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RESEARCH ARTICLE

Understanding spatiotemporal effects of food supplementation on host–parasite interactions using community-based science

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Abstract

1. Supplemental feeding can increase the overall health of animals but also can have variable effects on how animals defend themselves against parasites. However, the spatiotemporal effects of food supplementation on host–parasite interactions remain poorly understood, likely because large-scale, coordinated efforts to investigate them are difficult.
2. Here, we introduce the Nest Parasite Community Science Project, which is a community-based science project that coordinates studies with bird nest box 'stewards' from the public and scientific community. This project was established to understand broad ecological patterns between hosts and their parasites.
3. The goal of this study was to determine the effect of food supplementation on eastern bluebirds (*Sialia sialis*) and their nest parasite community across the geographic range of the bluebirds from 2018 to 2021. We received 674 nests from 69 stewards in 26 states in the eastern United States. Nest box stewards reported whether or not they provided mealworms or suet near nesting bluebirds, then they followed the nesting success of the birds (number of eggs laid and hatched, proportion that hatched, number and proportion of nestlings that successfully fledged). We then identified and quantified parasites in the nests.

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4. Overall, we found that food supplementation increased fledging success. The most common nest parasite taxon was the parasitic blow fly (*Protocalliphora sialia*), but a few nests contained fleas (*Ceratophyllus idius*, *C. gallinae* and *Orchopeas leucopus*) and mites (*Dermanyssus* spp. and *Ornithonyssus* spp.). Blow flies were primarily found at northern latitudes, where food supplementation affected blow fly prevalence. However, the direction of this effect varied substantially in direction and magnitude across years. More stewards fed bluebirds at southern latitudes than at northern latitudes, which contradicts the findings of other community-based science projects.
5. Overall, food supplementation of birds was associated with increased host fitness but did not appear to play a consistent role in defence against these parasites across all years. Our study demonstrates the importance of coordinated studies across years and locations to understand the effects of environmental heterogeneity, including human-based food supplementation, on host–parasite dynamics.

KEYWORDS
citizen science, disease ecology, ectoparasites, food supplementation, host–parasite interactions

1 | INTRODUCTION

Environmental factors, such as food availability, can influence host–parasite interactions (Becker et al., 2015, 2018; Sánchez et al., 2018). Host defence strategies against parasites, such as resistance, are often condition-dependent and affected by food availability. Resistance reduces the damage that parasites cause by reducing parasite fitness (Read et al., 2008). Resistance mechanisms can be condition-dependent because mounting these responses can be energetically costly (Howick & Lazzaro, 2014; Knutie, 2020; Lochmiller & Deerenberg, 2000; Sheldon & Verhulst, 1996). Therefore, only hosts with enough food resources are able to invest in a robust resistance response. Extra nutrients can directly increase immune cell production, which may account for the positive relationship between food availability and immune resistance (Strandin et al., 2018). For example, supplemented protein can increase the concentration of cellular and humoral immune cells (Coop & Kyriazakis, 2001; Datta et al., 1998). Consequently, food availability is expected to influence parasite abundance, but evidence for this phenomenon in the wild is mixed.

Humans can change resource availability for animals by intentionally providing food using wild bird feeders or unintentionally by leaving food waste in the environment (Murray et al., 2016). In fact, humans provide many wild bird species with a large proportion of their food (Cox & Gaston, 2018; Jones, 2011). In the United States alone, approximately 50 million households provide over half a million tons of supplemental food to attract wild birds to their property (Cox & Gaston, 2016; Robb et al., 2008). Supplemental feeding of birds can have several benefits to birds and humans. Feeding wild birds can improve the mental health of humans and strengthen their connection with nature (Cox & Gaston, 2016, 2018; Jones, 2011; Shaw et al., 2017). Birds that are supplemented with food are often in better condition, which, in turn, can increase their reproductive success (Bailey & Bonter, 2022; Tollington et al., 2019) and enhance some measures of immunity (Cornelius Ruhs et al., 2019; Lochmiller et al., 1993; Sánchez et al., 2018; Strandin et al., 2018; Wilcoxen et al., 2015). However, studies have found conflicting effects of food supplementation on clutch size, hatching success and fledging success of birds (reviewed in Robb et al., 2008). Because these studies often focus on a single year or population, the observed variation across studies might be explained by the influence of annual variation in environmental conditions or differences in local conditions.

