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Martay, Blaise; Leech, David I.; Shortall, Chris R.; Bell, James R.; Thackeray, Stephen J.; Hemming, Deborah L.; Pearce-Higgins, James W. 2023. **Aerial insect biomass, but not phenological mismatch, is associated with chick survival of an insectivorous bird.** *Ibis*, 165 (3) 790-807, which has been published in final form at <https://doi.org/10.1111/ibi.13190>.

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Running Head: Impacts of insect biomass on an insectivore

Aerial insect biomass, but not phenological mismatch, is associated with chick survival of an insectivorous bird

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This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process which may lead to differences between this version and the [Version of Record](#). Please cite this article as doi: [10.1111/ibi.13190](https://doi.org/10.1111/ibi.13190)

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ABSTRACT

Recent insect abundance declines may have affected populations of insectivorous bird species, but evidence for this is limited. Here, we use spatially overlapping 29-year time-series of aerial insect biomass and Barn Swallow *Hirundo rustica* numbers and breeding success from southern England to model the association between changes in invertebrate prey abundance, Swallow productivity, and population trends. We found a positive statistical relationship between Swallow chick survival and the biomass of aerial insects available for chicks. In nests where at least one chick fledged, 96.7% of chicks were predicted to survive to fledging where there was high insect biomass (an average of 0.62 g day⁻¹), compared to 87.4% of chicks surviving to fledging where there was the lowest insect biomass (0.02 g day⁻¹; excluding the greatest and smallest 5% of insect biomass measurements). The amount of food available for chicks was largely a function of annual variation in insect abundance rather than the phenology of egg laying and insect emergence. However, we did not find a correlation between annual insect abundance and subsequent Swallow population growth. In the context of concerns about declining insect abundance, this study shows how changes in insect biomass may affect the productivity of an insectivorous bird at a regional scale, but with uncertain implications for population size at that same scale.

Key words Barn Swallow; *Hirundo rustica*; populations; productivity; phenology

INTRODUCTION

There is increasing evidence that insects are declining globally, and this is linked to habitat loss, agricultural practices and climate change (Conrad *et al.* 2006, Dirzo *et al.* 2014, Habel *et al.* 2016, Eisenhauer *et al.* 2019, Sánchez-Bayo & Wyckhuys 2019, Raven & Wagner 2021).

However, there is uncertainty about the severity, magnitude, and geographic scope of this phenomenon (Simmons *et al.* 2019, Thomas *et al.* 2019). The observed decline is likely to have detrimental impacts on insectivores, such as many bird species, with potentially far-reaching implications for ecosystems (Tallamy & Shriver 2021). There are many examples of insect declines reducing the breeding success of insectivorous birds (Seress *et al.* 2018, Pearce-Higgins & Morris 2023) and indirect evidence of links between insect populations and insectivore populations, such as insectivorous bird population declines where there is high pesticide use or low rainfall (Kuijper *et al.* 2009, Hallmann *et al.* 2014, Vickery *et al.* 2014). However, it is rare to find studies that directly examine the link between insect and insectivore populations (Miller-Rushing *et al.* 2010, Vickery *et al.* 2014, Møller 2019). At the same time, predator populations may be impacted by climate-driven changes in the relative timing of prey abundance and peak predator needs (Durant *et al.* 2007). Food requirements for insectivores often peak during the breeding season, but in response to warming can become asynchronous with a more rapidly shifting peak in prey abundance (Thackeray *et al.* 2010, Visser *et al.* 2012). Although more recent studies have often found that the impact of phenological asynchrony on productivity and population size is limited (Reed *et al.* 2013a, Burgess *et al.* 2018, Franks *et al.* 2018), there has been little research into the relative impact of concurrent changes in insect populations and phenological matching on the abundance of prey for insectivores (Kharouba & Wolkovich 2020). Understanding the links between insect populations, insectivore populations and phenological matching is important for predicting and mitigating against the consequences of future changes in insect populations for ecosystems (Pearce-Higgins 2011). If insectivore abundance responds directly to abundance of their insect prey, then land-use interventions to increase insect populations could be effective (e.g. Carroll *et al.* 2011), but if insectivore declines are driven

by phenological mismatch or weather/climate effects, then alternative mitigation strategies may need to be investigated.

Phenological mismatch has been hypothesised as a potential driver of the long-term population declines seen in some insectivorous birds, and particularly migratory species (Visser & Gienapp 2019), and has been found to affect woodland birds, as they often have relatively specialist diets and rely on caterpillars with a short window of availability (Burgess *et al.* 2018). However, more generalist feeders may not experience detrimental phenological mismatch (Mallord *et al.* 2017), and we currently lack sufficient evidence to make general statements about the significance of mismatch for wild populations (Samplonius *et al.* 2021). Examining the relative impact of changes in insect abundance throughout the breeding season for insectivorous birds could give much-needed evidence for the potential link between changes in insect abundance and phenology and avian population trends (Vickery *et al.* 2014 Tallamy & Shriver 2021, Pearce-Higgins & Morris 2023).

In this study we used the Barn Swallow *Hirundo rustica* as a model species to examine whether changes in insectivore productivity and population growth across southern England could be linked to local variations in insect abundance and phenological synchrony between predator and prey. Barn Swallow (henceforth referred to as Swallow) populations in England during the study had large fluctuations but no significant linear trend (Robinson *et al.* 2003), although since 2010 UK Swallow populations have undergone a significant decline (45% decline, Woodward *et al.* 2020). It is unclear what demographic drivers underpin population change in Swallows (Spiller & Dettmers 2019); population change has variously been linked to adult survival rates (Robinson *et al.* 2014), post-fledging survival of juveniles (Grüebler *et al.* 2014) and recruitment and clutch sizes (Møller 1989, 2001). Carry-over

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effects of winter and migration route rainfall can have an impact on breeding success (Ockendon *et al.* 2013, Finch *et al.* 2014) and adult survival (Robinson *et al.* 2008) of long-distance migrants. Breeding season weather and food availability may also affect Swallow populations. Typically, food availability and quality for insectivorous birds has the biggest impact during the nesting period (Twining *et al.* 2016), but the extent to which Swallow populations are affected by variation in nesting success and insect abundance is less clear (Imlay *et al.* 2017, Møller 2021).

Swallow diet during nesting can be very broad and variable but generally consists largely of insects 2 - 9 mm in length in the taxa Diptera, Coleoptera, Hymenoptera and Hemiptera, with proportions depending on availability (Møller 1994, Orłowski & Karg 2011, McClenaghan *et al.* 2019b, Bumelis *et al.* 2022). During the study period it has been suggested that some groups of flying insects, such as many pollinators and moths, have declined in abundance across the UK (although there is variation in trends between species within these groups) (Powney *et al.*, 2019, Bell *et al.* 2020), whilst others, such as winged mayflies and stoneflies, have increased (Outhwaite *et al.* 2020). Swallow laying dates advanced by 2.2 days per decade from 1967-2016 (Woodward *et al.* 2018), less than the observed advance in insect phenology in the UK over a similar timescale of between 3.5 and 8.7 days per decade (Thackeray *et al.* 2010). Swallow breeding performance, therefore, could be negatively affected by mismatch between peak food requirements and changes in peak insect abundance (Visser *et al.* 2012). Alternatively, the broad and variable diet of Swallows may prevent phenological mismatch (McClenaghan *et al.* 2019b), although they may still be affected by changes in the abundance of aerial insect populations.

