

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

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Abstract

Supplemental feeding can increase the overall health of animals but also can have variable effects on animals dealing with parasites. Furthermore, the spatial and temporal effects of food supplementation on host-parasite interactions remain poorly understood, likely because large-scale, coordinated efforts are difficult. Here, we introduce the Nest Parasite Community Science Project (hereafter “Project”), which is a community-based science project that coordinates studies with bird nest box “landlords” from the public and scientific community. The Project was established to understand broad ecological patterns between box-nesting birds and their nest parasite community. The goal of this study was to use data collected by the Project 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 2018-2020. Nest box landlords either fed their bluebirds mealworms or not, then followed the nesting success of the birds (number of eggs, percent hatched, percent fledged). Nests were sent to our lab where we identified and quantified all nest parasite taxa. Birds from the western range laid more eggs than the eastern range, but this spatial effect was not observed for hatching success. However, food supplementation increased hatching success across years and the study area. We primarily found parasitic blow flies and fleas in the nests, which were restricted to northern latitudes. Within this geographic area, food supplementation affected blow fly abundance, but this effect varied across years, with abundances increasing, decreasing, or not changing, depending on the year. Interestingly, more landlords at southern latitudes fed bluebirds compared to northern latitudes, which contradicted the results of other community-based science projects. Our study demonstrates the importance of coordinated studies across years and locations to understand the effects of environmental heterogeneity on host-parasite dynamics.

Keywords: Citizen science, disease ecology, host-parasite interactions, *Protocalliphora*,
Ceratophyllus

Introduction

Environmental factors, such as food availability, can influence host-parasite interactions (Becker et al. 2015, 2018, Sánchez et al. 2018). Host defense strategies against parasites, such as resistance, are often condition-dependent and regulated by resource availability. Resistance, such as the immune response, reduces the damage that parasites cause by reducing parasite fitness (Read et al. 2008). Resistance can be condition-dependent because mounting immune responses can be energetically costly and therefore only hosts with enough food resources may be able to invest in immunity (Sheldon and Verhulst 1996, Lochmiller and Deerenberg 2000, Howick and Lazzaro 2014, Knutie 2020). One explanation for the positive relationship between food availability and immunity is that the extra nutrients directly increase the production of immune cells (Strandin et al. 2018). For example, supplemented protein can increase the concentration of cellular and humoral immune cells (Datta et al. 1998, reviewed in Coop and Kyriazakis 2001).

Humans can change resource availability for animals by increasing the abundance of unnatural food using wild bird feeders and the disposal of human waste (Murray et al. 2016, Start et al. 2018). In fact, humans provide many wild bird species with a large proportion of their food (Jones and James Reynolds 2008, Jones 2011, Cox and Gaston 2018). In the United States alone, c. 50 million households provide over a half a million tons of supplemental food to attract wild birds to their property (Robb et al. 2008, Cox and Gaston 2016). Supplemental feeding of birds can have several benefits to birds and humans. Feeding wild birds can improve the mental health of humans along with their connection with nature (Jones 2011, Cox and Gaston 2016, 2018,

Shaw et al. 2017). Birds that are supplemented with food are often in better condition, which, in turn, can increase their reproductive success (Tollington et al. 2019, Bailey and Bonter 2022) and enhance some measures of immunity (Lochmiller et al. 1993, Wilcoxon et al. 2015, Ruhs et al. 2018, Sánchez et al. 2018, Strandin et al. 2018).

Recent experimental work demonstrated that food supplementation increases resistance to parasitism in a wild bird species, but this study relied on only one 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 and Dickinson 2009, Sullivan et al. 2009). These projects have provided a wealth of data to understand the impact of environmental conditions, including food supplementation, on bird fitness (Bailey and Bonter 2022). However, these studies have limitations because they cannot provide insight into species interactions, such as host-parasite relationships. Thus, the Nest Parasite Community Science Project (hereafter “Project”), a community-based science project that works with bird nest box “landlords” from the public and scientific community, was established. This Project explores the effect of environmental conditions, such as food supplementation, 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 unnaturally fed by humans. In the 1970s, populations of bluebirds declined, which was thought to be linked to a loss of suitable foraging and nesting habitat (Gowaty and Plissner 2015). In response, humans built and established artificial nest boxes and started supplementing the birds’ natural diet of insects, spiders, and small fruits (Pinkowski 1977) with mealworms (larvae of

