

SYNTHESIS

The effect of insect food availability on songbird reproductive success and chick body condition: Evidence from a systematic review and meta-analysis

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Funding information

Division of Environmental Biology, Grant/Award Number: DEB-2225092; Office of Integrative Activities, Grant/Award Number: OIA-2019528; University of Connecticut; PEO International

Editor: Jonathan M. Chase

Abstract

Reports of declines in abundance and biomass of insects and other invertebrates from around the world have raised concerns about food limitation that could have profound impacts for insectivorous species. Food availability can clearly affect species; however, there is considerable variation among studies in whether this effect is evident, and thus a lack of clarity over the generality of the relationship. To understand how decreased food availability due to invertebrate declines will affect bird populations, we conducted a systematic review and used meta-analytic structural equation modelling, which allowed us to treat our core variables of interest as latent variables estimated by the diverse ways in which researchers measure fecundity and chick body condition. We found a moderate positive effect of food availability on chick body condition and a strong positive effect on reproductive success. We also found a negative relationship between chick body condition and reproductive success. Our results demonstrate that food is generally a limiting factor for breeding songbirds. Our analysis also provides evidence for a consistent trade-off between chick body condition and reproductive success, demonstrating the complexity of trophic dynamics important for these vital rates.

KEYWORDS

bird breeding success, insect decline, meta-analytic structural equation modelling, nestling body condition, prey availability, survival-reproductive success trade-off

INTRODUCTION

From the tropics to the tundra, entomologists have reported long-term declines in insect abundance, biomass and species richness over the past half century (Hallmann et al., 2017; Høye et al., 2013; Loboda et al., 2018; Roubik, 2001; Salcido et al., 2020; Wagner, 2020; Wagner et al., 2021). While not all insects are declining (Boyes et al., 2019; Van Klink et al., 2020), even local declines in insect abundance could have considerable ecological consequences. For example, nearly all terrestrial food webs include insects as critical links between plants and higher trophic levels (Kagata & Ohgushi, 2006; Yang & Gratton, 2014). For birds in particular, insect declines could have particularly influential impacts. Insects are the primary food source for 90% of all land birds, which

consume an estimated 400–500 million metric tonnes of insects annually (Nyffeler et al., 2018). Within passerines (songbirds)—which comprise the majority of all birds with roughly 6500 species—more than half have a diet composed of at least 70% invertebrates (Wilman et al., 2014). Even passerines considered primarily non-insectivorous as adults generally feed invertebrates to nestlings, suggesting a strong trophic link between insect populations and songbird productivity. Given this link, it is perhaps no surprise that parallel declines in insectivorous birds have also been reported over the past half century (Benton et al., 2002; Bowler et al., 2019; Reif & Hanzelka, 2020; Rosenberg et al., 2019; Thomas et al., 2004). The concurrent declines in insects and birds have raised concerns that insect decline could be having cascading effects on insectivores by reducing the

food supply (Bowler et al., 2019; Møller, 2019; Tallamy & Shriver, 2021).

Underlying these concerns is the fundamental assumption that food is generally limiting in bird species and that changes in the food supply can have large-scale consequences for their populations. Food resources are clearly important (Newton, 1980, 1998; White, 2008), but the degree to which they govern bird population dynamics is incompletely understood, despite being critically important for informed conservation decisions. For instance, previous reviews have shown that many experimental studies of food supplementation have failed to find the expected effects that would suggest food limitation (Dijkstra et al., 1990; Newton, 1998). There are many reasons why food may not be limiting for songbirds, or may not be detected. Adults may only choose to breed where there are sufficient food resources as is seen when there is an effect of habitat quality on nest site selection but not reproductive success (Chalfoun & Schmidt, 2012; Stillman et al., 2019). There is also evidence that females of many species adjust clutch sizes to account for anticipated food resources, obviating the importance of food availability on subsequent reproductive stages because broods are small enough that there are adequate resources (Lack, 1947). Dietary switching also could mitigate the effects of decreased availability of one food resource, such as insects, by substituting a more abundant resource (Holling, 1959; Real, 1977; Whelan et al., 1998), or food resources may simply be so abundant that other factors are limiting (Newton, 1980). In addition to the food supply, a tangled web of other factors can impact population processes, some of which may be far more important to insectivorous birds. For example, reproductive success can depend on factors as varied as predator abundance and nest predation pressure (Chalfoun et al., 2002), weather (Eeva et al., 2002; Imlay et al., 2018; Moreno & Møller, 2011; Shiao et al., 2015), pollution (Eeva & Lehikoinen, 2010), nest site availability (Samplonius & Both, 2019), mate attraction and pairing success (Dubois & Cézilly, 2002), among other factors (Newton, 1998). Further, the drivers of reproductive success can vary both inter- and intra-specifically (Boyle & Sigel, 2015), as well as changing over time and space, making it difficult to determine the degree to which food supply is an important factor at the population level compared to other drivers.

If food availability affects bird population dynamics, the two primary pathways proposed are through reproductive success and survival, which is mediated by body condition (Newton, 1980, 1998, 2004; White, 2008). The benefit of nesting when food resources are abundant is hypothesised to have led to synchrony between breeding activities and the timing of peak food abundance (Noor et al., 2005; Siikamäki, 1998), and is the mechanistic basis for many concerns about the phenological asynchrony that might result from climate change (Both et al., 2006; Stenseth & Mysterud, 2002). Uneven rates

of phenological change across trophic levels in response to climatic change (Thackeray et al., 2016; Youngflesh et al., 2021) may result in a scenario in which peak resource requirements (i.e., during chick rearing) are not temporally matched with peak resource availability (i.e., the seasonal peak in insect abundance). Under these conditions, breeding birds could face food shortages, leading to concerns that phenological ‘mismatch’ could have large-scale impacts on populations through reduced food supply (Both et al., 2009; Visser et al., 1998, 2004; Visser & Both, 2005; Zhemchuzhnikov et al., 2021).

Prey availability could also affect chick survival indirectly via body condition. Increased food supplies in the form of invertebrate abundance and biomass have been positively linked to higher chick immune function (Brzek & Konarzewski, 2007; Knutie, 2020), chick growth rates and mass at fledging (Shiao et al., 2019). Birds that can maintain high body mass have higher annual survival rates than those in worse condition (Cox & Cresswell, 2014; Danner et al., 2013; Rioux Paquette et al., 2014). When invertebrate prey abundance is low in a breeding season, adults may face a trade-off between allocating food resources to producing offspring, increasing offspring survival or maintaining their own body condition and increasing chances for future reproductive opportunities (Cox & Cresswell, 2014; Martin, 1987). Food-limited adult birds, such as those breeding in urban settings (Branston et al., 2021; Pollock et al., 2017) or out of synchrony with peak resources (Visser et al., 1998) must increase energy expenditure and foraging time to procure the same amount of food for nestlings. This expenditure can result in reduced adult body condition, nestling starvation or reduced condition, or increased risk of nest predation as parents become less attentive (Benton et al., 2002; Boulton et al., 2008; Martin, 1987).

Given concern about the cascading effects of insect decline on birds (Tallamy & Shriver, 2021), it is important to determine if food is generally limiting, and, when it is, how birds allocate limited resources. A holistic understanding of these questions through synthesis is complicated not only by the complexity of interacting factors, but also by the diverse ways in which researchers study food limitation. Multiple variables are used to estimate body condition (e.g., body mass standardised by age or size, pectoralis muscle shape and fat scores; see Brown, 1996; Labocha & Hayes, 2012) and reproductive success (e.g., number of fledglings, daily nest survival and recruitment). Similarly, food availability is quantified in multiple ways (e.g., total arthropod biomass, abundance of specific taxa and specialised indices using size classes) and measured with a variety of passive and active approaches (e.g., pitfall traps, sweep netting and caterpillar frass fall). In many cases, there is insufficient information about what birds actually eat to be able to quantify the food supply accurately for a given taxa. To get around this issue, many researchers have taken an experimental approach, using supplemental feeding to

test the effects of food limitation; however, food supplementation effects are influenced by natural variability in food abundance and species life history traits (Ruffino et al., 2014). Although some modelling methods (e.g., the approach used in this manuscript) can incorporate such variability, more unified and standardised data collection would facilitate stronger inferences in the long-term (Montgomery et al., 2021).