Recent experimental work with a wild bird species demonstrated that food supplementation increases resistance to parasitism, but this study relied on only 1 year of data in one population (Knutie, 2020). Due to environmental heterogeneity, studies are needed across years and populations to understand the broad impact of food supplementation on host–parasite interactions. Such studies are difficult to accomplish without coordinated efforts, such as community-based science projects (e.g. eBird, NestWatch; Phillips & Dickinson, 2009; Sullivan et al., 2009). These projects have provided a wealth of data to understand the impact of factors, including food supplementation, on bird fitness (Bailey & Bonter, 2022). However, these studies have limitations because they cannot provide insight into interspecific interactions, such as host–parasite relationships. Thus, the Nest Parasite Community Science Project (hereafter 'Project'), was established. This community-based science project works with the public and scientific community (hereafter 'stewards') across the eastern United States to monitor bird nest boxes, followed by the characterization of nest parasite taxa. Generally, the Project explores the effect of environmental conditions on spatiotemporal patterns of box-nesting birds, such as eastern bluebirds (*Sialia sialis*), and their nest parasite community.

The eastern bluebird (hereafter 'bluebird') is a North American bird species that is supplemented with food by humans. In the 1970s, populations of bluebirds declined, in part because of a loss of suitable foraging and nesting habitat (Gowaty & Plissner, 2020). In response, humans built and established artificial nest boxes and some began supplementing the birds' natural diet of insects, spiders, and small fruits (Pinkowski, 1977) with dried and live mealworms (larvae of *Tenebrio molitor*). Since the 1970s, the bluebird population size rebounded within approximately a decade (Sauer & Droege, 1990) and humans continue to maintain nest boxes and provide bluebirds with supplemental food. These continued efforts are likely important, as bluebirds face challenges, such as parasitic, nest-inhabiting flies, throughout much of their range (Grab et al., 2019). Past studies have found that blow fly (Calliphoridae: *Protocalliphora*) abundances are highly variable, and these flies either have a negative effect or no effect on fledging success of bluebirds (reviewed in Grab et al., 2019). A recent study in Minnesota found that bluebirds supplemented with mealworms had higher resistance (via an antibody response) to blow flies than unsupplemented birds (Knutie, 2020). However, even within populations, blow fly abundances and effects on survival were highly variable across years (Grab et al., 2019).

The goal of this study was to determine the effect of food supplementation on host–parasite interactions across years and geographic locations. Nest box stewards either fed their bluebirds mealworms and/or suet or not, then followed the nesting success of the birds (number of eggs laid and hatched, proportion of eggs hatched, number of fledglings, proportion of nestlings fledged) across the geographic range of the eastern bluebird from 2018 to 2021. Once the nests were empty, they were sent to the University of Connecticut and we identified and quantified nest parasite taxa. First, we used this information to determine spatial and temporal effects on nesting success and nest parasite presence and abundance. Second, we determined the effect of food supplementation on fledging success and parasite prevalence. Lastly, because stewards voluntarily fed or did not feed their bluebirds mealworms, we determined whether there was a spatial effect to bird feeding by stewards. Previous research suggests that citizen scientists who participate in bird feeding programs are most likely to be in the northern United States (Dunn & Tessaglia-Hymes, 2001). Thus, we predicted that stewards at northern latitudes would be more likely to feed their birds compared with stewards at southern latitudes. Overall, our integrative approach using a new community-based science project will provide a better understanding of how wild bird feeding can influence spatiotemporal patterns of host–parasite interactions.

2 | MATERIALS AND METHODS

2.1 | Field methods

Nest box stewards were recruited from 2017 to 2021 through social media platforms (e.g. Twitter and Facebook groups). From 2018 to 2021, we received a total of 674 nests from 69 stewards across 26 states in the eastern United States (Table S1). These stewards noted whether they provided no food or food (live or dried mealworms and/or suet) to bluebirds on their property. Suet contains animal fat and other items such as corn meal, peanuts, fruits and/ or dried insects and was provided consistently throughout the breeding season by the stewards. 38 stewards from 21 states provided mealworms in at least one of the years and 31 stewards from 18 states did not; eight stewards from seven states provided mealworms in some years but not the other years. The exact number of mealworms provided to the bluebirds varied by the steward. Stewards noted that they added 50–200 mealworms per day to the feeders, which were 0–27 m (mean = 12 m) from the nest boxes.

