1   Understanding spatiotemporal effects of food supplementation on

2   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.

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

47   *Ceratophyllus*

48

49   **Introduction**

50   Environmental factors, such as food availability, can influence host-parasite interactions

51   (Becker et al. 2015, 2018, Sánchez et al. 2018). Host defense strategies against parasites, such as

52   resistance, are often condition-dependent and regulated by resource availability. Resistance, such

53   as the immune response, reduces the damage that parasites cause by reducing parasite fitness

54   (Read et al. 2008). Resistance can be condition-dependent because mounting immune responses

55   can be energetically costly and therefore only hosts with enough food resources may be able to

56   invest in immunity (Sheldon and Verhulst 1996, Lochmiller and Deerenberg 2000, Howick and

57   Lazzaro 2014, Knutie 2020). One explanation for the positive relationship between food

58   availability and immunity is that the extra nutrients directly increase the production of immune

59   cells (Strandin et al. 2018). For example, supplemented protein can increase the concentration of

60   cellular and humoral immune cells (Datta et al. 1998, reviewed in Coop and Kyriazakis 2001).

61   Humans can change resource availability for animals by increasing the abundance of

62   unnatural food using wild bird feeders and the disposal of human waste (Murray et al. 2016, Start

63   et al. 2018). In fact, humans provide many wild bird species with a large proportion of their food

64   (Jones and James Reynolds 2008, Jones 2011, Cox and Gaston 2018). In the United States alone,

65   c. 50 million households provide over a half a million tons of supplemental food to attract wild

66   birds to their property (Robb et al. 2008, Cox and Gaston 2016). Supplemental feeding of birds

67   can have several benefits to birds and humans. Feeding wild birds can improve the mental health

68   of humans along with their connection with nature (Jones 2011, Cox and Gaston 2016, 2018,

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69   Shaw et al. 2017). Birds that are supplemented with food are often in better condition, which, in

70   turn, can increase their reproductive success (Tollington et al. 2019, Bailey and Bonter 2022) and

71   enhance some measures of immunity (Lochmiller et al. 1993, Wilcoxen et al. 2015, Ruhs et al.

72   2018, Sánchez et al. 2018, Strandin et al. 2018).

73   Recent experimental work demonstrated that food supplementation increases resistance

74   to parasitism in a wild bird species, but this study relied on only one year of data in one

75   population (Knutie 2020). Due to environmental heterogeneity, studies are needed across years

76   and populations to understand the broad impact of food supplementation on host-parasite

77   interactions. Such studies are difficult to accomplish without coordinated efforts, such as

78   community-based science projects (e.g., eBird, NestWatch) (Phillips and Dickinson 2009,

79   Sullivan et al. 2009). These projects have provided a wealth of data to understand the impact of

80   environmental conditions, including food supplementation, on bird fitness (Bailey and Bonter

81   2022). However, these studies have limitations because they cannot provide insight into species

82   interactions, such as host-parasite relationships. Thus, the Nest Parasite Community Science

83   Project (hereafter "Project"), a community-based science project that works with bird nest box

84   "landlords" from the public and scientific community, was established. This Project explores the

85   effect of environmental conditions, such as food supplementation, on spatiotemporal patterns of

86   box nesting birds, such as Eastern Bluebirds (*Sialia sialis*), and their nest parasite community.

87   The Eastern Bluebird (hereafter "bluebird") is a North American bird species that is

88   unnaturally fed by humans. In the 1970s, populations of bluebirds declined, which was thought

89   to be linked to a loss of suitable foraging and nesting habitat (Gowaty and Plissner 2015). In

90   response, humans built and established artificial nest boxes and started supplementing the birds'

91   natural diet of insects, spiders, and small fruits (Pinkowski 1977) with mealworms (larvae of

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92   *Tenebrio molitor*). Since the 1970s, the bluebird population size has rebounded (Sauer and

93   Droege 1990)but humans continue to maintain nest boxes and provide bluebirds with

94   supplemental food. Bluebirds also face challenges, as they are infested with parasitic nest flies

95   (especially *Protocalliphora spp.*) throughout much of their range (Grab et al. 2019). Past studies

96   have found highly variable blow fly abundances along with both a negative and no effect of blow

97   flies on fledging success of bluebirds across their range (reviewed in Grab et al. 2019). A recent

98   study in Minnesota found that bluebirds supplemented with mealworms had higher resistance

99   (via an antibody response) to blow flies than unsupplemented birds (Knutie 2020). However,

100   even in Minnesota, abundances and effects on survival are highly variable across years (Grab et

101   al. 2019).