To bring greater understanding to the potential effects of insect declines on birds, we conducted a systematic review and meta-analysis to synthesize information from studies on the effects of invertebrate food availability on chick body condition and reproductive success for songbirds. To identify general patterns across the heterogeneous landscape of studies on this topic, we selected measures that are consistently used across studies for quantitative synthesis. We used the meta-analytic approach of three-stage structural equation modeling (Cheung & Chan, 2005; Wilson et al., 2016), which allows for core concepts such as food availability, body condition, and reproductive success, to be estimated as latent variables that are informed by any number of measurement variables. Combining meta-analytic structural equation modeling with data from our systematic review, we evaluated the information strength of different measures as indicators of the latent variables of interest, estimated the effect of food availability on chick body condition and reproductive success, and tested for a trade-off between chick condition and reproductive success.

MATERIALS AND METHODS

Literature search and assembly

The conclusions drawn from a meta-analysis are highly dependent on the set of studies included. Following systematic review principles (Pullin et al., 2018), such as pre-registering a protocol and thoroughly searching the literature, can help ensure reliable findings, yet these steps are often neglected in ecological meta-analyses (Grames & Elphick, 2020; Romanelli et al., 2021). When designing our literature search (see pre-registered protocol, Grames, Montgomery, et al., 2019 for full details), we identified three elements that needed to appear in papers as a minimum for them to be considered for our review: (1) a measure of either body condition or reproductive success, (2) a measure of invertebrate food availability or supplementation and (3) data from songbirds (Order: Passeriformes). For each of these elements, we identified search terms (Table S2) using the R package litsearchr v0.1.0 (Grames, Stillman, et al., 2019b, 2019c) and translated the complete search from English into other languages (Russian, German, Spanish, French, Japanese, Chinese and Portuguese) using Google Translate accessed through the litsearchr package. We searched 22

bibliographic databases, five thesis and dissertation repositories, one data repository, and one organisational website (Table S1) using Boolean search logic. We assembled all article bibliographic data into a single data frame and removed all but one record for duplicates using a pre-alpha version of the R package synthesizr (Westgate & Grames, 2020). Because not all databases allowed us to restrict our search only to the title, abstract and keywords, we used text mining to re-apply our search terms to the assembled results and removed those that had been retrieved from databases for spurious reasons (e.g., records with one of our search terms included in the journal title, author names or indexing classification scheme).

Inclusion criteria and article screening

To be included in the synthesis, a study had to: (1) occur during a non-transitory period of a species' annual cycle (i.e., not during avian stopover or migration); (2) measure bird body condition or reproductive success; (3) be conducted on wild songbirds; (4) measure invertebrate (e.g., insects, spiders and terrestrial molluscs) availability as a food resource with a comparison to different levels or with experimental manipulation; (5) take place in a terrestrial, aerial or freshwater habitat (see Grames, Montgomery, et al., 2019 for full definitions). Because both body condition and reproductive success are multifaceted and can be operationalised with a variety of definitions and measurements, we did not restrict the types of variables we would include. We included any effects the original authors considered to represent these outcomes, including when multiple variables were used to indicate the same effect (e.g., a binary measure of nest success and number of fledglings both being reported in a single study as measures of reproductive success). For body condition, we did not include unstandardised measures (e.g., body mass with no correction for size or age), changes over time (e.g., chick growth rates) or transitory responses (e.g., stress hormone expression) even if original authors considered these measures as representing body condition. For reproductive success, we did not include measures that occur prior to the nestling stage (e.g., egg mass or clutch size) because we were primarily interested in the proximate, as opposed to lagged, effects of food availability. For measures of food availability, we were primarily interested in studies documenting changes in invertebrate abundance and biomass. We also included study designs with known effects on invertebrate food availability, such as insecticide applications in treatment plots compared to control plots with no insecticide, comparing years with superabundant food resources (e.g., periodical cicada emergence) to years with average invertebrate food availability or providing supplemental invertebrates (e.g., mealworms). We did not include studies using proxy measurements for food

availability, such as weather conditions or comparisons between habitat types or sites assumed to differ in food quality (e.g., coniferous forests compared to broadleaf forests) when food availability was not directly measured, as the effects are confounded with other habitat and site-level differences.

To determine if articles met our inclusion criteria, we screened all articles by title and abstract, and excluded any that clearly did not meet our criteria. Based on a power analysis to calculate the number of articles that should be screened in duplicate before calculating intercoder reliability, a subset of 618 articles were each screened by two people at the title and abstract stage. Conflicting decisions at this stage were resolved by a third party and these decisions were used to calculate false negative and false positive error rates for each screener. We used error rates as an alternative to the kappa statistic (Cohen, 1968), which does not account for direction of error when there are discrepancies. A single screener with low error rates (EMG false positive rate = 0.024, false negative rate = 0.011) then screened the remainder of the titles and abstracts singly. Articles that were included at the title and abstract stage were passed on to full text screening. Due to the large number of articles, we combined full text screening with data extraction for efficiency; if an article met inclusion criteria at the full text stage, we extracted metadata and calculated effect sizes before moving on to the next article. For databases from which we could not export results (e.g., Dryad), we screened articles on the platform and included any articles that met our criteria at the full text stage.

Data extraction

For each study that met our inclusion criteria at the full text stage, we extracted information on the type of article, the bird species studied, and when and where the study took place. We extracted the years during which data were collected for the study and the time in the annual cycle relative to the birds' life history (e.g., non-breeding, clutch initiation, nestling, etc.). For study locations, we used the latitude and longitude, if provided by the authors, or the most specific place name available (e.g., the name of a national park in which data were collected). If no latitude and longitude were specified, we approximated the coordinates based on the place names used. When the authors described the habitat type, we extracted their description (e.g., 'savanna-like Cerrado vegetation'); when no description was available, we inferred the habitat type based on taxon-specific references and the geographical location. From the EltonTraits database, we added a measure of the proportion of diet that is invertebrates and a categorical diet guild for each species (Wilman et al., 2014).

Our primary predictor variable, food availability, can be measured with multiple indicators with multiple means

of data collection. Because of the high degree of variability that may lead to heterogeneity in the effects detected, we extracted the authors' description of how food availability was estimated (e.g., total biomass, abundance or other indices), the method used to collect and measure food availability (e.g., malaise traps, sweep netting and visual surveys), the type of invertebrate prey available (e.g., all species collected and only lepidopteran larvae) and the comparator used (e.g., plots not treated with pesticide and nests not receiving supplemental mealworms). Similarly, for both of our outcome variables, body condition and reproductive success, we extracted which type of outcome was measured and how the authors measured or defined it (e.g., number of fledglings, proportion of nests that fledged at least one young, mass-tarsus residuals, etc.). For measures of body condition, we also extracted the age and sex of the birds, if reported by the study authors. When studies reported data on more than one measure of body condition or reproductive success or for different groups of birds (e.g., adult females and adult males separately), we extracted all measures used, since our modeling framework allows multiple responses per study. Because of the large number of ways in which researchers have measured reproductive success and body condition, we reduced the number of measures by using the original authors' definitions to reclassify some measures post-hoc to a standard measure. For example, 'mass at fledging', 'chick body mass at day 15' and 'mean nestling weight on day six' were consolidated into a single measure of chick body mass corrected by age.