Stewards were instructed to remove any old material from boxes in March–April each year. Stewards then monitored their nest boxes based on when bluebirds were expected to arrive on the breeding grounds (e.g. March for more southern latitudes and May for more northern latitudes). Once a nest box had nesting material, stewards confirmed that the nest box was occupied by bluebirds. The number of eggs laid in the box were counted visually once the clutches were complete. Once the eggs hatched, the stewards visually counted the number of nestlings. The stewards monitored the survival of nestlings until the nest was empty or dead nestlings were present. After the nest was empty, stewards removed the nest from the box and placed it individually in a gallon-sized, plastic ziplock bag. They placed a labelled piece of paper in the bag with the following information: collection date, full name and steward identification number (ID), city, county, state, zip code, bird species, whether mealworms and/or suet were fed, number of eggs laid, number of nestlings that hatched and number of nestlings that fledged or died. We also calculated the proportion of eggs that hatched and the proportion of nestlings that survived until fledging (i.e. fledging success). If infertile eggs or dead nestlings were found, stewards were instructed to remove these items with gloves before shipping the nests. Once the bags were labelled, stewards placed the bags in a cool, dry area. After the breeding season was complete, nests were compiled and shipped in a cardboard box or paper envelope to the University of Connecticut. All applicable international, national and/or institutional guidelines for the care and use of animals were followed. All bird handling and work was conducted according to approved UConn IACUC protocols (No. A18-005 and A21-002) with the appropriate state permits or waivers and US Fisheries and Wildlife Service Scientific Collecting Permit #MB11631D.

2.2 | Parasite identification, quantification and measurements

After nests were received, data provided by each steward were entered into a database and assigned to a nest dissector. Immediately prior to dissection, the ziplock bag was placed in a −80°C freezer for approximately 10 min (but sometimes up to an hour) to immobilize any live invertebrates. Once the nest was removed from the freezer, pieces of the nest material were removed from the bag and dissected over a white piece of paper, which took between 30 min to 2 h, depending on the number of invertebrates in the nest. All invertebrates were collected from the nest material and placed in 2 mL tubes with 90% ethanol. Specimens were then stored in a −80°C freezer until they were identified. We were unable to dissect 28 nests because they were too wet to dissect and thus reliably find the smaller parasites.

Specimens were identified into broad taxonomic groups and then identified. Blow fly pupae were identified under a dissecting scope after being removed from alcohol and dried; no further preparation was performed. Flea and mite specimens were slide-mounted in Hoyer's mounting medium or by clearing first in 10% KOH, washing and mounting in PVA (lactic acid, phenol, and polyvinyl alcohol); slides were left to cure on a slide warmer. Nests also contained commensal book lice (Liposcelididae), but since they were not parasitic we excluded them from the study.

Nests contained parasitic, commensal and predatory mites and therefore we separated these groups before identifying the parasitic genera. Identifications were confirmed to major groups: commensal dust mites (Pyroglyphidae), predatory mites of other mites (Cheyletidae), and parasitic mites (Mesostigmata). Mesostigmata specimens were slide-mounted and identifications of the genera *Ornythonyssus* and *Dermanyssus* were made using a compound microscope at various magnifications (200–1000X) and using published diagnostic keys (Di Palma et al., 2012; Knee & Proctor, 2006; Murillo & Mullens, 2017). Non-parasitic (commensal and predatory) mites were excluded from the study. Flea identifications were made using a compound microscope at various magnifications (200–400X) and using published diagnostic keys (Holland, 1951, 1985; Lewis, 2000). Blow flies were identified using available morphological keys for pupae (Whitworth, 2003a, 2003b). We also measured the width of empty pupal cases for up to 10 individuals per nest as a proxy for fly size, which is related to lifetime fitness in Diptera (Moon, 1980; Schmidt & Blume, 1973). We measured 1004 pupal cases from 126 nests of 13 stewards. We could not measure pupal case length because flies emerge from the top of the case, thus removing part of it.

2.3 | Statistical analyses

We used generalized linear mixed models (GLMMs) to examine spatiotemporal drivers of the five fitness components and abundances of each parasite taxa. All analyses were conducted in R (version 4.1.1; R Core Team, 2023), using the integrated nested Laplace approximation (INLA; Lindgren & Rue, 2015). All models were checked by simulating from the posterior and verifying the even distribution of residuals and verifying that the models' simulated data recapitulated the distribution of the input data.

2.3.1 | Host fitness models

We fitted models that examined each of our five fitness metrics as response variables. We used a Gaussian distribution for the number of eggs laid and hatched and number of nestlings that fledged, and binomial distribution for the proportion of eggs that hatched and the proportion of nestlings that successfully fledged (i.e. fledging success). For the former, the number of eggs laid represented the number of trials and the number of eggs hatched represented the number of successes and for the latter, the number of nestlings represented the number of trials and the number of fledglings represented the number of successes. Explanatory variables included year (categorical with four levels: 2018, 2019, 2020, 2021) and day-of-year that the nests were collected (1–365, representing number of days since January 1st). We included steward ID as a random effect to account for among-site variation in fitness. To ask whether supplementation improved fitness (i.e. for the number and proportion of nestlings fledged) we also fitted supplementation as a fixed effect. We did not include food supplementation as a fixed effect for the number of eggs laid and hatched and proportion hatched because supplementation did not always commence before eggs were laid, meaning that we would not be able to reliably infer effects of supplementation on these components of fitness. For models with supplementation, we tried to fit the effect of year-by supplementation on host fitness, but the inclusion of this interaction did not improve the model or show any notable significant variation, and thus was excluded.