Tenebrio molitor). Since the 1970s, the bluebird population size has rebounded (Sauer and Droege 1990) but humans continue to maintain nest boxes and provide bluebirds with supplemental food. Bluebirds also face challenges, as they are infested with parasitic nest flies (especially *Protocalliphora* spp.) throughout much of their range (Grab et al. 2019). Past studies have found highly variable blow fly abundances along with both a negative and no effect of blow flies on fledging success of bluebirds across their range (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 in Minnesota, abundances and effects on survival are 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 landlords either fed their bluebirds mealworms or not, then followed the nesting success of the birds (number of eggs, percent hatched, percent fledged) across the geographic range of the bluebird from 2018-2020. Once the nests were empty, they were sent to our team at the University of Connecticut and we identified and quantified nest parasite taxa. First, this information was used to determine spatial and temporal effects on nesting success and nest parasite presence and abundance. Second, we determined the effect of food supplementation on nesting success and parasite abundance. Lastly, because landlords voluntarily did or did not feed their bluebirds mealworms, we determined whether there was a spatial effect to bird feeding by landlords.

Methods

Field methods

Nest box landlords were recruited from 2017-2018 through social media platforms (e.g., Twitter and Facebook groups). From 2018-2020, we received a total of 390 nests from 59 landlords across 25 states in the eastern United States (Table S1). These landlords noted whether they provided live or dried mealworms to bluebirds on their property or not. Twenty-six landlords from 18 states provided mealworms and 26 landlords from 20 states did not; seven landlords 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 landlord. Landlords noted that they added approximately 50-200 mealworms per day to the feeders, which were 3-27 m (mean = 12 m) from the nest boxes.

Landlords were instructed to remove any old material from boxes in March-April each year. Landlords then monitored their nest boxes based on when bluebirds were expected to arrive on the breeding grounds (e.g., March for southern latitudes and May for northern latitudes). Once a nest box had nesting material, landlords confirmed that the nest box was occupied by bluebirds. Landlords monitored the nest boxes until eggs were laid in the nest box and then the number of eggs laid in the box were counted visually. Once the eggs hatched, the landlords visually counted the number of nestlings. The landlords monitored the survival of nestlings until the nest was empty or dead nestlings were present. After the nest was empty, landlords removed the nests from the box with gloves and placed nests individually in gallon-sized bags. They also placed a labeled piece of paper in the bag with the following information: collection date, full name and landlord ID, city, county, state, zip code, bird species, whether mealworms were fed, number of eggs laid, number of nestlings that hatched, and number of nestlings that died. Landlords were instructed to not touch the eggs or nestlings. However, if infertile eggs or dead nestlings were found, landlords were instructed to remove these items with gloves before shipping the nests.

Once the bags were labeled, landlords placed the bags in a cool, dry area. Once the breeding season was complete, nests were compiled and shipped in a cardboard box or paper envelope to the University of Connecticut.

Parasite identification, quantification, and measurements

After nests were received, they were logged into a database and assigned to a nest dissector (RMB, CW, MM, MN, RB, SG). Immediately prior to dissection, the ziplock bag was placed in a -80 °C freezer for up to 10 minutes 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. Specimens were identified into broad taxonomic groups then sent to MAB for identification. Blow fly puparia 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 contained parasitic, commensal, and predatory mites and therefore we separated these groups before identifying the parasitic genera. Identifications were confirmed to major groups, and Mesostigmata specimens (containing parasitic species) were slide-mounted. Identifications of the genera *Ornithonyssus* and *Dermanyssus* were made using a compound microscope at various magnifications (200-1000X) and using published diagnostic keys (Knee and Proctor 2006, di Palma et al. 2012, Murillo and Mullens 2017). 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 (Schmidt and Blume 1973, Moon 1980). We could not measure pupal case length because flies emerge from the top of the case, thus removing part of it.

Statistical analyses

We ran a series of generalized linear mixed models (GLMMs) to examine spatiotemporal drivers of the four fitness components and counts of both parasites. All analyses were conducted in R version 4.1.1 (Team and R Development Core Team 2016), using the integrated nested Laplace approximation (INLA; Lindgren and 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.