Because the meta-analytic approach we used requires pairwise effect sizes between all variables in the model to partition variance, we extracted effect sizes for relationships between all variables of interest. To calculate effect sizes, we used the raw data when possible or effects reported by the authors. We used the R package *metafor* 2.4.0 (Viechtbauer, 2010) to calculate effect sizes that were appropriate to the data presented by the authors (e.g., standardised mean difference when comparing treatment groups, odds ratio when proportions were presented, etc.). For studies with pre- and post-treatment measures for an experimental and control group, we created a custom function to calculate *dppc2*, the bias-corrected effect size estimate for pretest–posttest–control designs, using the formula by Morris (2008). We reverse-coded effects when variables indicated a negative relationship with our core concepts (e.g., effects associated with nest failure were reverse coded so that positive effects indicated higher reproductive success and pesticide application was reverse coded so that positive effects indicated higher food availability). We converted all effect sizes to correlation coefficients using *effectsize* 0.4.3 (Ben-Shachar et al., 2020). In several cases, the sample size was not reported and we inferred sample size from degrees of freedom or sample sizes that were reported for other measures on the population; for example, if the sample size was reported for tarsus length, but not for body mass corrected by tarsus

length, we assumed the sample size for each measure was identical. Effects presented separately for different species, sites or years in the same article were treated as separate studies based on their treatment as independent tests by the original authors.

Although we extracted all measures and effects of food availability, body condition and reproductive success as defined by the original study authors, we were only able to do a quantitative synthesis with variables that were consistently used across studies. To select such variables and reduce the number of missing pairwise effect sizes in our dataset, we created a square matrix of counts of effect sizes for all pairwise combinations of measures where rows and columns represent all possible variables. We iteratively reduced the dimensions of the matrix by dropping the variable with the most missing pairwise effect sizes until there were <10% missing effect sizes in the matrix for our response variables (Figure S1). We allowed missing effect sizes between pairwise combinations of our food availability variables, as it would be unreasonable to expect a study to report correlations between independent predictor variables (e.g., the correlation between whether a nest was provided with supplemental mealworms and frass fall in the surrounding area). We used variables that remained in the reduced matrix for subsequent analyses. To fill in the two remaining missing pairwise effect sizes, we introduced a non-existent study with an effect size of 0.001 and a sample size of two, giving them essentially no influence on the model results. To assess publication bias, we used Egger's regression test (Egger et al., 1997; Sterne & Egger, 2005) and a funnel plot across all pairwise effects of food availability on reproductive success or body condition, but not within-outcome measures which are secondary questions (e.g., the correlation between the number of nestlings and nest success) and therefore unlikely to be affected by publication bias.

Heterogeneity and moderator variable selection

We first used a multi-level random effects meta-analysis with random intercepts for study and effect nested within study to pool correlation coefficients with no adjustment for covariates. To assess heterogeneity, we used I^2 (Higgins & Thompson, 2002), a measure of the proportion of total heterogeneity that can be attributed to between-study variance as opposed to sampling error within studies. We then used meta-regression to determine which moderator variables explained heterogeneity in effects for the number of fledglings—the outcome variable with the most studies in response to one of the experimental food measures (i.e., supplementation and population suppression)—and the observational measures (i.e., biomass/abundance and frass fall). We assessed the magnitude of observed effects as a function of absolute latitude, proportion of diet that is invertebrates, if

the species is an insectivore, if the habitat studied was forest and an interaction between latitude and habitat. We collapsed habitat to a binary classification of whether a study was conducted in a forest or other habitat type.

To generate covariate-adjusted effects, we used the method described by Wilson et al. (2016). We fit a multi-level random effects meta-analysis with random effects for study and effect nested within study, and with fixed effects for habitat type, the proportion of the diet that is invertebrates, if the species is primarily an insectivore, absolute latitude and which two pairwise variables were represented by the effect. To calculate the covariate-adjusted effects, we added the predicted value at mean or modal values for the biological covariates (i.e., habitat, diet, diet guild and latitude) to the residuals from the model plus the adjustments for the two variables represented by the effect. We used the covariate adjusted effects for subsequent analyses.

We checked for heterogeneity in covariate-adjusted effect size estimates for each pairwise combination of the variables used to measure food availability with the outcome variables used to measure reproductive success and chick body condition. We did not check for heterogeneity in effect size estimates between outcome variables (e.g., the effect of the number of nestlings on the number of fledglings), as these are not of interest in our main model and are only used to partition variance. We estimated the amount of heterogeneity using τ^2 and Q-tests for heterogeneity (Cochran 1954), in addition to I^2 (Higgins & Thompson, 2002). Because we expected substantial heterogeneity, we also assessed whether our effect size estimates were stable for the measures that carry the most weight in our analysis. For pairwise variable combinations represented by at least 10 studies where we detected heterogeneity, we determined whether estimates were stable despite the heterogeneity by conducting a cumulative random-effects meta-analysis using the metafor package 2.4.0 (Viechtbauer, 2010) and calculating the difference in the cumulative mean effect size as each additional study was added. We bootstrapped a 95% confidence interval by randomly sorting the order in which new studies were added to the cumulative random-effects meta-analysis for 300 iterations. We considered the effect size estimate to be relatively stable if the absolute mean difference between two steps of the cumulative meta-analysis at any point was below a threshold of 0.05 and stayed below that point for three subsequent steps, meaning that the estimated correlation coefficient between two variables did not change by more than 0.05 as new studies were added.

Three-stage meta-analytic structural equation model

To investigate the connections between food availability and both chick body condition and reproductive success

across all types of measurements, we used three-stage meta-analytic structural equation modeling (Cheung & Chan, 2005; Wilson et al., 2016). This technique combines meta-analysis with structural equation modeling, a method that allows for causal inference (Pearl, 1998), resulting in a synthetic overview of relationships among variables of interest. Structural equation modeling also allows for latent variables, which are not directly observed but are instead measured by multiple indicator variables. Generally, meta-analytic structural equation modeling is a two-stage process in which meta-analysis is first used to generate a pooled correlation matrix across studies, which is then used to fit a structural equation model (Cheung & Chan, 2005). We used a three-stage approach more appropriate to complex datasets, however, in which effects are first adjusted for covariates (Wilson et al., 2016), as described above.

We pooled our covariate-adjusted effect size estimates across all studies using multilevel, random effects meta-analysis implemented in metafor 2.4.0 (Viechtbauer, 2010) with random intercepts for study and effect nested within study, resulting in a pooled correlation matrix and asymptotic covariance matrix. We adjusted our pooled correlation matrix to be positive-definite by finding the nearest positive-definite matrix using the Higham algorithm (Higham, 2002) with Dykstra's correction (Dykstra, 1983) as implemented in the R package Matrix 1.3–2 (Bates & Maechler, 2021). We then used the pooled covariate-adjusted effect sizes to fit the structural equation model using the R package metaSEM 1.2.5 (Cheung, 2015). In our structural model, we treated our predictor and response variables—food availability, chick body condition and reproductive success—as latent variables with the selected measures for each variable used as indicator variables (Figure S2).

RESULTS

Literature search and screening

Our systematic literature search retrieved 25,658 articles, of which 12,229 (48%) were duplicate records retrieved from multiple databases. After deduplication and using text mining to re-apply our search terms to the title, abstract and keywords of all retrieved studies, the full database for title and abstract screening contained 3004 records (Figure S3). After screening titles and abstracts only, we retained 1032 articles to screen at the full text stage, of which 417 articles (40%) met our inclusion criteria. We subsequently identified two additional articles from searching a data repository, resulting in 419 articles that met all of our inclusion criteria. For articles excluded at the full text stage, the most common reasons were that they did not contain a measure of invertebrate abundance ($n = 305$, 50%), did not report any measure of chick body condition or reproductive success ($n = 123$,

20%), or did not report original data ($n = 73$, 12%); though some studies could have been rejected for multiple reasons, we only recorded the most obvious reason for rejection for each study. We were unable to calculate effect sizes for 174 articles that met our criteria at the full text stage; these articles are included in our narrative and qualitative synthesis, but not in the quantitative synthesis. In most of the cases, the reason we could not calculate an effect size was because food availability was presented in a separate analysis of habitat quality that was not connected to analyses of body condition or reproductive success. The 125 remaining articles included in the meta-analysis represent 140 separate tests because we treated effects for different species, sites and years as separate if the tests were reported independently.