2.3.2 | Parasite models

Parasite models used blow fly prevalence as a binary response variable; for the other parasites, prevalence was too low to fit a reliable model, both for fleas (2.8%) and for mites (3.7%). Fixed effects included supplementation, year, day-of-year and number of eggs hatched, with steward ID as a random effect. When exploring the data, substantial among-year variation in the effects of supplementation on parasite prevalence was apparent; as such, we included supplementation as an interaction with year to examine the differences in the effect of supplementation on blow fly prevalence across years. This model showed stronger support (i.e. improved model fit when compared using deviance information criterion [DIC]) than including separate main effects of supplementation. We also added some elaborations to this model: first, because there were strong spatial patterns in blow fly prevalence, we also repeated the model including only the latitudes above which these parasites had been found (above 39.7° N), which is corroborated by past studies (Sabrosky et al., 1989). Second, we repeated the analysis with the highly overdispersed counts of blow fly abundances using a negative binomial distribution to investigate whether abundance showed the same trends as prevalence; the abundance models showed very similar effects to the prevalence, and so to be conservative, we only report the prevalence effects given that the abundance data were highly overdispersed.

2.3.3 | Blow fly size models

We also determined whether variation in blow fly size (pupal width [mm]) could be explained by any of the fixed effects. Fixed effects included year, year-by-supplementation interaction, number of nestlings and total parasite abundance. Nest ID and steward were included as random effects.

2.3.4 | Fitness–parasite models

To investigate whether parasites explained variation in fitness, we sequentially added main effects of blow fly and flea prevalence and food supplementation, and then interacting effects of each parasite with supplementation. Using DIC to distinguish competitive models, we examined whether these effects improved the fit of the model, and whether the effects were significant (i.e. with 95% credible intervals not overlapping with zero). We repeated this exercise both with the full data set and with the subset only considering the northern latitudes (above 39.77° N).

2.3.5 | Spatial autocorrelation effects

For all fitness and parasite models, we fitted a stochastic partial differentiation equation (SPDE) effect to control for and quantify spatial autocorrelation in the response variable (Lindgren et al., 2011; Lindgren & Rue, 2015). The SPDE effect uses samples' bivariate coordinates to model spatial dependence, examining whether samples from closer locations are more similar and then generating a two-dimensional spatial field that can be examined for spatial patterns. This approach has proved successful for investigating spatial patterns of parasite prevalence and intensity (Albery et al., 2019, 2022). We fitted an SPDE effect based on samples' latitude and longitude and examined whether it improved model fit by assessing whether it reduced the DIC of the model, using deltaDIC = 2 as a cut-off. INLA also allows fitting of separate spatial fields for different time periods, and therefore we also included between-year variation in the spatial field and assessed whether it improved model fit using the same cut-off.

2.3.6 | Steward models

Finally, we examined whether the probability of a steward providing food to their birds varied spatially. We fitted a model with the binary response variable of food supplementation (yes or no) and with fixed effects including year, the total number of nests submitted by the steward, latitude and longitude (all continuous). For all models, because there were two types of supplementation (mealworms and suet), we attempted to use each method on its own as an explanatory variable to investigate whether they had different implications for hosts and parasites. However, there were no notable differences among these specifications, and therefore we reported the fullest models—that is, those combining mealworm and suet supplementation—alone.

3 | RESULTS

3.1 | Host fitness models

Bluebirds laid between 2 and 6 eggs that hatched between 0 and 6 nestlings, which resulted in 0–6 fledglings ($n = 674$ nests). Our fitness models a revealed strong, significant effect of food supplementation on the number of fledglings (effect size = 0.317, confidence intervals [0.138, 0.495]; $p < 0.001$) and weaker but still a significant effect on the proportion of nestlings that survived out of the total number of nestlings (i.e. fledging success; effect size = 0.071, confidence intervals [0.018, 0.126]; $p = 0.01$; Figure 1a, Figure S1C). However, food supplementation did not affect other host fitness variables (Figure S1C). We detected strong spatial heterogeneity in the distribution of two out of five fitness metrics. For the number of fledglings, there was a patchy distribution with alternating hot- and coldspots (Figure 1c; ΔDIC = −6.580), and contrastingly, the east coast had a higher proportional fledging success than inland birds (Figure 1d; ΔDIC = −15.170). All other metrics did not show a significant improvement when the spatial effect was included (Figure S1; ΔDIC > −2). In addition, our models revealed a number of day-of-year effects (Figure S1; all $p < 0.001$). Nests sampled later in the year had fewer eggs (effect size = −0.335, CI [−0.414, −0.256]) and fewer hatchlings (effect size = −0.223, CI [−0.305, −0.142]), but had a greater proportion of fledgling success (effect size = 0.036, CI [0.014, 0.057]). On average, host fitness varied little among years (Figure S1), although number of fledglings differed significantly between 2018 and 2020, the intervals overlapped with zero in the spatial autocorrelation model, and thus this effect was removed in the spatial models (Figure S2). Otherwise, estimates for each year overlapped substantially with each other, demonstrating low among-year variation.