Fitness models. Our fitness models included eggs laid, eggs hatched, proportion eggs hatched, and fledging success as response variables. Eggs laid and hatched used a Gaussian distribution, while proportion hatched and fledging success used a binomial distribution wherein the number of eggs laid represented the number of trials. Explanatory variables included three fixed effects: mealworm supplementation (binary variable); year (categorical with 3 levels: 2018, 2019, 2020); and day-of-year ("DOY"; 1-365, representing number of days since January 1st). We included landlord ID as a random effect to account for between-site variation in fitness. To examine whether parasite variables determined fitness, we conducted a model addition approach where we began with the explanatory variables detailed above and then sequentially added parasite counts as explanatory variables. If a given variable improved model fit by reducing deviance

information criterion (DIC; $\Delta\text{DIC} > 2$), we kept that effect and repeated the procedure.

Because the parasite counts were extremely overdispersed, we coded them as a binary variable (infested/not infested).

Parasite models. Our parasite models included blow flies and fleas as response variables, both of which used a negative binomial specification. Explanatory variables included mealworm supplementation, year, and DOY as fixed effects and landlord ID as a random effect, all formulated as for the fitness models. When exploring the data there appeared to be substantial between-year variation in the effects of supplementation on parasites; as such, we fitted a single term fitting mealworm supplementation as an interaction with year to allow mealworm supplementation to have different effects across years. This model showed stronger support than including a fixed effect of mealworms alongside a separate interaction effect with year. Due to the overdispersed and uneven nature of the data distribution, the flea models were sensitive to the inclusion of our explanatory variables; as such, we repeated the model addition approach above with only year and landlord ID as explanatory variables, and then sequentially added the mealworm-by-year effect and the DOY effect to determine which effects were included in the final model.

Parasite size models. We also used the measures of blow fly pupal width as a response variable to examine whether our variables explained variation in the cumulative parasite size in the nest. We took the summed pupal width at each nest to use as the response variable, with a Gaussian specification. We then repeated the procedure that we used for the parasite models.

Spatial autocorrelation effects. For all 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 and Rue 2015). This approach 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 infection (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 spatial model, using 2 DIC as a cutoff. INLA also allows fitting of separate spatial fields for different time periods; as such, we also included between-year variation in the spatial field and assessed whether it improved model fit using the same cutoff.

Landlord models. Finally, to examine whether there were tangible spatial determinants of landlords' likelihood of feeding their birds, we fitted a model with mealworm supplementation as a binary response variable, and with explanatory variables including: the number of nests on the property, latitude, and longitude (all continuous).

Results

Fitness models. Bluebirds laid between 2-6 eggs that hatched between 0-6 young ($n = 354$ nests). Our fitness models revealed strong effects of supplementation on the proportion of eggs that hatched (0.31, CI (0.052, 0.567); $P=0.018$; Figure 1A, S1C), but on no other fitness variables (Figure S1C). There was strong spatial heterogeneity in the distribution of eggs laid (Figure 1B; S1A): fitting the SPDE effect improved model fit substantially ($\Delta\text{DIC}=-6.54$). The spatial distribution of the SPDE effect revealed that birds on the coast and to the northeast generally laid fewer eggs, while those in the midwest and southeast laid more (Figure 1B). However, no other fitness components showed similar spatial heterogeneity ($\Delta\text{DIC}>2$). In addition, our models revealed a number of DOY effects (Figure S1). Individuals sampled later in the year laid fewer

eggs (-0.293, CI (-0.404, -0.182), $P < 0.001$) and hatched fewer eggs (-0.161, CI (-0.275, -0.048), $P = 0.005$), but had more fledglings (0.208, CI (0.096, 0.32), $P < 0.001$).

Parasite models. Out of 373 nests that were dissected for parasites, 130 nests (34.9%) contained blow flies (*Protophormia sialia*; 1-139 individuals) and 17 nests (4.6%) contained fleas (1-179 individuals). Most flea taxa were identified as *Ceratophyllus idius*, but one nest contained *C. gallinae* and one nest contained *Orchopeas leucopus*. Fifteen nests (4.0%) contained between one to seven parasitic mites from the genera *Dermanyssus* and *Ornithonyssus*; because of these low numbers we did not statistically analyze the mite taxa. Nests also contained commensal dust mites (Pyroglyphidae), predatory mites (Cheyletidae), and commensal book lice (Liposcelididae) but since they were not parasitic, we excluded them from the models.