Characteristics of included studies

Most articles that met our inclusion criteria at the full text stage were published as journal articles ($n = 334$, 80%) or in theses and dissertations ($n = 78$, 19%). The datasets analysed in primary studies spanned from 1948 to 2018, with most of the studies taking place in the early 1990s to the early 2000s. On average, each study took place over 3.8 years (SE = 0.22), though the duration of studies ranged from a single season to over three decades (Perdeck et al., 2000; Vatka et al., 2011). All continents, except Antarctica, were represented by at least one study (Figure 1a); however, the dataset is heavily geographically biased, especially for studies included in the quantitative synthesis, of which only 15 (12%) were conducted outside Europe and North America. A total of 42 avian families (Figure 2a) were studied, comprising 201 bird species (Figure 2b) with a bias towards species that use nest boxes, such as *Parus major* ($n = 52$, 10%), *Parus caeruleus* ($n = 45$, 8%), *Ficedula hypoleuca* ($n = 22$, 4%) and *Tachycineta bicolor* ($n = 20$, 4%). The main habitats (Figure 2c) studied were temperate forest ($n = 152$, 28%), temperate grassland ($n = 102$, 19%) and arable land ($n = 64$, 12%).

When extrapolating the total estimated number of measures for each outcome, the accumulation rate did not approach an asymptote for either outcome (Figure S4). After reducing the number of variables (Figure S1), we were left with four widely used measures of invertebrate food availability: invertebrate abundance and biomass, frass fall, supplemental arthropods (primarily mealworms, *Tenebrio molitor*) provided to nesting pairs, and invertebrate population suppression due to pesticide application or invasive species. We retained five measures of reproductive success: hatching success, number of nestlings, number of fledglings, fledging success and nest success. Our final measures of chick body condition were tarsus length corrected by age, wing length corrected by age, body mass corrected by age and body mass residuals. In our set of studies for the meta-analysis,

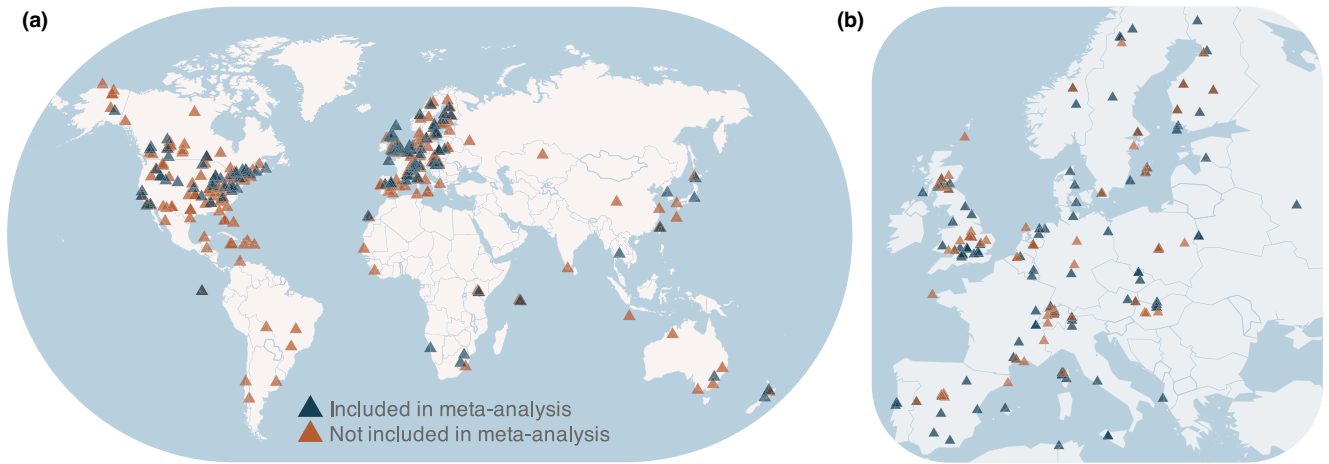


FIGURE 1 Locations of studies of songbirds documenting chick body condition or reproductive success in response to invertebrate prey availability (a) globally and (b) within Europe. Studies included in the meta-analytic structural equation model are shown in dark blue and those that were excluded due to duplicate data, uncommon measures or inability to calculate an effect are shown in orange. Study locations are approximate and have been adjusted to reduce overlap; when coordinates were not reported, a haphazard location based on the site description was assigned.

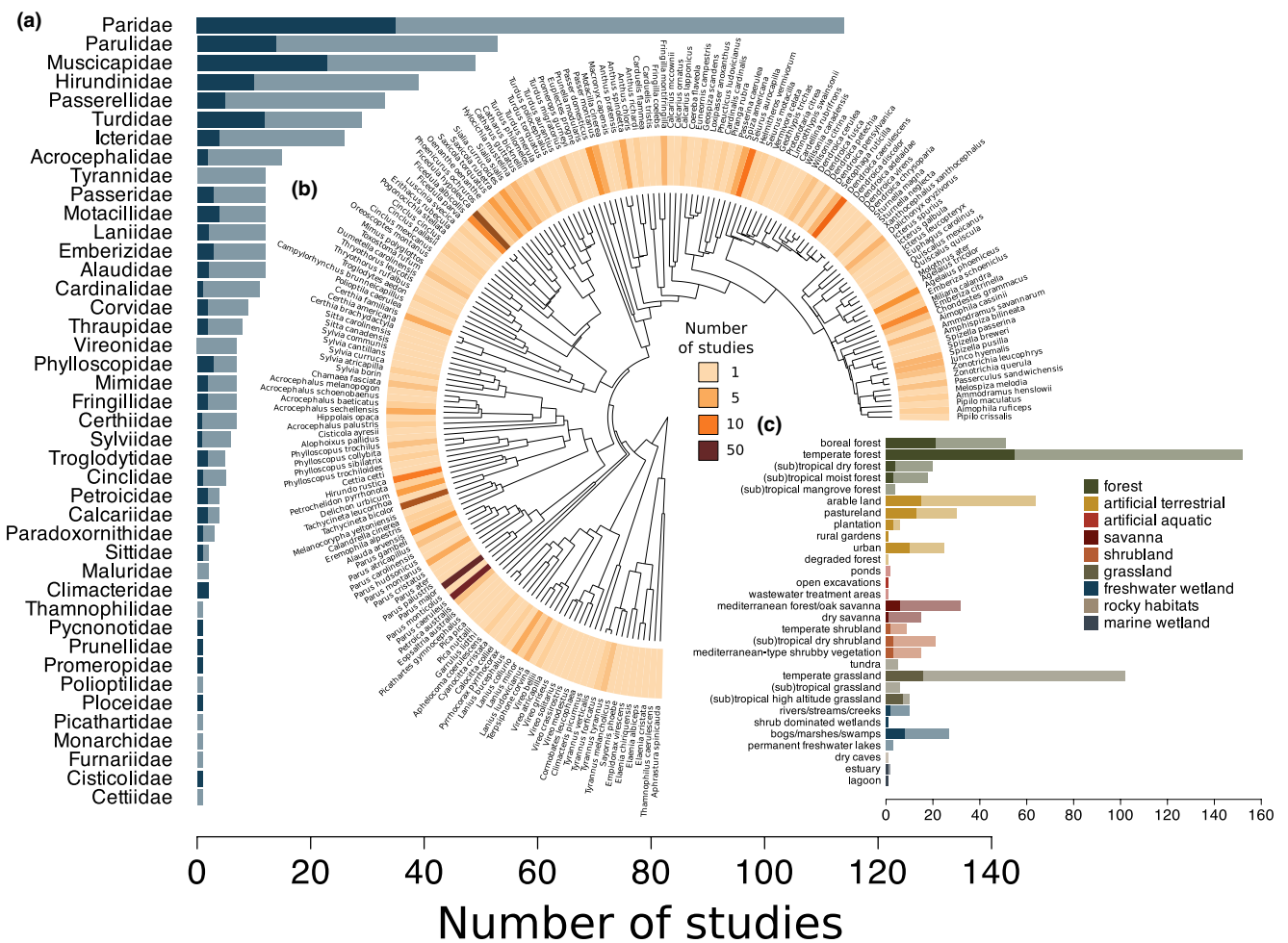


FIGURE 2 Number of studies of songbirds documenting chick body condition or reproductive success in response to invertebrate prey availability grouped by (a) family, (b) species and (c) habitat type(s) included in the study. In (a) and (c), the total number of studies is indicated by bar length, with darker portions of bars indicating the number included in the meta-analysis. In (b) darker colours indicate more studies regardless of inclusion in the meta-analysis.