3.2 | Parasite models

Out of 646 nests that were dissected for parasites, 171 nests (26.5%) from 20 stewards across 11 states contained 1–139 blow flies, which were all identified as *Protocalliphora sialia*. 18 nests (2.8%) from seven stewards across six states contained 1–179 fleas. Most flea taxa were identified as *Ceratophyllus idius*, but one nest contained *C. gallinae* and one nest contained *Orchopeas leucopus*. 24 nests (3.7%) from 10 stewards across nine states contained between one to over 4000 parasitic mites from the genera *Dermanyssus* and *Ornithonyssus*.

We found strong support for spatial variation in blow fly prevalence (ΔDIC = −5.800), with prevalence decreasing from north to south (Figure 2b). Notably, blow flies were only found as far south as 39.77° N (Figure 2b). We uncovered strong support for among-year effects of food supplementation on blow fly prevalence (ΔDIC = −5.560; Figure 2a, Figure S2). The effect of supplementation on blow fly prevalence was positive in 2018, negative in

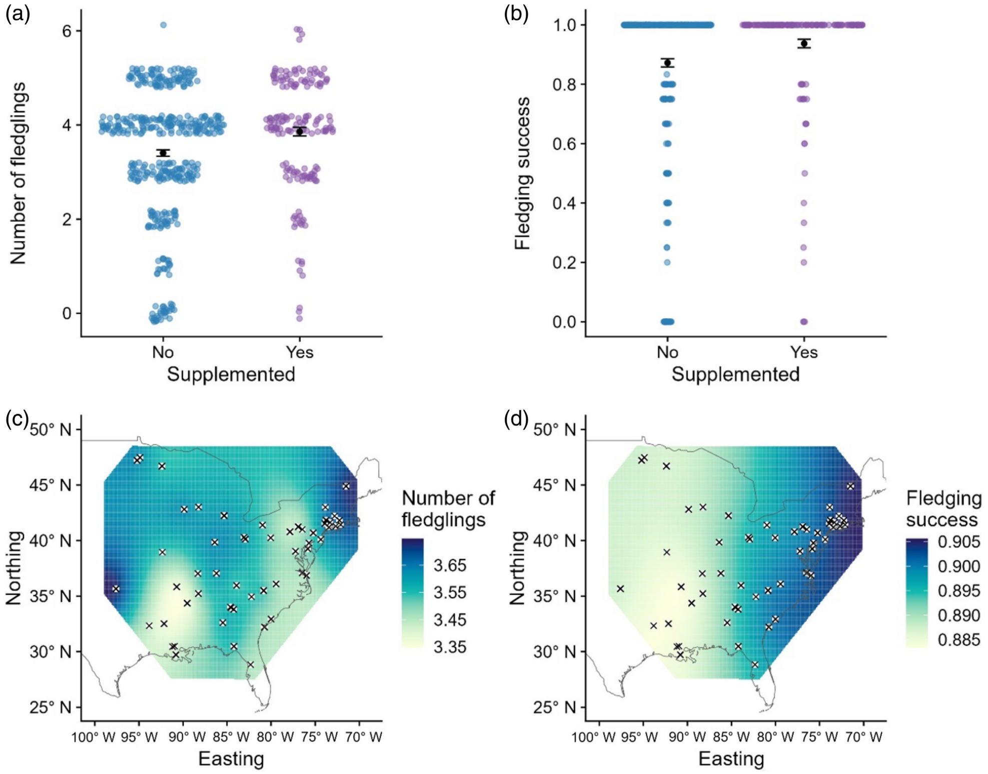

FIGURE 1 Nestling survival was affected by (a and b) food supplementation and (c and d) geographic location. In panels (a and b), each coloured point represents a nest; the black dot represents the mean, and the error bars denote the standard error around this estimate. Panels (c and d) display the geographic distribution of the spatial random effect for number of fledglings and proportional fledging success. Points with crosses represent sampling locations. Darker colours represent greater number of fledglings (c) and proportion of fledging success (d).

