, 1.05	10642	
	Site (intercept)	0.28	0.01, 0.81	11886	
	Nest Box	0.15	0.00, 0.39	7487	
	Clutch Size (intercept)	3.66	0.87, 7.19	4840	
PRODUCTIVITY (Poisson)	*FIXED TERMS*				
	Intercept	1.47	1.25, 1.70	2498	*
	Mismatch (linear)	-0.02	-0.03, -0.006	1640	*
	Mismatch^2	-0.0004	-0.0007, -0.0002	1023	*
	Peak Height (log)	0.05	0.03, 0.08	1916	*
	Mismatch : Peak Height	0.002	-0.000, 0.004	1713	*
	RANDOM TERMS				
	Year (intercept)	0.01	0.00, 0.03	1569	
	Site (intercept)	0.005	0.000, 0.015	1158	
	Nest Box	0.0004	0.0000, 0.0014	1272	
	Clutch Size (intercept)	0.06	0.02, 0.10	1212	

Table S7. Model estimates for Great Tit performance (success and productivity) with increasing mismatch and caterpillar abundance. Statistical significance indicated at the 0.05 (*) and 0.10 (*) levels. For model structure and interpretation, see Table S1. For a visual representation of model terms, see Figure S2.

		Estimate/ Variance	**CIs**	**Effective Sample Size**	
SUCCESS (Logistic)	*FIXED TERMS*				
	Intercept	-0.84	-3.61, 2.09	16633	
	Mismatch (linear)	-0.03	-0.15, 0.11	15798	
	Mismatch^2	-0.001	-0.002, -0.000	18645	*
	Peak Height (log)	0.23	-0.13, 0.62	17154	
	Mismatch : Peak Height	0.006	-0.017, 0.029	15412	
	RANDOM TERMS				
	Year (intercept)	0.26	0.00, 0.72	15243	
	Site (intercept)	1.49	0.15, 3.67	9793	
	Nest Box	0.18	0.00, 0.63	7106	
	Clutch Size (intercept)	6.44	0.98, 14.52	4968	
PRODUCTIVITY (Poisson)	*FIXED TERMS*				
	Intercept	1.08	0.76, 1.39	2910	*
	Mismatch (linear)	0.0008	-0.022, 0.021	1961	
	Mismatch^2	-0.0002	-0.0005, 0.0000	1484	*
	Peak Height (log)	0.08	0.04, 0.12	2466	*
	Mismatch : Peak Height	-0.0003	-0.003, 0.004	2075	
	RANDOM TERMS				
	Year (intercept)	0.003	0.000, 0.009	1655	
	Site (intercept)	0.006	0.000, 0.019	1684	
	Nest Box	0.0007	0.0000, 0.0025	2231	
	Clutch Size (intercept)	0.07	0.01, 0.16	1154	

Table S8. Model estimates for Pied Flycatcher performance (success and productivity) with increasing mismatch and caterpillar abundance. Statistical significance indicated at the 0.05 (*) and 0.10 (*) levels. For model structure and interpretation, see Table S1. For a visual representation of model terms, see Figure S2.

		Estimate/ Variance	**CIs**	**Effective Sample Size**	
SUCCESS (Logistic)	*FIXED TERMS*				
	Intercept	-0.97	-7.23, 5.09	4515	
	Mismatch (linear)	0.003	-0.24, 0.24	16739	
	Mismatch^2	-0.0004	-0.0021, 0.0029	17331	
	Peak Height (log)	0.29	-0.47, 1.06	14631	
	Mismatch : Peak Height	-0.015	-0.049, 0.016	16033	
	RANDOM TERMS				
	Year (intercept)	0.19	0.00, 0.56	15004	
	Site (intercept)	0.88	0.00, 3.42	5986	
	Nest Box	0.29	0.00, 0.91	4717	
	Clutch Size (intercept)	25.24	1.32, 75.61	744	
PRODUCTIVITY? (Poisson)	*FIXED TERMS*				
	Intercept	4.95	2.61, 7.45	19648	*
	Mismatch (linear)	-0.03	-0.15, 0.08	20000	
	Mismatch^2	0.0006	-0.0005, 0.0017	20000	
	Peak Height (log)	0.14	-0.16, 0.45	20000	
	Mismatch : Peak Height	-0.005	-0.021, 0.010	20000	
	RANDOM TERMS				
	Year (intercept)	0.05	0.00, 0.14	19935	
	Site (intercept)	0.10	0.00, 0.38	20000	
	Nest Box	0.09	0.00, 0.23	20000	
	Clutch Size (intercept)	2.41	0.33, 5.82	17251	