In this study we examined Swallow nest monitoring data and count data between 1973 – 2002 across 125,000 km² in southern England (Fig. 1). These years were chosen to temporally match aerial insect abundance data from four long-running suction traps (Shortall et al. 2009) with nests located within a 100km radius of any of the traps. Firstly, we quantified the correlation between insect biomass/abundance and clutch size, hatching success and chick survival in individual Swallow nests, whilst accounting for the effect of changes in laying date and weather. Secondly, we identified the degree to which variations in insect biomass and abundance available for Swallow chicks were associated with changes in annual insect biomass and abundance; or the relative seasonal timing of insect biomass and abundance and Swallow egg-laying. Finally, we tested whether there was a significant relationship between annual insect biomass and abundance and subsequent Swallow population change (Fig. 2).

METHODS

Swallow productivity data

Swallow nest data recorded by volunteers from 1973-2002 and within 100 km radii of each of four selected RIS suction traps in southern England (Fig. 1) were obtained from the BTO's Nest Record Scheme (NRS; Crick *et al.* 2003). We use a heuristic 100 km distance from the insect suction traps to impose an ecologically meaningful radius around each trap when spatially matching invertebrate and avian datasets. This is based upon the finding that the 95% confidence intervals of the spatial covariance of a swallow prey species overlap zero at distances greater than 150 km (Taylor 1974; Supporting Online Information Figure S1). We therefore judged 100 km (taking a conservative estimate of the spatial covariance of 150 km) a reasonable distance for spatial autocorrelation in swallow prey, whilst also relating the trap data to a reasonable sample of nests. Furthermore, as aerial insect density is largely

dependent on variations in daily weather conditions (Grüebler *et al.* 2008), we considered it reasonable to assume that trap catches are relatively representative of temporal variation of aerial insects within 100 km, even if there is spatial heterogeneity caused by micro- and macro-habitat variation (Evans *et al.* 2003; Grüebler *et al.* 2008). Any potential mismatch in scales between the insects sampled by the swallows and the aerial insect abundance data would simply be likely to introduce additional uncertainty in the data. Most NRS data are associated with a four-figure (1 km²) grid reference, but those records lacking a grid reference were also included if they originated from a county with at least 95% overlap with the 100 km buffer of a suction trap.

It is recommended that NRS volunteers monitor nests every 4-5 days from when nests are found until no chicks remain. However, the frequency and timing of the visits is at each volunteer's discretion. The standard phenological metric derived from each nest record is the median possible date of laying of the first egg of the clutch (lay date), derived from observations of nest contents and chick ages, as defined by feather development, made on dated visits (Crick *et al.* 2003). Nests were excluded from the analysis if there were more than 12 days between the earliest and latest possible dates in which the first egg could have been laid. From these nest records we then calculated three variables for each nest where possible:

1. Clutch size: the maximum number of eggs observed on any visit, provided a visit was carried out before hatching.
2. Hatching success: brood size divided by clutch size in nests with at least one chick.

The brood size was the maximum number of chicks observed, provided that the nest was examined in the period 22-26 days after the laying date of the first egg, when all eggs are likely to have hatched but before maximum chick growth (6-9 days after

hatching; Fernaz *et al.* 2012), and therefore peak brood reduction, is likely to have occurred. Nests not monitored in this window were excluded from analyses of hatching success.

3. Chick survival: the number of chicks in the final visit before fledging divided maximum number of chicks seen. This calculation is subject to the constraint that the final visit took place fewer than 39 days after the first egg date because after this fledging may have begun (Robinson 2005), and that the first visit with the maximum number of chicks seen occurred before the final visit.

In measures of hatching success and chick survival we only included nests where at least one chick had hatched or fledged, respectively. The inconsistent timing and frequency of visits will lead to a bias in knowledge about the fate of nests with total failure compared to nests with some survival. For example, the outcomes for broods that fail early are more likely to be known than the outcomes for broods that don't fail. Additionally, events such as adverse weather conditions or predation are more likely to cause total nest failure, while low food abundance is more likely to increase in chick mortality, but not necessarily lead to total nest failure (Schaub & Von Hirschheydt 2009). For these reasons, we did not include nests with total failure in the analysis.

We examined whether Swallow productivity metrics correlated with mean aphid abundance and insect biomass, daily mean temperature and total daily rainfall.

Insect data

Four Rothamsted Insect Survey (RIS) 12.2 m suction traps located in southern England (Fig. 1) were operated from April to September over the period 1973 to 2002 (Macaulay *et al.*

1988, Shortall *et al.* 2009). Although the suction traps continued to operate after 2002, the insects caught after 2002 have not yet been processed. Aerial insects captured by the traps were processed every fourth day: aphids were counted, and all other insects were weighed (wet weight after draining) (Shortall *et al.* 2009). These methods of quantifying aphid and other insect abundance were used because these long-term datasets were collected primarily for other uses and are the only source of long-term large-scale data on diurnal aerial insect abundance available in the UK, covering changes in the abundance of groups like Hemiptera, Diptera and Hymenoptera. Given the observed large-scale covariation between trap catches, the insect biomass (excluding aphids) and aphid abundance available for each nest were estimated as those from the nearest suction trap (Fig. 1).

Swallow forage heights can vary, with some studies finding typical foraging heights of around 1m (Bryant and Turner 1982, Warrick *et al.* 2016), 9 m (Bryant 1975) and one study found average flight heights of 34 m (Dreelin *et al.* 2018). The suction traps sample at a height of 12.2 m (Macaulay *et al.* 1988), which is within the range of typical foraging height for Swallows.

Insects smaller than Swallows' typical prey can be very abundant (McClenaghan *et al.* 2019b) and may therefore make up a large portion of the suction trap catches. However, trends in total insect biomass recorded at one of our trap sites closely matched the trends in biomass of insects greater than 2 mm (Shortall *et al.* 2009). The composition of the catch (no. individuals > 2 mm, split by taxonomic group) was examined at two suction traps in a pilot study and the catch was found to be roughly 57% Hemiptera (largely aphids), 17% Diptera, 17% Thysanoptera and 6% Hymenoptera (CR Shortall, personal communication, 28th February 2021).