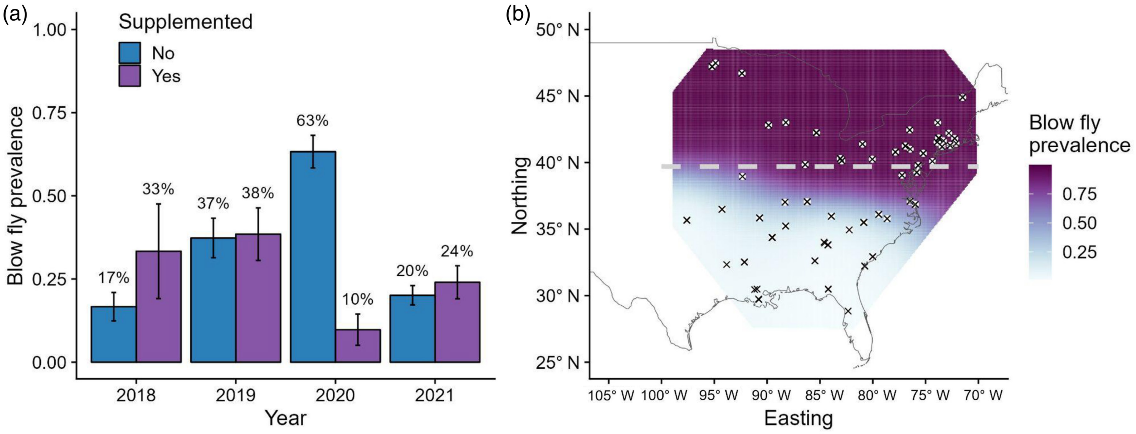

FIGURE 2 Parasite prevalence (i.e. the proportion of nests with blow flies) was affected by food supplementation in different years (a) and geographic location (b). Panel A presents the relationship between supplementation (yes or no; *x*-axis) and blow fly prevalence (*y*-axis). The proportion of nests with blow flies for supplemented birds compared to unsupplemented birds was higher in 2018, similar in 2019, lower in 2020 and similar in 2021. The percentage of nests with parasites is displayed above the bars. Panel (b) displays the geographic distribution of the spatial random effect for blow fly prevalence (b). Points with crosses represent sampling locations. Darker colours represent greater parasite prevalence. The grey dashed line represents the latitude below which no blow flies were found.

2020, and not significantly different in 2019 and 2021 (Figure 2a). Additionally, there was a substantial positive effect of day-of-year on blow fly prevalence (effect size = 0.681, CI [0.300, 1.069], $p < 0.001$; Figure S2). Blow fly size did not have strong spatial effects (ΔDIC > 2, Figure S3). Year and supplementation did not significantly affect blow fly size (Figure S3), but the number of nestlings in a nest and blow fly size correlated positively (effect size = 0.157, CI [0.034, 0.28], $p = 0.013$).

3.3 | Fitness-parasite models

We found no significant effect of parasite prevalence on host fitness, including no detectable effect of the interaction between supplementation and parasitism on host fitness (DeltaDIC < 2, $p > 0.05$; Figures S6 and S7). These results were consistent for both the overall dataset (Figure S6) and the subset of data from the range of the blow fly (i.e. northern latitudes, Figure S7).

3.4 | Steward models

Finally, our steward models uncovered a negative correlation between stewards' latitude and their probability of feeding their birds mealworms (effect size $= -0.891$, CI $[-1.401, -0.381]$; $p < 0.001$). That is, stewards at more southern latitudes were substantially more likely to feed their birds than those at more northern latitudes (Figure 3, Figure S4). In our models, we found no significant relationship between stewards' longitude and their probability of feeding their birds mealworms.

4 | DISCUSSION

Our study introduces the Nest Parasite Community Science Project, from which we assessed the effect of food supplementation on eastern bluebirds and their nest parasite community across years and the geographic range of bluebirds. Fledgling numbers were higher in the northeast and northwest, while proportional fledging success showed a consistent increase moving towards the East coast. Food supplementation increased fledging success, which has also been shown for bluebirds in a recent study (Bailey & Bonter, 2022). The main nest parasite taxa were parasitic blow flies, fleas and mites. Blow flies were found only in the northern latitudes, as observed in previous studies (reviewed in Sabrosky et al., 1989). Fleas and mites were rarer in bluebird nests and fleas were only found in the northern latitudes, which has been established in previous work (Sabrosky et al., 1989). Within the range of the blow flies, food supplementation affected blow fly prevalence but this effect varied across years. Finally, more stewards fed bluebirds at southern latitudes than at northern latitudes. Our results suggest that host–parasite dynamics can vary spatiotemporally, including in response to food supplementation of the host.