there were no studies reporting the effect of frass fall on chick wing length corrected by age, or for the effect of population suppression on chick body mass residuals. We did not examine adult body condition in our model, despite screening for this variable in our review, because there were too few studies reporting pairwise effect sizes for any measures of adult body condition with those for reproductive success or chick body condition. We found significant publication bias ($z = 2.06$, $p = 0.04$) across studies in the database (Figure S5).

Meta-regression and heterogeneity

When pooling correlation coefficients across studies for each pairwise combination of variables (Figure 3), a large proportion of heterogeneity in effects was attributed to between-study variation ($I^2 = 76.6\%$). Our meta-regression of the effects of invertebrate biomass/abundance on the number of fledglings (Figure 4a–c) showed heterogeneity that was not explained by the covariates ($Q = 133.58$, $p < 0.001$), though there was no evidence for heterogeneity in the corresponding meta-regression for supplemental invertebrates (Figure 4d–f) as the measure of food availability ($Q = 21.80$, $p = 0.29$). In the biomass/abundance model, studies conducted in habitats other than forests had smaller effect sizes ($\beta = -1.08$, 95% confidence interval = -1.79 , -0.38) and there was an interaction whereby

forest studies had even larger effects than those in other habitats at more polar latitudes ($\beta = 0.02$, 95% CI = 0.01 , 0.04). Latitude did not have an independent influence on effect size magnitude (est = 0.00 , 95% CI = -0.01 , 0.01), nor did proportion of the diet composed of invertebrates ($\beta = 0.00$, 95% CI = -0.01 , 0.01) or if a species was primarily insectivorous ($\beta = 0.09$, 95% CI = -0.25 , 0.43). In the meta-regression testing moderator relationships for the effect of supplemental invertebrates on number of fledglings, there was again a significant effect of habitat with smaller effects for studies conducted in habitats other than forest ($\beta = -1.05$, 95% CI = -1.69 , -0.41) and an interaction with latitude ($\beta = 0.03$, 95% CI = 0.01 , 0.04), but no clear effect for latitude on its own ($\beta = -0.01$, 95% CI = -0.01 , 0.00). There was an effect of proportion of diet that is insectivorous on the magnitude of effect sizes ($\beta = -0.01$, 95% CI = -0.02 , -0.01), with species more specialised on invertebrates showing weaker responses to food supplementation; there was no evidence for an effect of diet guild ($\beta = 0.19$, 95% CI = -0.04 , 0.42). Despite diet guild not having an effect in the meta-regressions, we included in the model for covariate adjustment (Figures S6 and S7) because removing it increased the proportion of heterogeneity attributed to between-study outcomes in the supplemental invertebrate meta-regression by 8.7% (I^2 without diet guild = 26.6%).

Q-tests indicated there was heterogeneity in the true outcomes for 14 of our 20 pairwise comparisons for

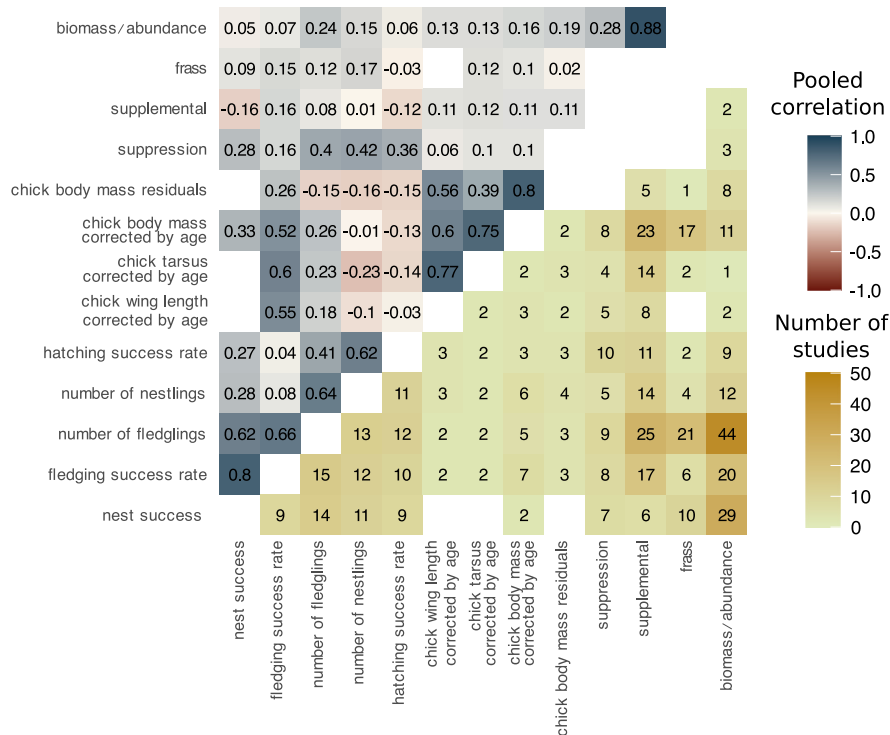


FIGURE 3 Heatmap of pooled correlation coefficients across studies before adjusting for covariates and the number of studies reporting each correlation, reported above and below the leading diagonal respectively. Stronger positive (blue) and negative (red) correlations are indicated by darker colours. Darker yellows indicate more studies; missing values are shown in white. See Figure S7 for covariate-adjusted correlations.