We uncovered strong support for among-year variable mealworm effects on blow flies (deltaDIC=-13; Figure 2A, S2). The effect of mealworms was significantly positive in 2018, indeterminate in 2019, and significantly negative in 2020 (Figure 2A). There was strong support for spatial effects in both blow flies (deltaDIC=-20.8) and fleas (deltaDIC=-5.98; Figure S2); both decreased in burden moving from North to South (Figures 2B-C). Notably, the furthest south that blow flies were discovered was 39.2°N (Figure 2B); the equivalent point for fleas was 41.8°N (Figure 2C). Finally, there was a substantial positive effect of DOY on blow fly burden (0.464, CI (0.087, 0.858; $P = 0.01$; Figure S2). By contrast, our blow fly size models found nothing significant (Figure S3), and the models were not improved by incorporation of the SPDE effect (deltaDIC>2; S3).

Landlord models. Finally, our landlord models uncovered a negative correlation between landlords' latitude and their probability of feeding their birds mealworms (-0.206 (-0.343, -

0.087); $P < 0.001$). That is, landlords in the south were substantially more likely to feed their birds than those in the north (Figure 3, S4).

Discussion

Our study introduces the Nest Parasite Community Science Project from which we determined the effect of food supplementation on eastern bluebirds (*Sialia sialis*) and their nest parasite community (fleas, blow flies) across years and the geographic range of bluebirds. We found that the number of eggs laid was higher in the midwestern United States compared to the East Coast, but this effect was not observed for hatching success. However, food supplementation increased hatching success across years and the study area. We primarily found parasitic blow flies and fleas in nests, which were restricted to northern latitudes. Seven or fewer parasitic mites were found in 4% of nests, suggesting that they were rare in the nests. Within the range of the blow flies, food supplementation affected blow fly abundance, but this effect varied across years, with abundances increasing, decreasing, or not changing depending on the year. Finally, more landlords at southern latitudes fed bluebirds compared to northern latitudes, which contradicted the results of other community-based science projects (Horn and Johansen 2013, Lepczyk et al. 2013). Our results suggest that host-parasite dynamics can vary spatiotemporally, including in response to food supplementation of the host.

On average, bluebirds in the Midwest laid more eggs, with the number of eggs laid decreasing moving towards the East Coast. The average number of eggs laid within a population can be constrained by resource availability and energetic constraints. Not only can the number of eggs laid be constrained by food availability, but also the number of offspring that the parents can feed (Food Limitation Hypothesis) (Lack 1947). Therefore, food might be more abundant in

the Midwest compared to the East Coast, allowing for females to lay more eggs. However, the number of nestlings that hatched did not differ spatially. One explanation is that midwestern bluebirds might have a higher rate of egg infertility than other areas and therefore these bluebirds “hedge their bets” by laying more eggs. Using a metaanalysis of 99 bird species, Spottiswoode and Møller (2004) found that species with higher genetic similarity have lower hatching success. Midwest bluebird populations might have higher genetic similarity than East Coast populations, resulting in higher egg infertility, which could help explain this difference in egg laying behavior.

Food supplementation increased the proportion of eggs that hatched. The effect of supplementation has had varying effects on other species, which likely depends on the type of macronutrient used. For example, supplementation with high protein insects increased bluebird brood size by 5% (Bailey and Bonter 2022). In contrast, fat-rich and protein-poor peanut cakes decreased brood size for (Eurasian) blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*) (Harrison et al. 2010). Our study found that high-protein mealworms led to an increase in hatching success, thus corroborating the trend of other studies where protein-focused supplements can increase clutch and brood sizes (Abell 1999). Our study did not find annual variation in the effect of food supplementation on hatching success of bluebirds. During low resource availability, brood size can decrease (Abell 1999), but can be rescued by food supplementation (Ruffino et al. 2014). Either bluebirds are able to find ample food in years of lower food availability or our study did not include years with a large enough effect of low food availability. Continuing our long-term community-based science project will add the necessary information to address these hypotheses.