102   The goal of this study was to determine the effect of food supplementation on host-

103   parasite interactions across years and geographic locations. Nest box landlords either fed their

104   bluebirds mealworms or not, then followed the nesting success of the birds (number of eggs,

105   percent hatched, percent fledged) across the geographic range of the bluebird from 2018-2020.

106   Once the nests were empty, they were sent to our team at the University of Connecticut and we

107   identified and quantified nest parasite taxa. First, this information was used to determine spatial

108   and temporal effects on nesting success and nest parasite presence and abundance. Second, we

109   determined the effect of food supplementation on nesting success and parasite abundance. Lastly,

110   because landlords voluntarily did or did not feed their bluebirds mealworms, we determined

111   whether there was a spatial effect to bird feeding by landlords.

112

113   **Methods**

114   *Field methods*

115 Nest box landlords were recruited from 2017-2018 through social media platforms (e.g.,

116 Twitter and Facebook groups). From 2018-2020, we received a total of 390 nests from 59

117 landlords across 25 states in the eastern United States (Table S1). These landlords noted whether

118 they provided live or dried mealworms to bluebirds on their property or not. Twenty-six

119 landlords from 18 states provided mealworms and 26 landlords from 20 states did not; seven

120 landlords from seven states provided mealworms in some years but not the other years. The exact

121 number of mealworms provided to the bluebirds varied by the landlord. Landlords noted that

122 they added approximately 50-200 mealworms per day to the feeders, which were 3-27 m (mean

123 = 12 m) from the nest boxes.

124 Landlords were instructed to remove any old material from boxes in March-April each

125 year. Landlords then monitored their nest boxes based on when bluebirds were expected to arrive

126 on the breeding grounds (e.g., March for southern latitudes and May for northern latitudes). Once

127 a nest box had nesting material, landlords confirmed that the nest box was occupied by bluebirds.

128 Landlords monitored the nest boxes until eggs were laid in the nest box and then the number of

129 eggs laid in the box were counted visually. Once the eggs hatched, the landlords visually counted

130 the number of nestlings. The landlords monitored the survival of nestlings until the nest was

131 empty or dead nestlings were present. After the nest was empty, landlords removed the nests

132 from the box with gloves and placed nests individually in gallon-sized bags. They also placed a

133 labeled piece of paper in the bag with the following information: collection date, full name and

134 landlord ID, city, county, state, zip code, bird species, whether mealworms were fed, number of

135 eggs laid, number of nestlings that hatched, and number of nestlings that died. Landlords were

136 instructed to not touch the eggs or nestlings. However, if infertile eggs or dead nestlings were

137 found, landlords were instructed to remove these items with gloves before shipping the nests.

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138   Once the bags were labeled, landlords placed the bags in a cool, dry area. Once the breeding

139   season was complete, nests were compiled and shipped in a cardboard box or paper envelope to

140   the University of Connecticut.

141   *Parasite identification, quantification, and measurements*

142   After nests were received, they were logged into a database and assigned to a nest

143   dissector (RMB, CW, MM, MN, RB, SG). Immediately prior to dissection, the ziplock bag was

144   placed in a -80 °C freezer for up to 10 minutes to immobilize any live invertebrates. Once the

145   nest was removed from the freezer, pieces of the nest material were removed from the bag and

146   dissected over a white piece of paper, which took between 30 min to 2 h, depending on the

147   number of invertebrates in the nest. All invertebrates were collected from the nest material and

148   placed in 2 mL tubes with 90% ethanol. Specimens were then stored in a -80 °C freezer until

149   they were identified. Specimens were identified into broad taxonomic groups then sent to MAB

150   for identification. Blow fly puparia were identified under a dissecting scope after being removed

151   from alcohol and dried; no further preparation was performed. Flea and mite specimens were

152   slide-mounted in Hoyer's mounting medium or by clearing first in 10% KOH, washing, and

153   mounting in PVA (lactic acid, phenol, and polyvinyl alcohol); slides were left to cure on a slide

154   warmer.