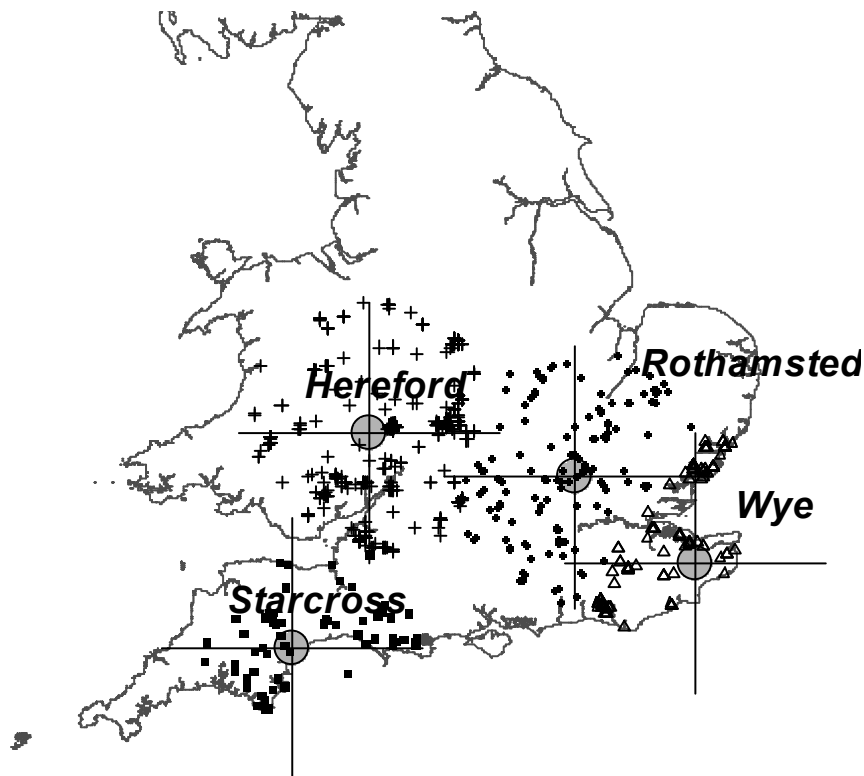


Figure 1. Location of Rothamsted Insect Survey suction traps. Four 12.2 m suction traps (large circles) in southern England, UK with 100 km radii shown (large crosses). Swallow nests within 100 km of a suction trap are shown by symbols, indicating which suction trap is the nearest to each nest.

Meteorological data

We extracted daily temperature and rainfall data from 5-km gridded UK climate data (Perry *et al.* 2009), as these variables could also affect Swallow productivity, and more proximately, access to food. Other weather variables which could affect aerial insect availability, such as wind speed was not available at the necessary temporal and spatial resolution. Mean daily temperature and total daily rainfall were spatially matched to each nest. Nests that lacked a grid reference but were located in a county with a 95% overlap with the 100 km buffer of a

suction trap (19% of nests included in this study) were assigned rainfall and temperature data spatially matched to the nearest suction trap.

To account for potential carry-over effects on clutch size and laying dates (Ockendon *et al.* 2013; Finch *et al.* 2014), we obtained values for the sum of rainfall during the wet season preceding the breeding season in question, across the area of southern Africa that matched the majority of wintering recaptures of Swallows ringed in the UK (Wernham *et al.* 2002) (November – March, 35° S–23° S, 17° E–33° E). We also obtained values for the sum of wet-season rainfall at Swallows' Sahel stop-over region (Jones 1995) (May – October, 11° N–17° N, 17° W–13° E). Rainfall data for these areas came from dataset TS3.20 (University of East Anglia Climatic Research Unit 2008) (Nicholson *et al.* 2000, Ockendon *et al.* 2013), created from station weather anomalies interpolated into 0.5° latitude/longitude grid cells to obtain monthly values (Harris *et al.* 2014).

Temporal matching of Swallow breeding data with insect abundance and meteorological variables

To match Swallow productivity variables with the insect abundance and meteorological variables in time, we calculated mean values for each variable in three time-windows:

1. Pre-laying: days -7 to -1, if the date in which egg laying was initiated is designated as day 0.
2. Incubation: days 0 to 17, the mean hatching date (Robinson 2005).
3. Nestling period: the day from the first visit after hatching to the day before the last visit before fledging.

Data analysis

All analyses were carried out using R version 3.3.1 (R core team 2016). All Generalized Linear Models (GLMs) and Mixed Models (GLMMs) were fitted using the ‘lme4’ package (Bates *et al.* 2015) unless stated otherwise. For all GLMs and GLMMs we standardised and centred all explanatory variables by subtracting the variable mean from values and dividing the result by the variable’s standard deviation. Where possible, we used the R-package ‘MuMIn’ to examine the model-averaged values of parameters from GLMMs including all possible combinations of explanatory variables (without interactions), weighting models by their Akaike weights (Barton 2009). 95% confidence intervals (CIs) for each model parameter were obtained, using the ‘full’ average. This assumes that each variable is included in every model, but in some models the corresponding coefficient (and its respective variance) is set to zero, making it a more conservative estimate than the ‘conditional’ average (Burnham & Anderson 2002). We considered a variable to be a significant predictor if its 95% confidence intervals (CIs) did not overlap zero, and 95% CIs throughout are presented in square brackets after parameter estimates.

For all models we checked for correlations between pairs of explanatory variables and found that none had a Pearson correlation coefficient r of > 0.7 , the threshold considered to prevent reliable model estimation (Dormann *et al.* 2013).

Analysis 1: The association of Swallow productivity with insect abundance and weather

Firstly, we determined whether Swallow productivity correlated with spatially and temporally matched insect biomass and aphid abundance. We hypothesised that correlations would be

strongest when food requirements were highest, between brood hatching and fledging. We used three GLMMs to determine whether any of the three productivity variables (clutch size, hatching success and chick survival) were associated with temperature, rainfall, aphid abundance and insect biomass (Fig. 2). In each of the three GLMMs we included nested random factors of trap-site and nest location, using 1-km grid references as the nest location, and we assessed the significance of explanatory factors using the methods described above (Supporting Online Material Table S1 for a summary of variables and structure).

For the clutch size model, we included the following explanatory variables: mean daily rainfall, temperature, aphid abundance and biomass of other insects (both log-transformed), with all variables calculated for the pre-laying week. Winter rainfall and stop-over rainfall from the preceding winter, and lay date were also included as explanatory variables, as these variables may correlate with clutch size (Bańbura & Zieliński 1998, Finch *et al.* 2014) (Fig. 2, Supporting Online Material Table S1). Clutch size variance was much smaller than the mean (0.5 and 4.6 respectively) making the data too under-dispersed for a standard Poisson model. We therefore modelled clutch size using a generalized Poisson distribution (a mixture of Poisson distributions which allows the variance to be greater than the mean (Brooks *et al.* 2019)) with a log link function, carried out using the ‘glmmTMB’ package in R (Brooks *et al.* 2017). We assessed the dispersion and residual distribution of this model using the ‘DHARMA’ package (Hartig 2016) and found it to be a good distribution for this data set.

For hatching success we included daily temperature and rainfall, aphid abundance and biomass of other insects (both log-transformed) as explanatory variables, all calculated for the incubation period (Fig. 2). We also included clutch size as a covariate because this could

affect the proportion of eggs hatching. We used a binomial distribution with a logit link function (Supporting Online Material Table S2 for a summary of variables and structure).

For chick survival, we included mean daily rainfall and temperature, aphid abundance and biomass of other insects (both log-transformed) as explanatory variables, all calculated for the nestling period. Mean chick age (i.e. mean of the age at the first visit after hatching and last visit before fledging) was also included as a response variable. The two-way interactions between chick age and each of the explanatory variables were also included to test for possible age-dependent relationships between chick survival and environmental variables. We also included brood size as a covariate. The observation period (i.e. the number of days between first visit after hatching and last visit before fledging) was included as an offset, to allow us to model daily chick survival probability. This was achieved by using a binomial error distribution with a complementary log-log link function (Bolker 2019) (Supporting Online Material Table S3 for a summary of variables and structure).