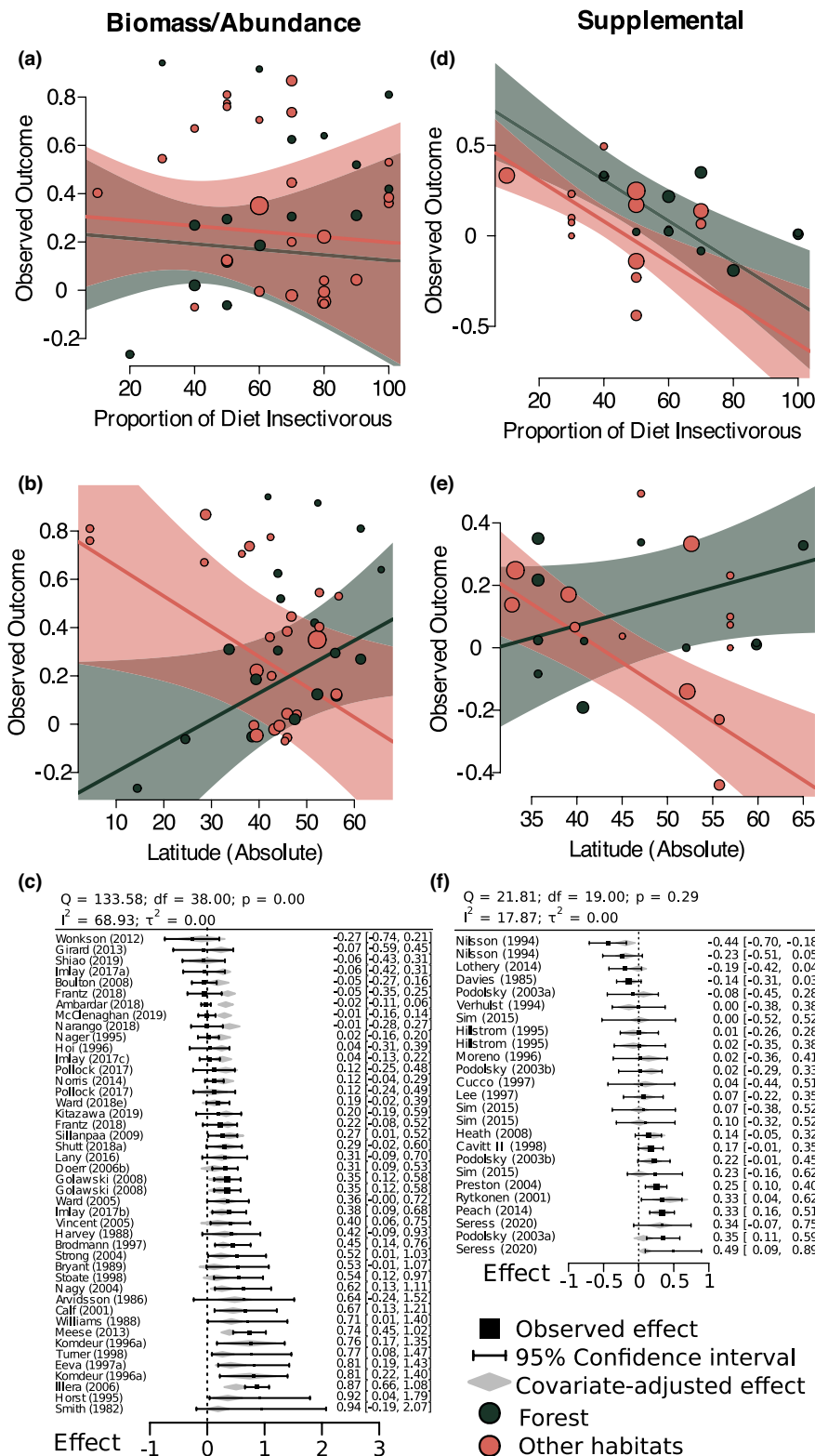


FIGURE 4 Results of meta-regressions estimating the effects of habitat type, the proportion of the diet that is invertebrates, if the functional guild for a species is insectivore and absolute latitude, on the estimated relationship between the number of fledglings and food availability, measured as biomass and abundance (a, b, c) or experimentally manipulated by food supplementation (d, e, f). Relationships between diet (a, d) and latitude (b, e) are shown at the mean or modal values for the other variables separately for forests (green) and other habitat types (coral; primarily grassland and urban areas) with 95% confidence intervals. Forest plots for each meta-regression are shown (c, f) along with tests for heterogeneity. Black squares and bars indicate the observed effect and 95% confidence intervals for each study, which are identified with text; grey diamonds indicate the covariate-adjusted effect estimates for each study after accounting for moderator variables. No overall effect is estimated with this method (see Figures S8 and S39).

measures of reproductive success and food availability and for nine of our 16 pairwise comparisons for measures of body condition and food availability when using the covariate-adjusted effect sizes (Figures S8–S39). The estimated total heterogeneity out of the total variability (I^2 values) for each pairwise meta-analysis ranged from 0.0% to 81.9% for reproductive success and from 0.0% to 86.1% for body condition (Figures S8–S39). Statistics for all pairwise comparisons are included in the Supplemental Information and a summary of estimated effects from the random-effects meta-analyses are shown in Figure 5. The regression tests indicated funnel

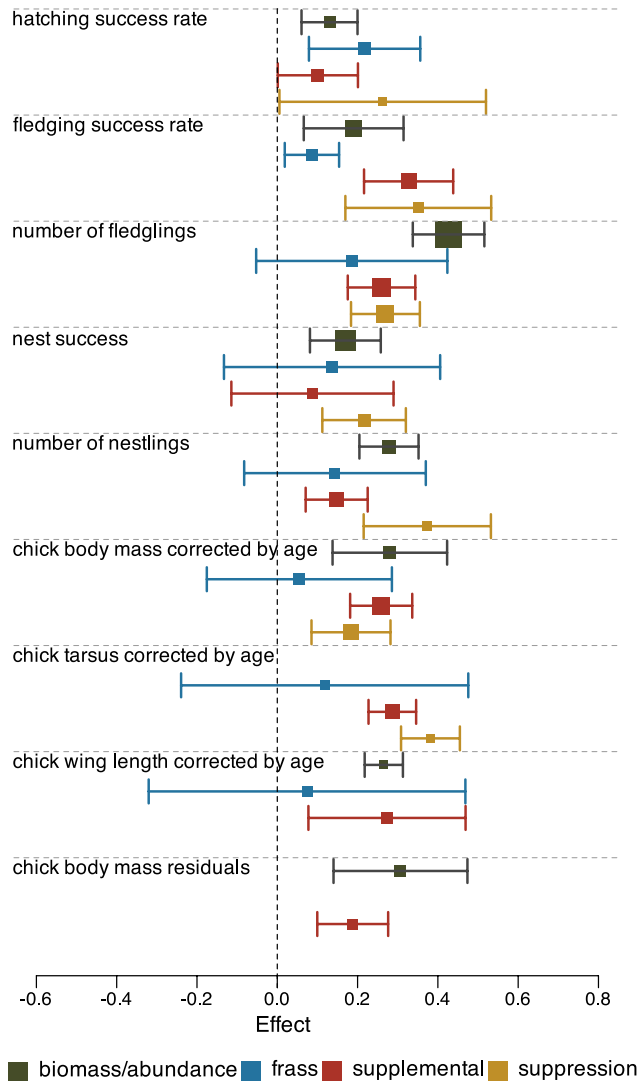


FIGURE 5 Effects of invertebrate food availability measured as biomass and abundance (green), frass fall (blue), supplemental invertebrates (red) and population suppression (orange) on the nine most commonly used measures of bird reproductive success and chick body condition found by our systematic review. Each square indicates the estimated overall effect from a random effects meta-analysis using the covariate adjusted effect sizes, with bars showing 95% confidence intervals, for a single food availability measure and a single outcome for all pairwise combinations that were represented by at least two studies. The number of studies included in a meta-analysis is indicated by the size of the square (see Figure 3).

plot asymmetry and potential publication bias in six out of 31 cases with at least three studies available to estimate bias, more than would be expected based on chance alone (approximately 1.55). The cases in which there was potential publication bias were for the effect of invertebrate biomass or abundance on fledging success rate ($t = 2.3, p = 0.062$), nest success ($t = 2.3, p = 0.029$), number of fledglings ($t = 4.9, p < 0.001$) and number of nestlings ($t = 4.2, p = 0.002$); there was also publication bias detected for the effect of invertebrate population suppression on the number of fledglings ($t = 2.5, p = 0.042$) and chick body mass corrected by age ($t = 3.7, p = 0.01$). Other pairwise combination tests showed no evidence of publication bias (Figures S8–S39).

Three-stage structural equation model

Our structural equation model converged normally after 39 iterations. Goodness of fit tests indicated that the structure of our model was acceptable but not optimal (RMSEA = 0.006, 95% CI = 0.005, 0.007; CFI = 0.76). Because we have a priori ecological reasons for structuring the model as it is and defined each latent variable based on measures used in the literature, however, we made inference on the model despite there being potentially better fitting structures, albeit ones that may make less biological sense. The meta-analytic structural equation model based on pooled effects (Figure 6) indicated that food availability has a positive effect on reproductive success (mean = 1.25, Wald 95% CI = 0.96, 1.54), where a one unit increase in food availability would result in an estimated 1.25 unit increase in reproductive success. Similarly, the model indicated that food has a positive effect on chick body condition (mean = 0.83, Wald 95% CI = 0.62, 1.05) and that reproductive success and body condition are inversely related (mean = -0.46, Wald 95% CI = -0.90, -0.03). Based on the factor loadings, most variables were reasonably good indicators of the latent variables they were intended to measure, although the measurement error—indicating inter-study reliability of that variable—was high (Kang & Ahn, 2021), particularly for indicators of food availability (Figure 4).