155   Nests contained parasitic, commensal, and predatory mites and therefore we separated

156   these groups before identifying the parasitic genera. Identifications were confirmed to major

157   groups, and Mesostigmata specimens (containing parasitic species) were slide-mounted.

158   Identifications of the genera *Ornythonyssus* and *Dermanyssus* were made using a compound

159   microscope at various magnifications (200-1000X) and using published diagnostic keys (Knee

160   and Proctor 2006, di Palma et al. 2012, Murillo and Mullens 2017). Flea identifications were

161   made using a compound microscope at various magnifications (200-400X) and using published

162   diagnostic keys (Holland 1951, 1985, Lewis 2000). Blow flies were identified using available

163   morphological keys for pupae (Whitworth 2003a, 2003b). We also measured the width of empty

164   pupal cases for up to 10 individuals per nest as a proxy for fly size, which is related to lifetime

165   fitness in Diptera (Schmidt and Blume 1973, Moon 1980). We could not measure pupal case

166   length because flies emerge from the top of the case, thus removing part of it.

167   *Statistical analyses*

168   We ran a series of generalized linear mixed models (GLMMs) to examine spatiotemporal

169   drivers of the four fitness components and counts of both parasites. All analyses were conducted

170   in R version 4.1.1 (Team and R Development Core Team 2016), using the integrated nested

171   Laplace approximation (INLA; Lindgren and Rue 2015). All models were checked by simulating

172   from the posterior and verifying the even distribution of residuals and verifying that the models'

173   simulated data recapitulated the distribution of the input data.

174   **Fitness models.** Our fitness models included eggs laid, eggs hatched, proportion eggs hatched,

175   and fledging success as response variables. Eggs laid and hatched used a Gaussian distribution,

176   while proportion hatched and fledging success used a binomial distribution wherein the number

177   of eggs laid represented the number of trials. Explanatory variables included three fixed effects:

178   mealworm supplementation (binary variable); year (categorical with 3 levels: 2018, 2019, 2020);

179   and day-of-year ("DOY"; 1-365, representing number of days since January 1st). We included

180   landlord ID as a random effect to account for between-site variation in fitness. To examine

181   whether parasite variables determined fitness, we conducted a model addition approach where

182   we began with the explanatory variables detailed above and then sequentially added parasite

183   counts as explanatory variables. If a given variable improved model fit by reducing deviance

184   information criterion (DIC; deltaDIC>2), we kept that effect and repeated the procedure.

185   Because the parasite counts were extremely overdispersed, we coded them as a binary variable

186   (infested/not infested).

187   **Parasite models.** Our parasite models included blow flies and fleas as response variables, both

188   of which used a negative binomial specification. Explanatory variables included mealworm

189   supplementation, year, and DOY as fixed effects and landlord ID as a random effect, all

190   formulated as for the fitness models. When exploring the data there appeared to be substantial

191   between-year variation in the effects of supplementation on parasites; as such, we fitted a single

192   term fitting mealworm supplementation as an interaction with year to allow mealworm

193   supplementation to have different effects across years. This model showed stronger support than

194   including a fixed effect of mealworms alongside a separate interaction effect with year. Due to

195   the overdispersed and uneven nature of the data distribution, the flea models were sensitive to the

196   inclusion of our explanatory variables; as such, we repeated the model addition approach above

197   with only year and landlord ID as explanatory variables, and then sequentially added the

198   mealworm-by-year effect and the DOY effect to determine which effects were included in the

199   final model.