Analysis 2: The association of annual insect abundance and phenology with prey availability for Swallow chicks

In this analysis we examined the extent to which prey availability for Swallow chicks was determined by the overall annual insect abundance, and by the phenological match between when insects were abundant and when Swallows were breeding.

Firstly, we calculated the mean daily insect biomass and aphid abundance available for chicks in each nest (days 18-37 after laying), averaged within each of the four trap sites and each year (*insects_{Swallow_food}* and *aphids_{Swallow_food}*). Secondly, we calculated mean daily insect

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biomass and aphid abundance within each site and year, in the months in which insect biomass was recorded (April to September) (*insectspop_size* and *aphidspop_size*). The additional values we estimated were annual Swallow, insect and aphid phenology (*phenologySwallows*, *phenologyinsects* and *phenologyaphids*). We characterised insect and aphid phenology (*phenologyinsects* and *phenologyaphids*) as the date by which 5% of the total insect biomass or aphid abundance had been recorded in each site and year (following the approach used by Conrad *et al.* 2006 to characterise moth phenology). Annual variation in Swallow phenology was estimated by identifying the annual peak in initiation of first broods from a weekly moving average of the number of nests with their lay date on each day (Franks *et al.* 2018). Data were too sparse to directly calculate separate Swallow phenology values for nests around each of the four trap-sites, so these were calculated indirectly: we added the mean site phenology (site peak lay date across all years – peak across all years and sites) to the annual phenology estimates for all sites, to estimate Swallow phenology in each year and site (*phenologySwallows*). Given that only 5-13 nests were recorded annually prior to 1981, and 23-76 nests recorded from 1981-2002 across the four sites, this analysis was only conducted on the data collected after 1980.

We used a GLMM to examine whether prey availability (*insectSwallow_food*) correlated with *insectspop_size*, *phenologySwallows*, *phenologyinsects* and the interaction between *phenologySwallows* and *phenologyinsects*. Site was included as a random factor. We then repeated this analysis, replacing insect availability, biomass and phenology with aphid availability, abundance and phenology.

We also examined whether annual Swallow, insect and aphid phenology changed over time, modelling the annual Swallow phenology estimates (without the site-specific adjustments), $phenology_{insects}$ and $phenology_{aphids}$ in response to the year. We included site as a random factor in the models of insect and aphid phenology.

Analysis 3: The association of aphid and other insect abundance with Swallow population growth

We tested whether annual Swallow population growth in year I ($population_i/population_{i-1}$) in the 100 km radius around the four suction-trap sites correlated with annual aphid abundance or annual biomass of other insects in the previous year ($insects_{pop_size_i-1}$ and $aphids_{pop_size_i-1}$). Adult Swallows are generally faithful to previous nest sites (Shields 1984) so a population increase is most likely to be due to increased productivity in the previous year or increased survival of adults. The mean natal dispersal distance of Swallows was 14 km in one study (Paradis *et al.* 1998) although it is known to vary spatially (Balbontín *et al.* 2009). This is low enough to assume that most returning juveniles hatched within the 100 km radius.

First, we calculated an annual index of Swallow abundance in the circle of 100 km radius around each suction trap using Common Bird Census (CBC) data collected between 1973 and 2000, after which the CBC was not carried out (Marchant *et al.* 1990). This is the standard data used for calculating UK bird population trends prior to 2000 (Marchant *et al.* 1990). In this survey volunteers carried out territory mapping over 10 visits from mid-March to late June to estimate the number of breeding adults in areas selected by the volunteer of around 70 ha in farmland (or around 20 ha in woodland) (Marchant 1983). Breeding population was estimated in a mean of 32 areas around each trap-site in each year (minimum 9 areas, maximum 100 areas); 30.5% of these had at least one breeding pair of Swallows.

The annual population change at each CBC site was calculated ($\text{count}_{\text{year}_i} / \text{count}_{\text{year}_{i-1}}$). The log-transformed population change was modelled using a GLM with year and CBC site as explanatory factors. There were no sites with multiple observers, so observer did not need to be included as a random factor. We specified a Poisson error distribution and included the log of the site area as an offset. The population index for each 100 km radius surrounding trap sites was taken as the exponentially transformed year effects (Marchant *et al.* 1990), anchored to 1 in the first year of count data (1972) by adding $1 - \text{population}_{1972}$ to each value. Annual population growth at each trap-site was calculated as $\text{population}_i / \text{population}_{i-1}$.

Swallow population growth in year I was modelled using a GLMM (normal distribution with trap as a random factor) as a linear function of the site mean annual aphid abundance and insect biomass in year $i-1$. Annual rainfall on Swallow wintering grounds (southern Africa) and stop-over regions (the Sahel) in the winter between year $i-1$ and year i were also included as explanatory variables as they may affect adult survival. We found that there was some negative temporal autocorrelation ($\text{Phi} = -0.14$) so we included a first order autoregressive term in the GLMM ('corAR1' term in the 'nlme' R-package (Pinheiro *et al.* 2020)). The correlations between Swallow population growth and the response variables were taken to be the parameter estimates from the full models. To obtain confidence intervals around these parameter estimates we carried out bootstrapping with 1000 repeats on the counts at each trap-site, recalculating population indices and GLMM parameter estimates for each bootstrap. We repeated this analysis on detrended data to ensure any correlations were not an artefact of response and explanatory variables correlating with external factors (Votier *et al.* 2008).

Finally, we examined long-term trends in Swallow population index, aphid abundance and insect biomass (log-transformed means of daily aphid counts or insect biomass between April and September). For each time-series we fitted linear models of annual values at each trap-site with Gaussian distributions. To obtain confidence intervals around the trends in the Swallow population index we carried out bootstrapping with 1000 repeats on the counts at each trap-site, removing bootstraps if models did not converge.

RESULTS

In total, 945 nests were monitored in our recording period and area. Of these, 57 nests failed before hatching, 24 suffered complete brood loss and 505 successfully produced at least one fledgling. The brood outcome was not known for the remaining 359 nests.

Analysis 1: The association of Swallow productivity with insect abundance and weather

Clutch size could be calculated for 589 nests. Clutch size negatively correlated with lay date, indicating that early clutches were generally larger than late clutches (lay date parameter estimate = -0.042, [-0.057; -0.026], $z = 5.20$, $P < 0.001$) (Fig. 3; Supporting Online Material Table S1). All but the most extreme 5% of lay dates were between the 8th May and 29th July. The clutch size predicted on these lay dates were a mean of 4.9 eggs/nest and 4.3 eggs/nest respectively.

Of the 791 nests with at least one chick, hatching success could be calculated for 203 nests. Hatching success did not significantly correlate with any variables, using parameters averaged over all possible models (Supporting Online Material Table S2).