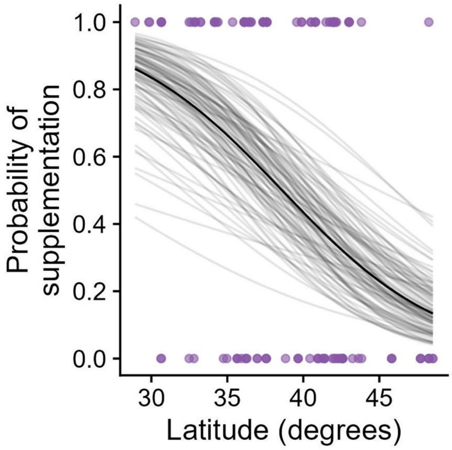

FIGURE 3 Stewards in higher latitudes were substantially less likely to feed birds compared to stewards in lower latitudes. Points represent an individual steward in a given year and the grey lines represent 100 random draws from the posterior distribution of our model estimates for the effect of latitude, which displays uncertainty in the estimate. The black line represents the mean of this distribution, thereby showing the mean effect estimate.

On average, fledging success of bluebirds in the East was higher relative to the rest of the study region. The ability to raise offspring to fledging may be constrained by food availability and energetic constraints, and by the number of offspring that the parents can feed (Food Limitation Hypothesis; Lack, 1947). Therefore, food might be more abundant on the East Coast, allowing for females to raise fledglings more successfully. The other fitness components (i.e. those related to egg laying and hatching) did not differ spatially, implying that there was not a similar geographic effect on egg production, fertility or viability. Regardless of the cause, this spatial heterogeneity could play an important role when examining the fitness consequences of a wide range of ecological and societal processes for wild bird populations, and so spatial autocorrelation should be accounted for where possible in such scenarios.

Interestingly, we found that few bluebird nests contained mites, which were from the genera *Dermanyssus* and *Ornithonyssus*. These two genera have been found in the nests of many species of passerines and on the bodies of domestic poultry, such as chickens (Proctor et al., 2000). In passerine nests, mites either overwinter in old nests and then infest new nests the following year, or they transmit into the nests on nesting material or adult birds (Proctor et al., 2000). Tree swallows, which are another common box-nesting bird, are often highly infested by parasitic nest mites (Knutie, unpublished data; Winkler, 1993). This species often incorporates chicken feathers into their nests, which not only provides the opportunity for mites to invade the nests, but also results in higher mite abundance (Winkler, 1993). Bluebird or mite behaviour might alternatively explain the lack of mites in bluebird nests. For example, bluebirds might choose boxes that are not apparently infested by mites, as found in other species with their roost sites (Christe et al., 1994). Mites might prefer other hosts compared to bluebirds if bluebirds have suboptimal characteristics (e.g. small brood sizes; Burtt Jr. et al., 1991) or effective defences against mites (e.g. preening, immune response). The differing infestation rates among box-nesting host species deserves further attention and would provide more insight into multi-host–parasite dynamics (Albert et al., 2023; Grab et al., 2019).

Food supplementation had contrasting effects on blow fly abundance in different years. In 2018, supplemented nests had more parasites than non-supplemented nests, in 2019 and 2021, there was no difference between treatments, and in 2020, supplemented bird nests had fewer parasites. One possible driver for these patterns is variation in food availability from natural sources. Food supplementation can improve host immune responses (Tschirren et al., 2007), and experimental work has demonstrated that supplemented bluebirds invest more in resistance mechanisms, which reduces parasite abundance (Knutie, 2020). However, this effect was primarily observed only early in the season when resource availability was low. Thus, immune investment by bluebirds might have varied across years due to changing food resource availability. For example, aerial insect abundance and activity can increase with temperature (Winkler et al., 2013), so temperature differences across years could have resulted in differing food (insect) availability. Blow flies themselves might be responding to changes in annual temperatures, with survival and fecundity changing in response to dynamic winter or summer temperatures (Musgrave et al. 2019). Although mean blow fly abundance in supplemented nests remained constant, abundances did vary across years in non-supplemented nests. Overall, our results suggest that annual variation in environmental conditions likely affects both host defences and blow fly fitness. Furthermore, these results suggest that environmental effects can vary among years and provides further evidence that researchers must consider that a single year of data might not provide the whole story. Characterizing the effect of other environmental factors on host–parasite interactions is beyond the scope of this study, but can be explored further with this community-based science project.

Food supplementation also increased fledging success of bluebirds, which corroborates a recent, large-scale citizen science study using NestWatch data (Bailey & Bonter, 2022). However, we did not find evidence that the presence of parasites mediated this relationship. Knutie (2020) found that food supplementation of bluebirds decreased the number of blow flies, thereby increasing fledging success. Although the study was experimental, it focused on one population in one year and thus might not be representative of the overall effects of food supplementation on host–parasite interactions across years and the range of the bluebird. More generally, our study does support the results of most studies showing that blow fly parasitism has no significant effects on fledging success (reviewed in Grab et al., 2019). This result could be explained by the long-standing relationship between bluebirds and blow flies, which has resulted in the evolution of effective host defences against the parasites (Grab et al., 2019).