Fleas (*Ceratophyllus spp.*) and blow flies (*Protocalliphora sialia*) were found only in northern latitudes. Decades of past work has also shown that the geographical range of *Protocalliphora spp.* is restricted to northern latitudes (Sabrosky et al. 1989). These patterns might be because ectotherm survival is dependent on environmental temperature (Munch and Salinas 2009). Parasites were only found in areas where they experience temperate winter conditions, such as freezing temperatures. In turn, these insects have evolved strategies to deal with the winter conditions. For example, shorter days and lower temperatures can signal insects to enter into a state of developmental arrest, called diapause, to survive these winter conditions (Vinogradova and Reznik 2013). During diapause, reduced metabolic rate can slow down the process of aging and increase survival (Denlinger 2008, Keil et al. 2015). For example, higher temperatures can reduce diapause survival in butterflies (*Lycaena tityrus*) and the rice stem borer (*Chilo suppressalis*) (Xiao et al. 2017, Klockmann and Fischer 2019). Thus, parasites might be unable to survive the higher winter temperatures in the south for long enough to take advantage of the next host breeding season. Higher summer temperatures at southern latitudes might also reduce the fitness of fleas and blow flies. Mean summer temperature can negatively predict nest parasite load (Mennerat et al. 2019; Musgrave et al. 2019). Temperature-dependent production of pigments like AGE, which is a marker of cellular senescence, can accumulate more quickly at higher temperatures in the related brown blow fly (*Calliphora stygia*) (Kelly et al. 2013). Experimental studies are needed to determine how seasonal temperatures affect the survival and evolution of fleas and blow flies, which would then causally explain the patterns observed in our study.

Interestingly, we found that few bluebird nests contained mites and the nests that contained mites included 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 and Owens 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 and Owens 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 behavior might alternatively explain the lack of mites in bluebird nests. For example, bluebirds might choose boxes that are not apparently infested by mites. Mites might prefer other hosts compared to bluebirds if bluebirds have suboptimal characteristics (small brood sizes; Burt et al. 1991) or effective defenses against mites (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 (Grab et al. 2019, Albert et al. 2021).

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 there was no difference between treatments, and in 2020 supplemented bird nests had fewer parasites. Food supplementation can improve host immune responses (Tschirren et al. 2007). For example, experimental work 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. Although mean blow fly abundance in supplemented nests remained constant, abundances did vary across years in unsupplemented nests. Overall, our results suggest that annual variation in environmental conditions likely affects both host defenses 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.

Close to 50 million Americans feed birds in their backyards or around their homes (Robb et al. 2008, Cox and Gaston 2016). We found that landlords fed bluebirds in the southern United States more than in the north, which contradicts other studies. For example, several studies have found that more people from northern latitudes feed birds compared to the south (Horn and Johansen 2013, Lepczyk et al. 2013). Systemic reporting biases could potentially explain our results. For example, southern bird-feeding enthusiasts or hobbyists are more likely to volunteer in community science projects, as opposed to their northern counterparts (Lepczyk et al. 2013). Furthermore, our contradictory spatial patterns could be specific to bluebirds, given that none of the aforementioned studies focused exclusively on bluebirds. Spatial biases are common in citizen science projects (Geldmann et al. 2016) and can be explained by human population density; higher population density, which is higher in the north (United States Census Bureau, 2022), correlates with higher sampling efforts. Future studies could focus on explaining why

bluebirds are fed by more landlords in the south, compared to the north, which could have conservation implications for the species.

Community-based science projects can provide a wealth of data that can help researchers explore broad 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, who are not infested with fleas or blow flies, have evolved the same immune defenses against ectoparasites as northern bluebirds (Knutie 2020). 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, given the amount of training and permits involved in handling animals for research.

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Figure Legends

Fig. 1. Fitness components were affected by A) food supplementation and B) geographic location. In panel A, samples are divided into those that received mealworms and those that did not (x axis), plotted against their proportion hatching success (y axis). Individuals that received supplementation hatched a greater proportion of eggs (P value displayed at top). Panel B displays the geographic distribution of the spatial random effect for numbers of eggs laid. Points with crosses represent sampling locations. Darker colors represent greater numbers of eggs laid.