While there were 727 nests with at least one chick present in the final visit before fledging, only 345 of these were visited twice after hatching, allowing chick survival to be calculated. Removing records where there were gaps in weather and insect records, or second visits were more than 38 days after laying (after which fledging may have occurred), chick survival could be determined for 286 nests. Chick survival increased with insect biomass (parameter estimate for insect biomass = 0.429 [0.050; 0.808], $z = 2.21$, $P = 0.027$; Fig. 3; Supporting Online Material Table S3). There were no significant interactions between predictor variables and chick age. Assuming mean rainfall, temperature and chick age, and exposure of 20 days (the typical time between hatching and fledging), variation in insect biomass was linked to a change from 87.4% of chicks fledging where insect biomass was low (0.02 g day⁻¹, the lowest daily biomass excluding bottom 2.5% of values) to 96.7% fledging where insect biomass was high (0.62 g day⁻¹, the highest value excluding top 2.5% of values).

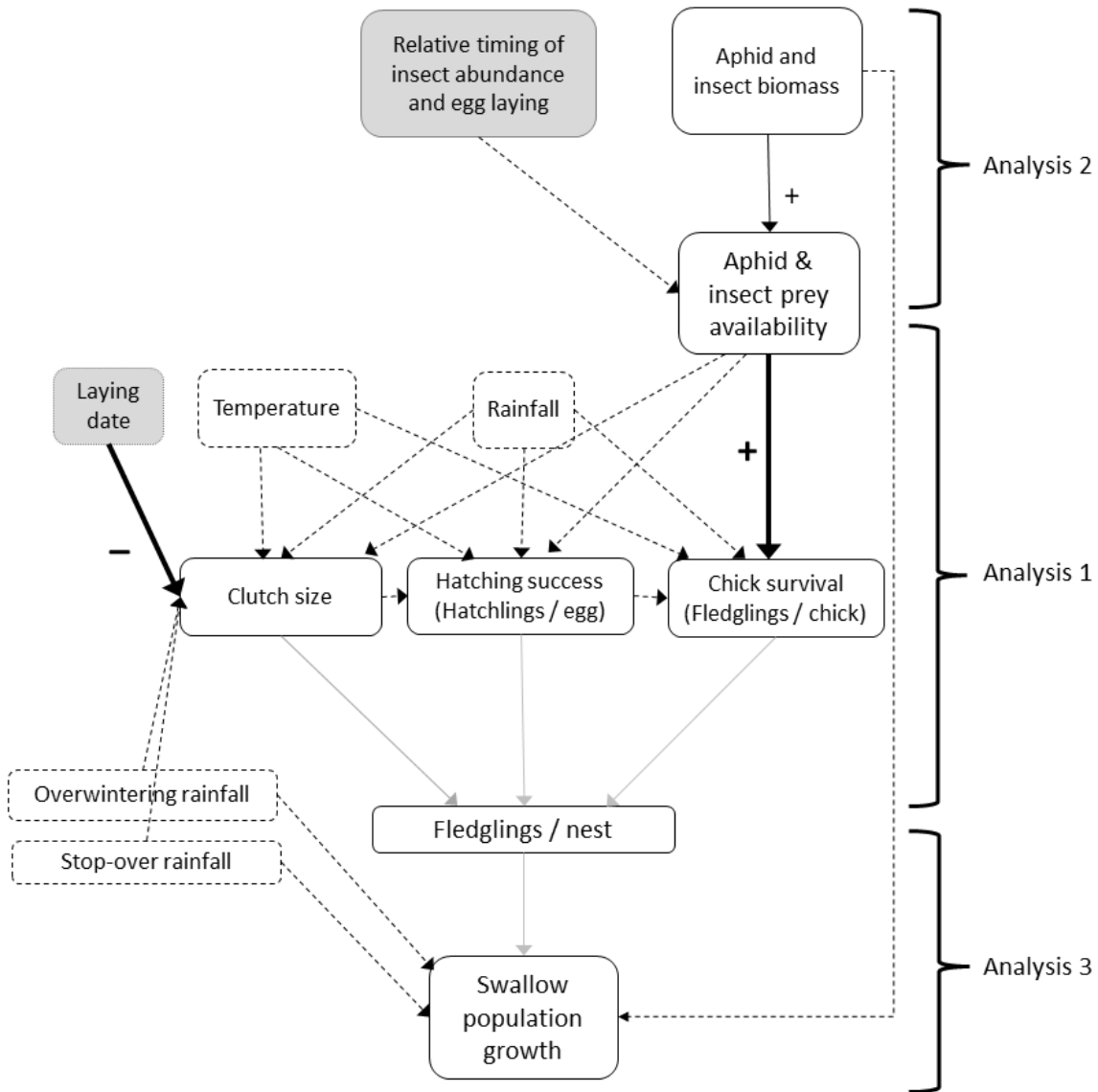


Figure 2. Schematic of all relationships tested in this paper. The hypothesised links between insect biomass, phenology, weather and Swallow populations. Significant relationships are shown with solid arrows, with the direction of influence and whether the relationship was negative or positive shown. Non-significant relationships are shown with dashed lines. Relationships that could not be tested are shown in grey. Weather variables are shown in dashed boxes and phenological variables are shown in grey boxes.

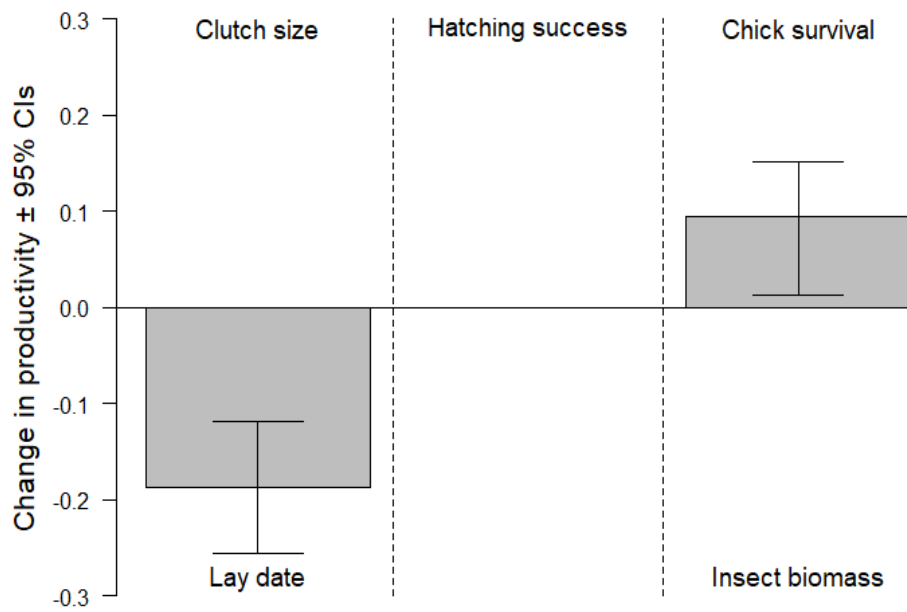


Figure 3. Factors significantly correlating with Swallow productivity. The change in productivity for significant factors associated with Swallow productivity \pm 95% confidence intervals. This was the predicted change in number of eggs laid (for clutch size) or change in number of chicks surviving. Chick survival was calculated from predicted daily survival rates, assuming a mean number of hatchlings and maximum exposure (20 days), given a change in the explanatory variable of 1 standard deviation within the observed values. Insect biomass was the mean biomass spatially matched to each nest from the week before the final pre-fledging nest visit.