200   **Parasite size models.** We also used the measures of blow fly pupal width as a response variable

201   to examine whether our variables explained variation in the cumulative parasite size in the nest.

202   We took the summed pupal width at each nest to use as the response variable, with a Gaussian

203   specification. We then repeated the procedure that we used for the parasite models.

204   **Spatial autocorrelation effects.** For all models, we fitted a stochastic partial differentiation

205   equation (SPDE) effect to control for and quantify spatial autocorrelation in the response

206   variable (Lindgren et al. 2011, Lindgren and Rue 2015). This approach uses samples' bivariate

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207   coordinates to model spatial dependence, examining whether samples from closer locations are

208   more similar and then generating a two-dimensional spatial field that can be examined for spatial

209   patterns. This approach has proved successful for investigating spatial patterns of parasite

210   infection (Albery et al. 2019, 2022). We fitted an SPDE effect based on samples' latitude and

211   longitude and examined whether it improved model fit by assessing whether it reduced the DIC

212   of the spatial model, using 2 DIC as a cutoff. INLA also allows fitting of separate spatial fields

213   for different time periods; as such, we also included between-year variation in the spatial field

214   and assessed whether it improved model fit using the same cutoff.

215   **Landlord models.** Finally, to examine whether there were tangible spatial determinants of

216   landlords' likelihood of feeding their birds, we fitted a model with mealworm supplementation as

217   a binary response variable, and with explanatory variables including: the number of nests on the

218   property, latitude, and longitude (all continuous).

219

220   **Results**

221   **Fitness models.** Bluebirds laid between 2-6 eggs that hatched between 0-6 young (n = 354

222   nests). Our fitness models revealed strong effects of supplementation on the proportion of eggs

223   that hatched (0.31, CI (0.052, 0.567); P=0.018; Figure 1A, S1C), but on no other fitness variables

224   (Figure S1C). There was strong spatial heterogeneity in the distribution of eggs laid (Figure 1B;

225   S1A): fitting the SPDE effect improved model fit substantially (deltaDIC=-6.54). The spatial

226   distribution of the SPDE effect revealed that birds on the coast and to the northeast generally laid

227   fewer eggs, while those in the midwest and southeast laid more (Figure 1B). However, no other

228   fitness components showed similar spatial heterogeneity (deltaDIC>2). In addition, our models

229   revealed a number of DOY effects (Figure S1). Individuals sampled later in the year laid fewer

230 eggs (-0.293, CI (-0.404, -0.182), P<0.001) and hatched fewer eggs (-0.161, CI (-0.275, -0.048),

231 P=0.005), but had more fledglings (0.208, CI (0.096, 0.32), P<0.001).

232 **Parasite models.** Out of 373 nests that were dissected for parasites, 130 nests (34.9%) contained

233 blow flies (*Protocalliphora sialia*; 1-139 individuals) and 17 nests (4.6%) contained fleas (1-179

234 individuals). Most flea taxa were identified as *Ceratophyllus idius*, but one nest contained *C.*

235 *gallinae* and one nest contained *Orchopeas leucopus*. Fifteen nests (4.0%) contained between

236 one to seven parasitic mites from the genera *Dermanyssus* and *Ornithonyssus*; because of these

237 low numbers we did not statistically analyze the mite taxa. Nests also contained commensal dust

238 mites (Pyroglyphidae), predatory mites (Cheyletidae), and commensal book lice (Liposcelididae)

239 but since they were not parasitic, we excluded them from the models.

240   We uncovered strong support for among-year variable mealworm effects on blow flies

241 (deltaDIC=-13; Figure 2A, S2). The effect of mealworms was significantly positive in 2018,

242 indeterminate in 2019, and significantly negative in 2020 (Figure 2A). There was strong support

243 for spatial effects in both blow flies (deltaDIC=-20.8) and fleas (deltaDIC=-5.98; Figure S2);

244 both decreased in burden moving from North to South (Figures 2B-C). Notably, the furthest

245 south that blow flies were discovered was 39.2°N (Figure 2B); the equivalent point for fleas was

246 41.8°N (Figure 2C). Finally, there was a substantial positive effect of DOY on blow fly burden

247 (0.464, CI (0.087, 0.858; P=0.01; Figure S2). By contrast, our blow fly size models found

248 nothing significant (Figure S3), and the models were not improved by incorporation of the SPDE

249 effect (deltaDIC>2; S3).