Close to 50 million Americans feed birds in their backyards or around their homes, and more than half of these people also manage nest boxes (Cox & Gaston, 2016; Robb et al., 2008). In a 2008 survey, respondents expressed that they fed birds because they wanted to feel closer to nature, it brought them pleasure as a hobby, and/or they wanted to help the birds (Galbraith et al., 2014; Horn & Johansen, 2013). Although studies have not determined why people manage nest boxes, they likely engage in this activity for similar reasons to bird feeding. In our study, we found that stewards feed bluebirds in the southern United States more than in the north (Figure 3), which conflicts with the results of a previous study (Dunn & Tessaglia-Hymes, 2001). Since all of our participants manage nest boxes, the reasons stated above for not engaging in bird feeding is unlikely. Instead, participants might not feed bluebirds because it is expensive; in 2011, an average household in the United Kingdom spent £0.35 per day (Orros & Fellowes, 2015), which is approximately £0.53 per day in 2024. Alternatively, participants might be aware of studies that show that bird feeding can increase transmission of disease-causing pathogens, such as the Avipoxvirus or *Mycoplasma gallisepticum* (Galbraith et al., 2014; Wilcoxen et al., 2015), or reduce the reproductive success of bird species (Robb et al., 2008).

Over 15% of the US population engage in bird feeding and most feeder bird species are affected by nest ectoparasites (Sabrosky et al., 1989; US Fisheries and Wildlife, 2012). Therefore, understanding the broad-scale effects of food supplementation on host–parasite interactions is needed. Community-based science projects can provide a wealth of data that can help researchers explore spatial and temporal ecological patterns that might not otherwise be possible. The main result of our study demonstrates that food supplementation can have varying effects on host–parasite interactions across years and thus, cautions the interpretation of results from only one year of data. Additionally, we found that fleas and blow flies are restricted to the northern geographic range of bluebirds, which begs the question of whether southern bluebirds, which are not infested with fleas or blow flies, have evolved the same immune defences against ectoparasites as northern bluebirds (Knutie, 2020). Given the amount of training and permits involved in handling animals for research, a coordinated study on the evolution of host immune differences across geographic areas would only be possible with the academic scientists involved in the Nest Parasite Community Science Project.

AUTHOR CONTRIBUTIONS

Sarah A. Knutie and Rachel Bahouth conceived the ideas and designed methodology. Sarah A. Knutie, Rachel Bahouth, Matthew A. Bertone, Caroline Webb, Mahima Mehta, Mia Nahom, Rachael M. Barta, Sharan Ghai, Ashley C. Love, Sydney Horan, Alexandria Soldo, Elizabeth Cochrane, Jenna Bartholomew, Emily Cowan, Heather Bjerke, Susan L. Balenger, Michael W. Butler, Allison Cornell, Ashley C. Kennedy, Virginie Rolland, Elizabeth M. Schultz, Mark Stanback and Conor C. Taff collected the field data. Matthew A. Bertone, Sydney Horan and Alexandria Soldo identified parasites. Gregory F. Albery analysed the data. Sarah A. Knutie, Matthew A. Bertone and Gregory F. Albery led the writing of the drafts. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from figshare https://doi.org/10.6084/m9.figshare.26045368.v1 (Knutie & Albery, 2024).

STATEMENT ON INCLUSION

Our study brings together authors throughout the United States, where the study took place. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent were considered from the onset.

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SUPPORTING INFORMATION

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

Appendix 1. Understanding spatiotemporal effects of food supplementation on host-parasite interactions using community-based science.

Table S1. The number of nests collected from stewards based on state and year.

Figure S1. DIC values associated with model fits (top row) and fixed effect estimates (bottom row) for the fitness variable models.

Figure S2. DIC values associated with model fits (left panel) and fixed effect estimates (right panel) for the blow fly prevalence models, examining the factors determining infection with blow flies.

Figure S3. DIC values associated with model fits (left panel) and fixed effect estimates (right panel) for the parasite size models, examining the factors determining the size of blowfly pupae.

Figure S4. DIC values associated with model fits (left panel) and fixed effect estimates (right panel) for the steward supplementation models, testing the factors that determined whether a steward supplemented their nests.

Figure S5. DIC values associated with model fits (left panel) and fixed effect estimates (right panel) for the models of blowfly prevalence, fitted solely to data from above the 39.7' Latitude to control for a latitudinal bias in parasite presence.

Figure S6. Effect estimates for our models examining fitness effects, to examine how parasite counts influence fitness variables.

Figure S7. Effect estimates for our models examining fitness effects, to examine how parasite counts influence fitness variables, fitted solely to data from above the 39.7' Latitude to control for a latitudinal bias in parasite presence.

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