Analysis 2: The association of annual insect abundance and phenology with prey availability for Swallow chicks

We identified two distinct annual peaks in egg laying, the first on 19 May and the second on 10 July, broadly corresponding to first and second clutches (Fig. 4a). Aphid abundance and insect biomass increased to a relatively stable level by mid-May (Fig. 4c, e). Swallow laying date advanced by 6.2 days/decade (parameter estimate = -0.620 [-1.18; -0.057], $P = 0.043$; Fig. 4b), while insect and aphid emergence phenology advanced by 4.2 and 5.9 days/decade respectively (insect parameter estimate = -0.419 [-0.681; -0.157], $P = 0.002$; aphid parameter estimate = -0.587 [-0.894; -0.281], $P < 0.001$; Fig. 4d, f).

Mean annual insect availability to Swallow broods correlated closely to annual insect biomass (parameter estimate = 0.852 [0.735; 0.969], $z = 14.29$, $P < 0.001$), and mean annual aphid availability to Swallow broods correlated closely to annual aphid count (parameter estimate = 0.578 [0.392; 0.764], $z = 6.10$, $P < 0.001$). Annual insect availability had no significant correlations with Swallow phenology, insect phenology or the interaction between Swallow and insect phenology (P -values respectively = 0.793, 0.870 and 0.997). Likewise, annual aphid availability had no significant correlations with Swallow phenology, aphid phenology or the interaction between Swallow and aphid phenology (P -values respectively = 0.720, 0.964 and 0.915). The fixed terms in the top models (i.e., insect abundance only or aphid biomass only) respectively explained 72.3% and 32.9% of the variation in annual aphid and insect availability for Swallow chicks. Thus, the main drivers of food availability for Swallows were overall insect and aphid abundance rather than the relative phenologies of insect and aphid emergence or Swallow laying dates.

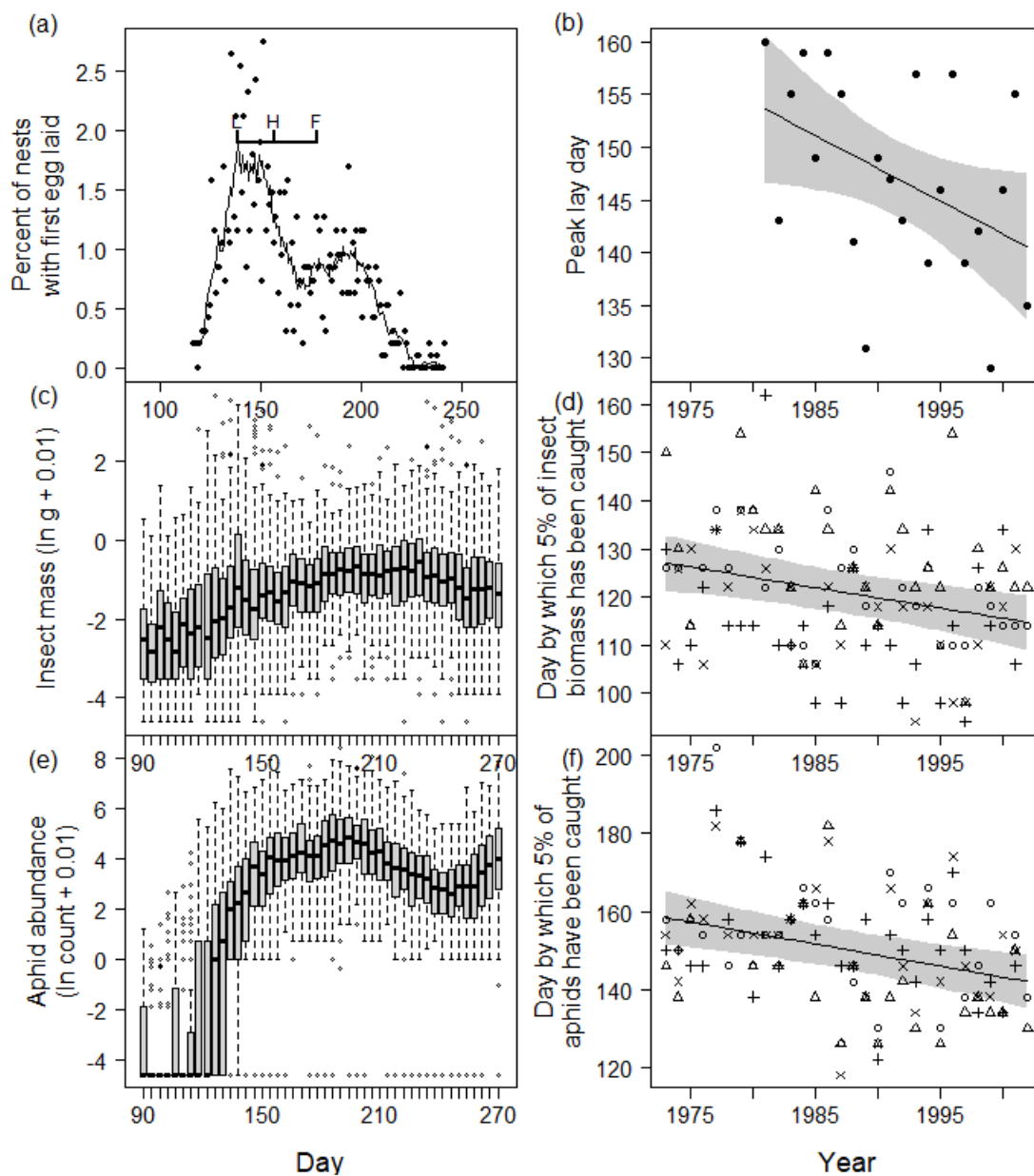


Figure 4. Phenology of Swallows, insects and aphids. Swallow laying dates (a and b) and insect biomass (c and d) and aphid abundance (e and f) are shown, within years (a, c and e) and across years (b, d and f) from 1973 to 2002 in southern England. In the seasonal distribution of Swallow lay dates (a), the points show the percentage of nests with lay date on each day, across all years and sites. The line shows the weekly moving average. Horizontal bars on (a) show mean laying (L), hatching (H) and fledging (F) for nests initiated at the peak of egg laying (Robinson 2005). The peak lay date in each year is identified and plotted in (b). In the seasonal distribution of insect biomass and aphid abundance (c and e), the

boxplots show the distribution of log-transformed biomass or counts recorded in each four-day period across all years and sites. Annual insect and aphid phenology (d and f) at each of the four trap sites are shown using site-specific symbols: Hereford (circles), Rothamsted (triangles), Starcross (plusses) and Wye (crosses). 95% confidence intervals around linear trends in Swallow, insect and aphid phenology are shown by the grey blocks.

Analysis 3: The association of aphid and other insect abundance with Swallow population growth

Annual Swallow population growth-rate between 1973 and 2000 (calculated from 3564 CBC records) associated with each suction trap was not correlated with annual aphid abundance (parameter estimate = 1.54×10^{-4} [95% CIs derived from bootstrapping (915/1000 bootstraps with converging models) = -2.29×10^{-3} ; 5.16×10^{-3}]) or annual insect biomass (parameter estimate = -6.56×10^{-4} [-2.34×10^{-3} ; 6.40×10^{-4}]) (Fig. 5). Population growth also did not correlate with Sahelian stop-over rainfall (parameter estimate = 1.67×10^{-3} [-1.12×10^{-3} ; 4.61×10^{-3}]) or southern African over-wintering rainfall (parameter estimate = 4.23×10^{-4} [-2.42×10^{-3} ; 4.31×10^{-3}]) (Supporting Online Material Table S4). All relationships were also non-significant when all variables were detrended (Supporting Online Material Table S5).