250 **Landlord models.** Finally, our landlord models uncovered a negative correlation between

251 landlords' latitude and their probability of feeding their birds mealworms (-0.206 (-0.343, -

252 0.087); P<0.001). That is, landlords in the south were substantially more likely to feed their birds

253 than those in the north (Figure 3, S4).

254

255 **Discussion**

256   Our study introduces the Nest Parasite Community Science Project from which we

257 determined the effect of food supplementation on eastern bluebirds (*Sialia sialis*) and their nest

258 parasite community (fleas, blow flies) across years and the geographic range of bluebirds. We

259 found that the number of eggs laid was higher in the midwestern United States compared to the

260 East Coast, but this effect was not observed for hatching success. However, food

261 supplementation increased hatching success across years and the study area. We primarily found

262 parasitic blow flies and fleas in nests, which were restricted to northern latitudes. Seven or fewer

263 parasitic mites were found in 4% of nests, suggesting that they were rare in the nests. Within the

264 range of the blow flies, food supplementation affected blow fly abundance, but this effect varied

265 across years, with abundances increasing, decreasing, or not changing depending on the year.

266 Finally, more landlords at southern latitudes fed bluebirds compared to northern latitudes, which

267 contradicted the results of other community-based science projects (Horn and Johansen 2013,

268 Lepczyk et al. 2013). Our results suggest that host-parasite dynamics can vary spatiotemporally,

269 including in response to food supplementation of the host.

270   On average, bluebirds in the Midwest laid more eggs, with the number of eggs laid

271 decreasing moving towards the East Coast. The average number of eggs laid within a population

272 can be constrained by resource availability and energetic constraints. Not only can the number of

273 eggs laid be constrained by food availability, but also the number of offspring that the parents

274 can feed (Food Limitation Hypothesis) (Lack 1947). Therefore, food might be more abundant in

275   the Midwest compared to the East Coast, allowing for females to lay more eggs. However, the

276   number of nestlings that hatched did not differ spatially. One explanation is that midwestern

277   bluebirds might have a higher rate of egg infertility than other areas and therefore these bluebirds

278   "hedge their bets" by laying more eggs. Using a metaanalysis of 99 bird species, Spottiswoode

279   and Møller (2004) found that species with higher genetic similarity have lower hatching success.

280   Midwest bluebird populations might have higher genetic similarity than East Coast populations,

281   resulting in higher egg infertility, which could help explain this difference in egg laying

282   behavior.

283   Food supplementation increased the proportion of eggs that hatched. The effect of

284   supplementation has had varying effects on other species, which likely depends on the type of

285   macronutrient used. For example, supplementation with high protein insects increased bluebird

286   brood size by 5% (Bailey and Bonter 2022). In contrast, fat-rich and protein-poor peanut cakes

287   decreased brood size for (Eurasian) blue tits (*Cyanistes caeruleus*) and great tits (*Parus major*)

288   (Harrison et al. 2010). Our study found that high-protein mealworms led to an increase in

289   hatching success, thus corroborating the trend of other studies where protein-focused

290   supplements can increase clutch and brood sizes (Abell 1999). Our study did not find annual

291   variation in the effect of food supplementation on hatching success of bluebirds. During low

292   resource availability, brood size can decrease (Abell 1999), but can be rescued by food

293   supplementation(Ruffino et al. 2014). Either bluebirds are able to find ample food in years of

294   lower food availability or our study did not include years with a large enough effect of low food

295   availability. Continuing our long-term community-based science project will add the necessary

296   information to address these hypotheses.