Fig. 2. Parasite infection was affected by food supplementation in different years (A) and geographic location (B-C). In panel A, samples are divided into those that received mealworms and those that did not (x axis), plotted against their log-transformed blow fly burden (y axis). Individuals that received supplementation hatched a greater burden in 2018, a similar burden in 2019, and a lower burden in 2020 (P-values displayed at top). Panels B-C display the geographic distribution of the spatial random effect for blow flies (B) and fleas (C). Points with crosses represent sampling locations. Darker colors represent greater parasite burdens. Grey dashed lines represent latitudes at which no parasites were found. See Figure 1B for the easting and northing values.

Fig. 3. Landlords in higher latitudes were substantially less likely to feed birds on their property. The grey lines represent 100 random draws from the posterior distribution of our GLMM's estimate for the effect, to display uncertainty in the estimate. The black line represents the mean of the posterior. The estimate, 95% credibility intervals, and P-value are displayed at the top.

Figure 1.

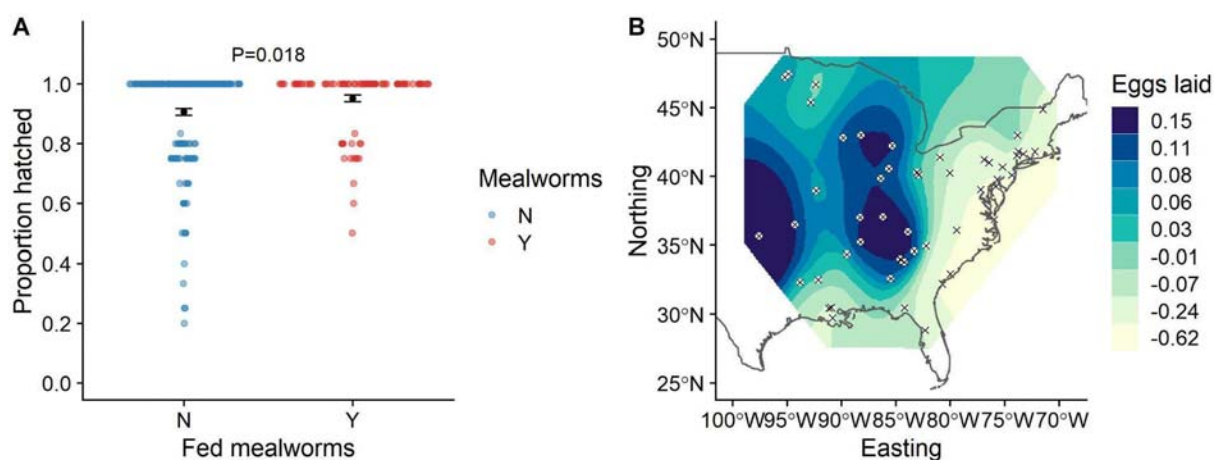
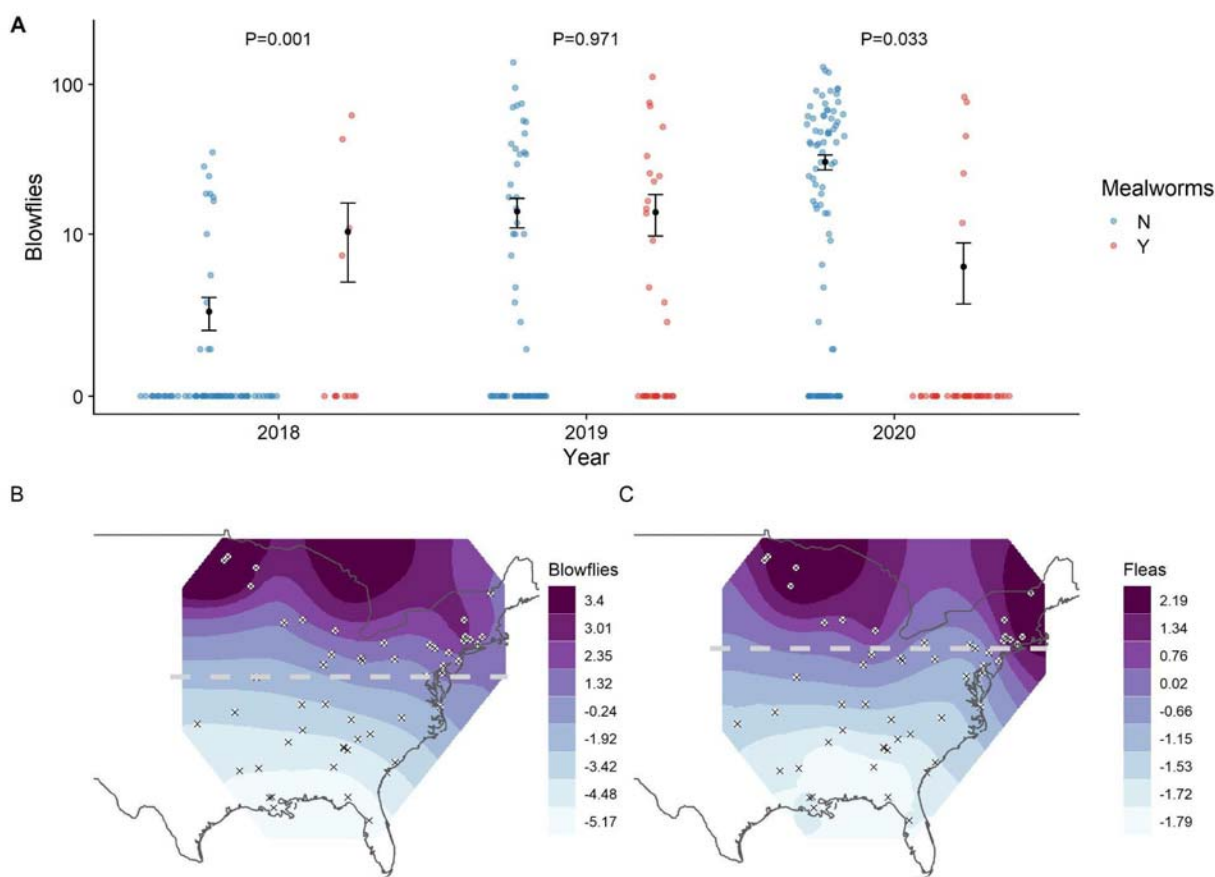
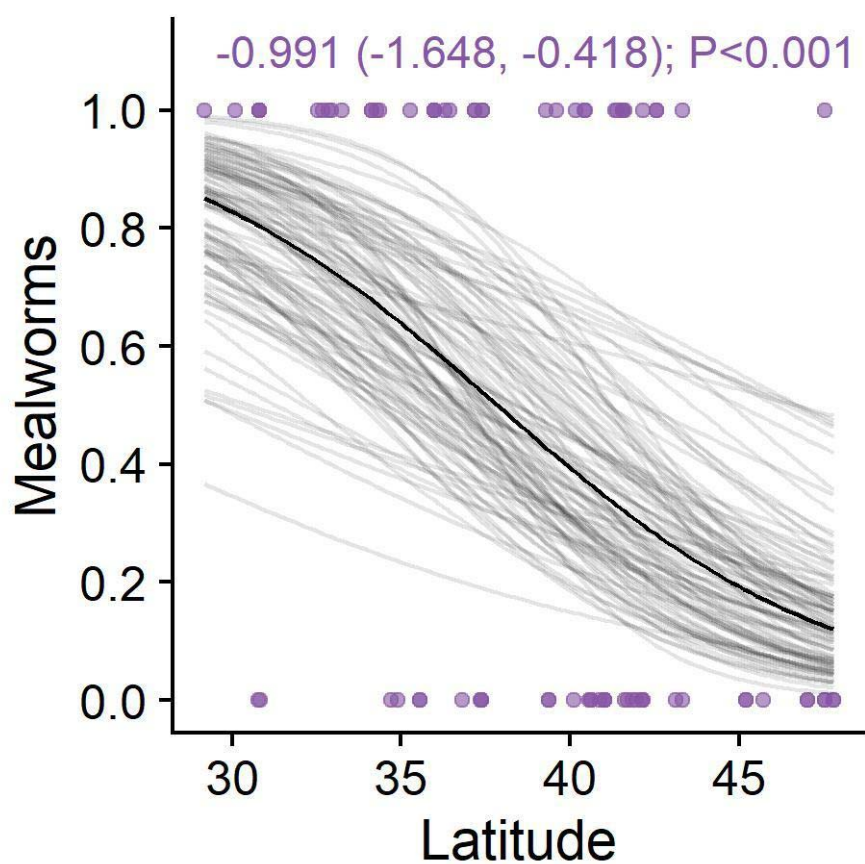


Figure 2.



605 **Figure 3.**



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