Swallow populations in our study period were stable within a 100km radius of two suction trap sites, Hereford (parameter estimate = 2.3×10^{-4} [-3.5×10^{-4} ; 7.2×10^{-4}]) and Rothamsted (parameter estimate = 2.5×10^{-4} [-2.6×10^{-4} ; 6.8×10^{-4}]), increased within a 100km radius of Starcross (14 non-convergent bootstraps removed, parameter estimate = 0.003 [0.002; 0.004]), and declined within a 100km radius of Wye (63 non-convergent bootstraps removed, parameter estimate = -5.8×10^{-4} [-0.008 ; -9.5×10^{-5}]) (Fig. 5). Annual insect biomass declined at the Hereford suction trap between 1973 and 2002 (parameter estimate = -0.045 [-

0.073; -0.016], $t = -3.1$, $P = 0.005$), increased at Rothamsted (parameter estimate = 0.024 [0.003; 0.045], $t = 2.2$, $P = 0.038$) and remained stable at Starcross and Wye (parameter estimate = 0.004 [-0.012; 0.021] and 0.008 [-0.006; 0.022], $P = 0.624$ and 0.265 respectively; Fig. 5). Aphid abundance showed no significant trend at any site ($P = 0.658, 0.723, 0.331, 0.728$ respectively; Fig. 5).

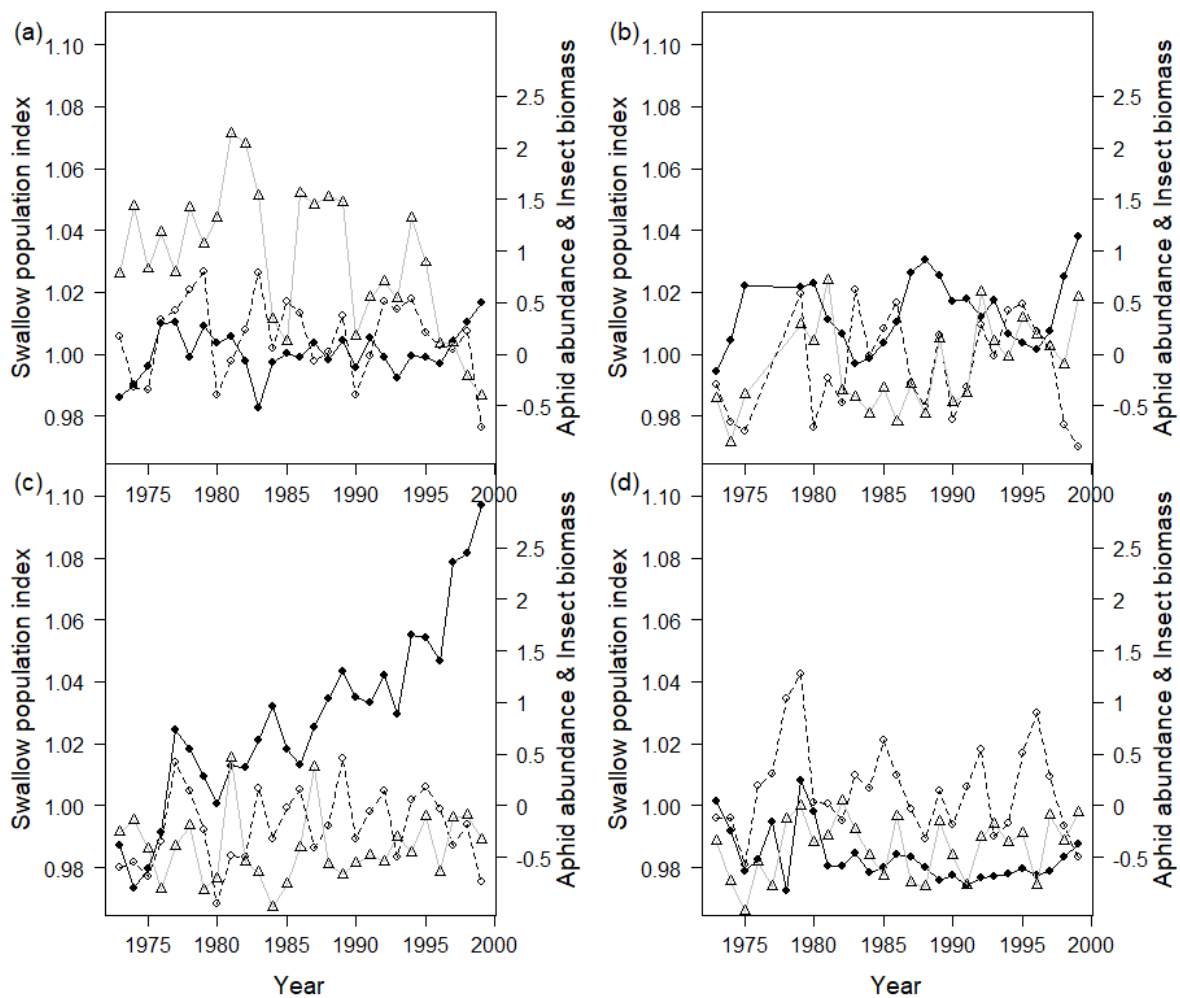


Figure 5. Trends in Swallow populations, insect biomass and aphid abundance. For four suction trap sites, (a) Hereford, (b) Rothamsted, (c) Starcross and (d) Wye, we show the Swallow population index (closed circles and solid black lines) within a 100km radius, and log-transformed aphid abundance (open triangles and solid grey lines) and insect biomass (open circles and dashed black lines) from each trap. Swallow population index was

calculated from a Poisson model of counts from the annual Common Bird Census in a 100 km radius around the trap-site, modelled against a factorial term for year and monitoring area. The resulting indices were anchored to 1 in 1972. Aphid abundance and insect biomass is the natural log of mean daily counts or weights between April and September in each year, subtracted from the log of the mean across all sites and years.

DISCUSSION

Using a 30-year time-series, we identified that Swallow chick survival in nests where at least one chick fledged was positively correlated with insect biomass, excluding aphids. This biomass consisted largely of Diptera which are usually the main component of Swallow diets (Møller 1994, McClenaghan *et al.* 2019b, Bumelis *et al.* 2022). This relationship means that in nests where at least one chick fledged, 96.7% of chicks were predicted to survive to fledging where there was high insect biomass (a mean biomass of 0.62 g day^{-1}) compared to 87.4% of chicks surviving to fledging where there was low insect biomass (0.02 g day^{-1}). Chick survival was still relatively high when insect abundance was very low, suggesting that foraging Swallows are still able to find prey for their chicks at these times. This may be because of variation in the relationship between the measure of insect abundance from the aerial traps and insect abundance as the swallows experience it, or because the adults are able to compensate for low insect abundance through their foraging ability. We found no evidence that the link between chick survival and insect abundance varied with chick age. Similar relationships demonstrating the importance of insect abundance in determining the breeding success of insectivores have been identified in other birds (Pearce-Higgins & Yalden 2004, Reed *et al.* 2013b, Ruffino *et al.* 2014, Imlay *et al.* 2017, McClenaghan *et al.* 2019a, Møller *et al.* 2021). While Swallow productivity was linked to insect biomass, we did not find evidence that subsequent Swallow population growth rate was correlated with annual insect

biomass, although Møller *et al.* (2021) did find that insect and Swallow abundance are correlated.