297   Fleas (*Ceratophyllus spp.*) and blow flies (*Protocalliphora sialia*) were found only in

298   northern latitudes. Decades of past work has also shown that the geographical range of

299   *Protocalliphora spp.* is restricted to northern latitudes (Sabrosky et al. 1989). These patterns

300   might be because ectotherm survival is dependent on environmental temperature (Munch and

301   Salinas 2009). Parasites were only found in areas where they experience temperate winter

302   conditions, such as freezing temperatures. In turn, these insects have evolved strategies to deal

303   with the winter conditions. For example, shorter days and lower temperatures can signal insects

304   to enter into a state of developmental arrest, called diapause, to survive these winter conditions

305   (Vinogradova and Reznik 2013). During diapause, reduced metabolic rate can slow down the

306   process of aging and increase survival (Denlinger 2008, Keil et al. 2015). For example, higher

307   temperatures can reduce diapause survival in butterflies (*Lycaena tityrus*) and the rice stem borer

308   (*Chilo suppressalis*) (Xiao et al. 2017, Klockmann and Fischer 2019). Thus, parasites might be

309   unable to survive the higher winter temperatures in the south for long enough to take advantage

310   of the next host breeding season. Higher summer temperatures at southern latitudes might also

311   reduce the fitness of fleas and blow flies. Mean summer temperature can negatively predict nest

312   parasite load (Mennerat et al. 2019; Musgrave et al. 2019). Temperature-dependent production of

313   pigments like AGE, which is a marker of cellular senescence, can accumulate more quickly at

314   higher temperatures in the related brown blow fly (*Calliphora stygia*) (Kelly et al. 2013).

315   Experimental studies are needed to determine how seasonal temperatures affect the survival and

316   evolution of fleas and blow flies, which would then causally explain the patterns observed in our

317   study.

318   Interestingly, we found that few bluebird nests contained mites and the nests that

319   contained mites included the genera *Dermanyssus* and *Ornithonyssus*. These two genera have

320   been found in the nests of many species of passerines and on the bodies of domestic poultry,

321   such as chickens (Proctor and Owens 2000). In passerine nests, mites either overwinter in old

322   nests and then infest new nests the following year, or they transmit into the nests on nesting

323   material or adult birds (Proctor and Owens 2000). Tree swallows, which are another common

324   box-nesting bird, are often highly infested by parasitic nest mites (Knutie, unpublished data,

325   Winkler 1993). This species often incorporates chicken feathers into their nests, which not only

326   provides the opportunity for mites to invade the nests, but also results in higher mite abundance

327   (Winkler 1993). Bluebird or mite behavior might alternatively explain the lack of mites in

328   bluebird nests. For example, bluebirds might choose boxes that are not apparently infested by

329   mites. Mites might prefer other hosts compared to bluebirds if bluebirds have suboptimal

330   characteristics (small brood sizes; Burtt et al. 1991) or effective defenses against mites (preening,

331   immune response). The differing infestation rates among box-nesting host species deserves

332   further attention and would provide more insight into multi-host-parasite dynamics (Grab et al.

333   2019, Albert et al. 2021).

334   Food supplementation had contrasting effects on blow fly abundance in different years.

335   In 2018 supplemented nests had more parasites than non-supplemented nests, in 2019 there was

336   no difference between treatments, and in 2020 supplemented bird nests had fewer parasites. Food

337   supplementation can improve host immune responses (Tschirren et al. 2007). For example,

338   experimental work demonstrated that supplemented bluebirds invest more in resistance

339   mechanisms, which reduces parasite abundance (Knutie 2020); however, this effect was

340   primarily observed only early in the season when resource availability was low. Thus, immune

341   investment by bluebirds might have varied across years due to changing food resource

342   availability. For example, aerial insect abundance and activity can increase with temperature

343   (Winkler et al. 2013), so temperature differences across years could have resulted in differing

344   food (insect) availability. Blow flies themselves might be responding to changes in annual

345   temperatures, with survival and fecundity changing in response to dynamic winter or summer

346   temperatures. Although mean blow fly abundance in supplemented nests remained constant,

347   abundances did vary across years in unsupplemented nests. Overall, our results suggest that

348   annual variation in environmental conditions likely affects both host defenses and blow fly

349   fitness. Furthermore, these results suggest that environmental effects can vary among years and

350   provides further evidence that researchers must consider that a single year of data might not

351   provide the whole story. Characterizing the effect of other environmental factors on host-parasite

352   interactions is beyond the scope of this study but can be explored further with this community-

353   based science project.