DISCUSSION

The relationships among food availability, reproductive success, and chick survival in songbirds have long been of interest (Lack, 1947; Newton, 1980). Although food availability clearly influences both vital rates in some circumstances, it is only one of a constellation of—possibly stronger—influential factors. This complexity, and conflicting evidence across individual studies (Newton, 1998), leaves open the question of whether food is a limiting factor that consistently influences avian reproductive success and chick survival across systems.

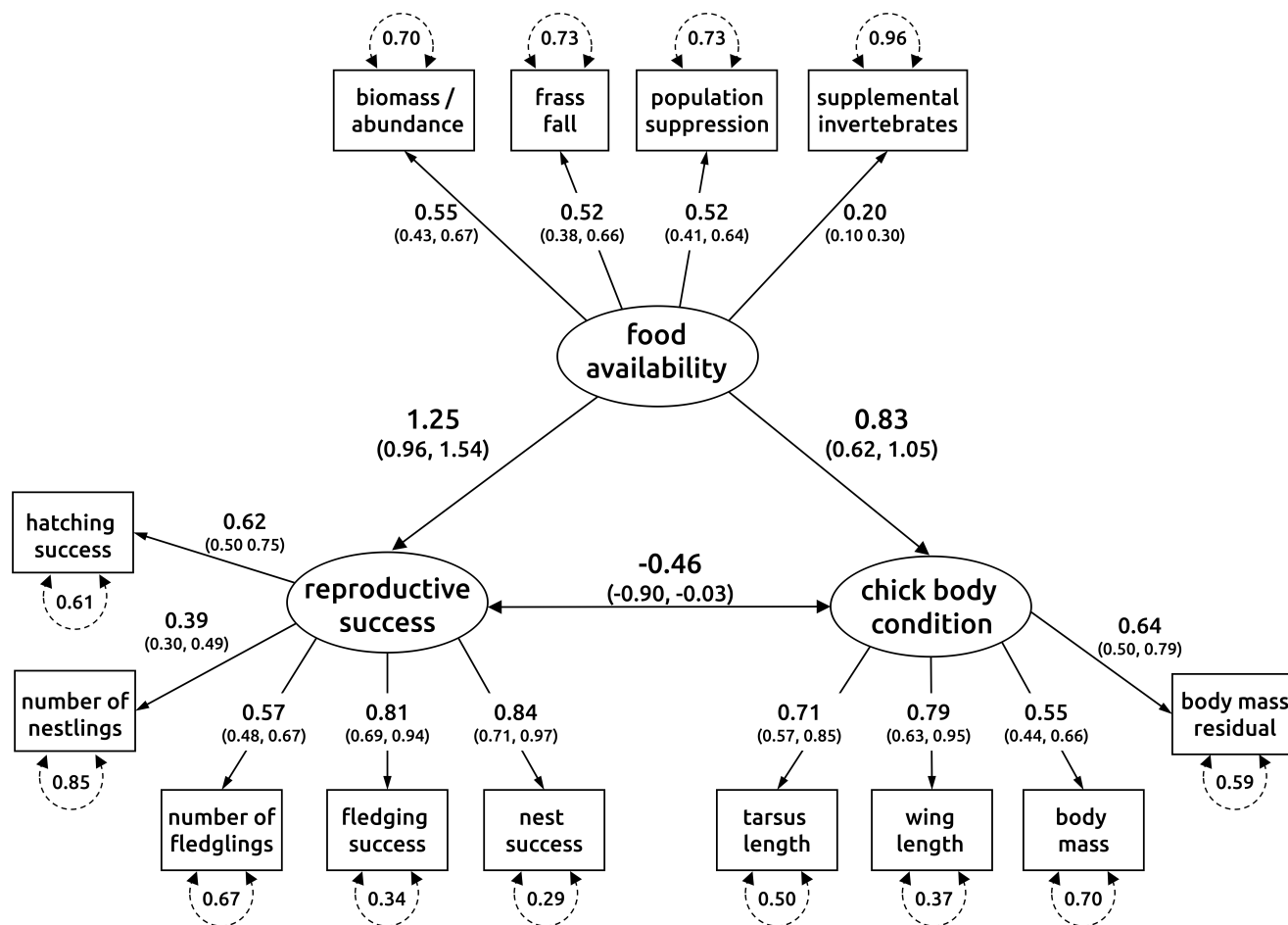


FIGURE 6 Meta-analytic structural equation model demonstrating strong effects of invertebrate prey availability on both songbird reproductive success and chick body condition. Latent variables (ovals) are measured by indicator variables (rectangles) for which measurement error is shown by dashed circular arrows. Single-headed arrows between latent variables indicate direction of implied causal relationships; the double-headed arrow between reproductive success and body condition indicates covariance; arrows going from latent variables to indicator variables indicate measurement relationships. Path coefficients (and Wald 95% confidence intervals) were estimated with a three-stage meta-analytic structural equation model using effects adjusted by bird family and broad habitat classification (open, forested or wetland) for 125 studies (total sample size = 49,028 samples, typically individuals, territories or whole broods depending on level of analysis in the primary study).

Prior reviews have summarised available evidence, but have not used systematic search methods, instead relying on narrative discussion and ‘vote-counting’ (Koricheva & Gurevitch, 2013) to summarise the literature (e.g., Newton, 1998) or on experimental studies such as food supplementation, which do not necessarily reflect true variation in food availability (Ruffino et al., 2014). Thus, we have heretofore lacked a comprehensive assessment that synthesizes effects quantitatively across studies.

Here, we demonstrate that food availability generally increases both reproductive success and chick body condition, a proxy for survival, across insectivorous bird species (Figure 6), suggesting that invertebrate populations are generally a limiting resource for songbirds during the breeding period. The observed pattern of food limitation we found was weaker for supplemental food, which could also indicate that food is not as limiting as the main model results suggest and that the observed positive correlations between food availability and bird

outcomes is driven by unmeasured confounding factors or potentially by publication bias. For example, a positive correlation between bird reproductive success and insect biomass could also indicate that both insects and birds are responding to some shared aspect of habitat or site quality. We did find that the magnitude of effects varied across habitat types and there was substantial heterogeneity in the biomass and abundance effects that were unexplained by our covariates. We suspect much of this variation can be attributed to the variety of ways researchers sampled invertebrate biomass and abundance. Despite including both observational and experimental studies, though, we still found consistent evidence that food is generally a limiting resource for birds, suggesting that decreases in invertebrate food availability will reduce bird population sizes. The links among food availability, reproductive success and body condition shown here illustrate how insect declines are likely to have cascading effects on insectivorous birds (Wagner, 2020): if

food availability is a limiting factor on a macro scale, then declines in the food supply will reduce insectivorous bird population sizes.

If food is limiting, then one would also expect a trade-off between survival and reproduction. Relationships between the number of offspring and the probability of adult survival have been demonstrated in several avian systems (Ghalambor & Martin, 2001; Martin, 1987). The general idea of the survival-reproductive success trade-off has also been long debated, however, and lacks evidence in many other systems (Roff & Fairbairn, 2007; Santos & Nakagawa, 2012). To add to this ongoing debate, our meta-analysis finds clear evidence of a trade-off between chick body condition and reproductive success for insectivorous birds (Figure 6). Beyond the overall effect between the latent variables in our model, this trade-off was also evident in the pooled correlation matrix for both unadjusted effects (Figure 3) and covariate-adjusted effects (Figure S7) with a cluster of negative correlations between the measures of reproductive success and body condition. Too few studies reported effects for both reproductive success and adult body condition in response to food availability to include adult condition in the model, however, indicating that further evidence is needed to adequately resolve the survival-reproductive success trade-off debate.