Insect biomass was measured up to 100 km away from the Swallow nests and using suction traps which will not be entirely representative of Swallow prey composition (McClenaghan *et al.* 2019b). Our measurements of insect availability were therefore crude and do not incorporate differences in insect abundances across differing macro- and microhabitats (Evans *et al.* 2003, Gruebler *et al.* 2010). Our estimate of the importance of insect biomass for Swallow productivity could therefore be an underestimate. However, we have no way of validating this, because long-term, high resolution insect monitoring is very rare. Potentially, the low resolution of spatial matching between insect trapping and Swallow counts could have limited our ability to identify a link between Swallow and insect populations. We suggest that future monitoring of insect populations in the immediate vicinity of monitored nests and populations would be a useful way to better quantify the link between insect populations and insectivorous bird productivity and populations (Pearce-Higgins & Morris 2023). Importantly, better monitoring of insect populations would improve our understanding of how best to conserve ecosystem functions in a changing world.

The biomass of insects during the period of peak food requirements of an insectivorous species (prey availability) can be determined by a combination of changes in insect population sizes (Pearce-Higgins 2010) and in the timing of their availability, for example as a result of phenological mismatch (Durant *et al.* 2005, Visser *et al.* 2012). Taking the example of Swallows, we showed that variation in annual insect biomass could account for 72% of the annual variation in insect prey availability. Swallow egg-laying and insect emergence advanced over the study period but we found no evidence that variation in the

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timing of egg-laying and insect emergence was significantly associated with annual prey availability to the Swallows as measured by the suction traps. Thus, there was no evidence that these predator populations were affected by phenological mismatch using the criteria set out by Samplonius *et al.* (2021): there was no asynchrony between the timing of prey availability and predator food requirements, and no evidence that asynchrony was affecting Swallow fitness or breeding population size. Previous work has highlighted a strong effect of phenological mismatch on some insectivorous woodland birds (Both *et al.* 2006, Visser *et al.* 2006, 2012, Reed *et al.* 2013b) which feed on caterpillars with a unimodal peak of abundance (e.g., Van Noordwijk *et al.* 1995, Both *et al.* 2006, Visser *et al.* 2006, Smith *et al.* 2011). The more generalist and variable nature of Swallow diet may reduce dependence on the abundance peak of a single prey taxon. Further, the lack of a simple unimodal peak in aerial insect abundance could remove or dampen the influence of phenological mismatch on Swallow breeding success (McClenaghan *et al.* 2019b).

We did not find that Swallow population growth correlated with insect or aphid abundance in the previous year, contrary to previous literature (Møller *et al.* 2021), which has found that productivity, recruitment and adult survival can all affect Swallow population growth. Møller (1989, 2001) showed that decreases in Swallow populations were linked to small clutch size and low recruitment of yearling Swallows. Rainfall in wintering areas can affect Swallow productivity: Swallows have been found to arrive and breed earlier in years when wintering-ground rainfall was high, which in turn led to an increased frequency of second broods (Saino *et al.* 2004, Ockendon *et al.* 2013). However, if winter rainfall affects productivity, the effect will not be seen in the adult population until the following year, which was not tested in this study. Unfortunately, our data did not allow us to examine variations in the frequency of second broods. Swallow population changes are also likely to be influenced

by mortality after fledging but prior to their first migration as this is when most post-fledging mortality occurs (Grüebler *et al.* 2014). Insect biomass during this post-fledging period could therefore have a large impact on Swallow populations and further research into this is needed.

There is mounting evidence for insect declines globally (Conrad *et al.* 2006, Dirzo *et al.* 2014, Habel *et al.* 2016, Eisenhauer *et al.* 2019, Raven & Wagner 2021) although this is not ubiquitous (Macgregor *et al.* 2019, Bell *et al.* 2020). Agricultural intensification is likely to have had a negative impact on aerial insect population sizes (Benton *et al.* 2002, Paquette *et al.* 2013, Møller *et al.* 2021), which has been shown to affect the foraging behaviour of another swallow species (Stanton *et al.* 2016). In this study, we found a long-term decline in insect biomass at one of four sites (Hereford), an increase at one site (Rothamsted) and stable populations at two sites, although subsequent analyses have also identified a decline in Diptera abundance (trends in biomass were not tested) at the Rothamsted suction trap (Grabener *et al.* 2020). Swallow population trends were also variable between the four trap-sites, although there was no obvious link between trends in insects and Swallows. Aphid abundance was stable at all sites. Swallow diet is diverse and the response of different insect taxa to environmental change will differ: warming may alter aphid population dynamics (Bell *et al.* 2015), but have a negative impact on Diptera associated with wet soils (Pearce-Higgins 2010, Pearce-Higgins & Morris 2023), both of which form a significant component of Swallow diets. In this study we found that Swallow chick survival was more dependent on the biomass of other insects, largely Diptera, than on aphids, and they may therefore be sensitive to declines in Diptera abundance (Grabener *et al.* 2020). We call for further studies of the contribution that large-scale declines in insect abundance may have had upon insectivore population trends.

In conclusion, this study provides evidence that changes in insect populations have the potential to generate population-level impacts at higher trophic levels. However, direct evidence of this is still lacking. In the UK, population trends of some insects are more negative in the south than elsewhere (Conrad *et al.* 2002, Fox *et al.* 2021), as are the population trends of many insectivorous birds (Massimino *et al.* 2015). Insectivore declines in the south could therefore be due to insect declines, but alternatively both groups of species may be responding negatively to other factors, such as agricultural intensification, habitat loss or climate change. Clearly, large-scale insect monitoring combined with existing large-scale data on populations of insectivorous species that feed on them, are required to better understand the extent to which insect populations have collapsed around the world, and the cascading implications of such declines for the wider food web.

Acknowledgements

This project was funded by NERC (project: NE/J02080X/1) and we are grateful to the SPACE II consortium. Additional funding was donated by Simon Cooke. The Rothamsted Insect Survey, a National Capability, is funded by the Biotechnology and Biological Sciences Research Council under the Core Capability Grant BBS/E/C/000J0200.

Debbie Hemming was supported by the Joint UK BEIS/Defra Met Office Hadley Centre Climate Programme (GA01101). We acknowledge the voluntary and professional contributions to the BTO NRS and the Rothamsted Insect Survey. We would also like to thank Simon Gillings, Alexandre Millon, Jeremy Wilson and reviewers for their comments on the manuscript, and Philipp Boersch-Supan for statistical advice.

Data Availability Statement

The data that support the findings of this study are available on request from the British Trust for Ornithology and Rothamsted Research.

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