To synthesize findings across studies and reach general conclusions, it is necessary for primary studies to report results that are comparable and to use standardised measures. Even after consolidating related measures (e.g., fledglings per egg and fledglings per nestling being combined as a single measure of fledging success), we still found a large number of ways that researchers have defined body condition and reproductive success, with each new study seemingly adding a new measure (Figure S4). The meta-analytic approach we used allowed flexibility to include some of this variation with multiple indicator variables, however, we could only include nine out of 74 potential outcome measures that authors reported in the literature because they were the only ones consistently reported across studies. Though researchers may consider some metrics to be more internally reliable, we advocate also collecting and reporting commonly used measures to facilitate synthesis across studies. For example, although local swelling in response to phytohaemagglutinin injection (Bańbura et al., 2013; Lifjeld et al., 2002) or rectrix regrowth rate (Strong, 1999) may be good indicators of body condition, they were used in so few studies that we could not include data from these studies in our quantitative synthesis. Had these studies also reported more common measures (e.g., body mass residuals) in addition to more specialized metrics, some of the results would be more comparable to the rest of the field and these studies could have contributed to our synthetic understanding. Based on the frequency with which measures exist in the current literature and the measurement error from the model, we recommend that

researchers make it regular practice to report nestling size measures (e.g., wing chord and tarsus length) corrected by age and whole nest success or fledging success in addition to other measures. Researchers should also consider reporting standardised outcomes such as those used by the Studies of Populations of Individual Birds (SPI-Birds) network (Culina et al., 2021).

The low degree of inter-study reliability indicated by the model's estimates of measurement error for indicators of food availability suggests that the ways in which ornithologists generally measure invertebrates may not consistently reflect food availability. We excluded studies that inferred invertebrate abundance based on indirect measures such as temperature or rainfall, or from nearby locations or other years at the same site—even though many studies that we screened for inclusion treated these metrics as measures of invertebrate abundance. Invertebrate populations vary wildly over space and time, with large interannual fluctuations (Pimm & Redfearn, 1988; Roubik, 2001). Inferring abundance based on relationships to other covariates could thus lead to spurious findings in primary studies and add heterogeneity to data syntheses. Similarly, frass fall, an indirect measure of caterpillar biomass, had relatively high measurement error compared to invertebrate abundance or biomass, suggesting that proxy measures are inferior to direct measures. Though one might expect supplemental invertebrates to be a good indicator of food availability because it is a direct, experimental manipulation, we found this not to be the case. A previous meta-analysis found that the effects of food supplementation on breeding success varied widely depending on experimental design (e.g., timing of supplementation and accessibility of supplemental food to nesting pairs) and the amount of natural food available (Ruffino et al., 2014). It is likely that the high measurement error we detected for supplemental invertebrates can be attributed to these types of factors, as not all supplemental food is administered in the same way or is of the same quality. Many of the supplemental food studies included in our analysis relied on mealworms (*Tenebrio molitor*), which can vary in nutritional quality depending on how they were reared and can often be poor sources of necessary nutrients like calcium and carotenoids (Eeva et al., 2009; Klasing et al., 2000; Martin et al., 1976), and are thus not an adequate substitute for natural foods that are carotenoid-rich. We also found that the effect of supplemental food on the number of fledglings varied with the proportion of a species' diet that is invertebrates, suggesting that supplemental feeding is less effective for species with more highly specialized diets. Similarly, we found weaker effects of supplemental food in non-forest habitats; however, this research question has predominantly been addressed in forest systems, and therefore our understanding of food limitation may be influenced by where studies have been conducted. The best indicators of food availability—population suppression and

invertebrate biomass or abundance—both document changes in the overall abundance of the invertebrate community. Despite being the best indicators, they still had relatively high measurement error, which we suggest may indicate sampling methods that do not consistently or completely capture invertebrate taxa that represent specific food for the birds studied.

Many studies included the full community of invertebrates sampled through various methods, such as pitfall trapping, malaise traps or sweep netting without attempting to distinguish which invertebrates are consumed by the birds studied. These methods may result in a mismatch between what researchers measured as prey, and what birds are able, or choose, to capture and consume. Several studies limited their measures of food availability to only taxa that birds were observed to use for provisioning their young or to consume (e.g., Madliger & Love, 2016); however, in many cases there was insufficient information about what birds eat, and researchers used data on all invertebrates captured by the sampling method (e.g., Mwangi et al., 2018). The emergence of meta-barcoding techniques for diet analysis could improve our understanding of what birds eat (Rytönen et al., 2019), and which measurements of invertebrate food abundance are appropriate. Following the recommendations of entomologists, we had initially intended to calculate the proportion of invertebrates collected that were noxious or otherwise unpalatable to birds (Grames, Montgomery, et al., 2019), however, this information was not reported in any of the studies that met our inclusion criteria. More collaboration between entomologists and ornithologists is necessary to improve the sampling methods and reporting standards for monitoring invertebrate populations (Montgomery et al., 2021) and to clarify which invertebrates should be included in measures of food available to birds.

Although the primary drivers of insect declines are varied (Wagner et al., 2021) and overall insect population trends are largely unknown, the documented declines in some formerly abundant taxa (Conrad et al., 2006; Warren et al., 2021) are enough to expect that global insect declines will have profound effects on species interactions and disrupt population processes at higher trophic levels (Tallamy & Shriver, 2021; Wagner, 2020). In this synthesis, we have investigated the potential for insect decline to result in parallel declines in insectivorous birds through the proximate mechanisms of reproductive success and chick body condition, the latter of which is linked to annual survival and juvenile recruitment (Cox & Cresswell, 2014). The results of our meta-analysis illustrate the importance of food availability for both bird body condition and reproductive success, suggesting that fluctuations in insect abundance may have a substantial impact on bird demographics. This has important implications for understanding and conserving birds, particularly given large-scale declines in bird abundance in

some parts of the world over the last several decades (Rosenberg et al., 2019).

AUTHOR CONTRIBUTIONS

EG and CE developed the project idea; EG, GM and CY screened articles for inclusion with conflicts resolved by MT and CE; EG extracted effect sizes and performed the meta-analysis; EG wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

ACKNOWLEDGEMENTS

We thank all the researchers who spent countless hours in the field collecting the primary data that underlies our analysis, especially those who provided data on request: Medhavi Ambardar, Davide Dominini, Tapio Eeva, Becky Harris, Tara Imlay, Ming-Tang Shiao and Travis Wilcoxon. We also thank Robi Bagchi, Mike Singer, Austin Spence and David Wagner for advice in designing the protocol for the meta-analysis. We thank the editor, two anonymous reviewers and Ellen Welti for helpful comments on previous versions of the manuscript. We acknowledge support from the National Science Foundation (OIA-2019528, DEB-2225092), PEO International, and the University of Connecticut Graduate School.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.14178>.

OPEN RESEARCH BADGES




This article has earned Open Data, Open Materials and Preregistered Research Design badges. Data, materials and the preregistered design and analysis plan are available at [[insert provided URL(s) on the Open Research Disclosure Form]].


DATA AVAILABILITY STATEMENT

All data and scripts used for the meta-analysis are archived on Figshare, DOI: [10.6084/m9.figshare.21545424.v1](https://doi.org/10.6084/m9.figshare.21545424.v1)

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Grames, E.M., Montgomery, G.A., Youngflesh, C., Tingley, M.W. & Elphick, C.S. (2023) The effect of insect food availability on songbird reproductive success and chick body condition: Evidence from a systematic review and meta-analysis. *Ecology Letters*, 00, 1–16. Available from: <https://doi.org/10.1111/ele.14178>