354   Close to 50 million Americans feed birds in their backyards or around their homes (Robb

355   et al. 2008, Cox and Gaston 2016). We found that landlords fed bluebirds in the southern United

356   States more than in the north, which contradicts other studies. For example, several studies have

357   found that more people from northern latitudes feed birds compared to the south (Horn and

358   Johansen 2013, Lepczyk et al. 2013). Systemic reporting biases could potentially explain our

359   results. For example, southern bird-feeding enthusiasts or hobbyists are more likely to volunteer

360   in community science projects, as opposed to their northern counterparts (Lepczyk et al. 2013).

361   Furthermore, our contradictory spatial patterns could be specific to bluebirds, given that none of

362   the aforementioned studies focused exclusively on bluebirds. Spatial biases are common in

363   citizen science projects (Geldmann et al. 2016) and can be explained by human population

364   density; higher population density, which is higher in the north (United States Census Bureau,

365   2022), correlates with higher sampling efforts. Future studies could focus on explaining why

366   bluebirds are fed by more landlords in the south, compared to the north, which could have

367   conservation implications for the species.

368   Community-based science projects can provide a wealth of data that can help researchers

369   explore broad spatial and temporal ecological patterns that might not otherwise be possible. The

370   main result of our study demonstrates that food supplementation can have varying effects on

371   host-parasite interactions across years and thus, cautions the interpretation of results from only

372   one year of data. Additionally, we found that fleas and blow flies are restricted to the northern

373   geographic range of bluebirds, which begs the question of whether southern bluebirds, who are

374   not infested with fleas or blow flies, have evolved the same immune defenses against

375   ectoparasites as northern bluebirds (Knutie 2020). A coordinated study on the evolution of host

376   immune differences across geographic areas would only be possible with the academic scientists

377   involved in the Nest Parasite Community Science Project, given the amount of training and

378   permits involved in handling animals for research.

379

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400   **Author contributions:** SAK and RB designed the project, SAK, MAB, RB, CW, MM, MN,

401   RMB, SG, SB, MWB, AK, BS, and CCT collected data, GFA conducted analyses, MAB

402   identified parasites, SAK, MAB, RB, CW, MM, MN, RMB, SG and GFA wrote the manuscript

403   and all authors revised the manuscript.

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576 **Figure Legends**

577 **Fig. 1.** Fitness components were affected by A) food supplementation and B) geographic

578 location. In panel A, samples are divided into those that received mealworms and those that did

579 not (x axis), plotted against their proportion hatching success (y axis). Individuals that received

580 supplementation hatched a greater proportion of eggs (P value displayed at top). Panel B displays

581 the geographic distribution of the spatial random effect for numbers of eggs laid. Points with

582 crosses represent sampling locations. Darker colors represent greater numbers of eggs laid.

583 **Fig. 2.** Parasite infection was affected by food supplementation in different years (A) and

584 geographic location (B-C). In panel A, samples are divided into those that received mealworms

585 and those that did not (x axis), plotted against their log-transformed blow fly   burden (y axis).

586 Individuals that received supplementation hatched a greater burden in 2018, a similar burden in

587 2019, and a lower burden in 2020 (P-values displayed at top). Panels B-C display the geographic

588 distribution of the spatial random effect for blow flies   (B) and fleas (C). Points with crosses

589 represent sampling locations. Darker colors represent greater parasite burdens. Grey dashed lines

590 represent latitudes at which no parasites were found. See Figure 1B for the easting and northing

591 values.

592 **Fig. 3**. Landlords in higher latitudes were substantially less likely to feed birds on their property.

593 The grey lines represent 100 random draws from the posterior distribution of our GLMM's

594 estimate for the effect, to display uncertainty in the estimate. The black line represents the mean

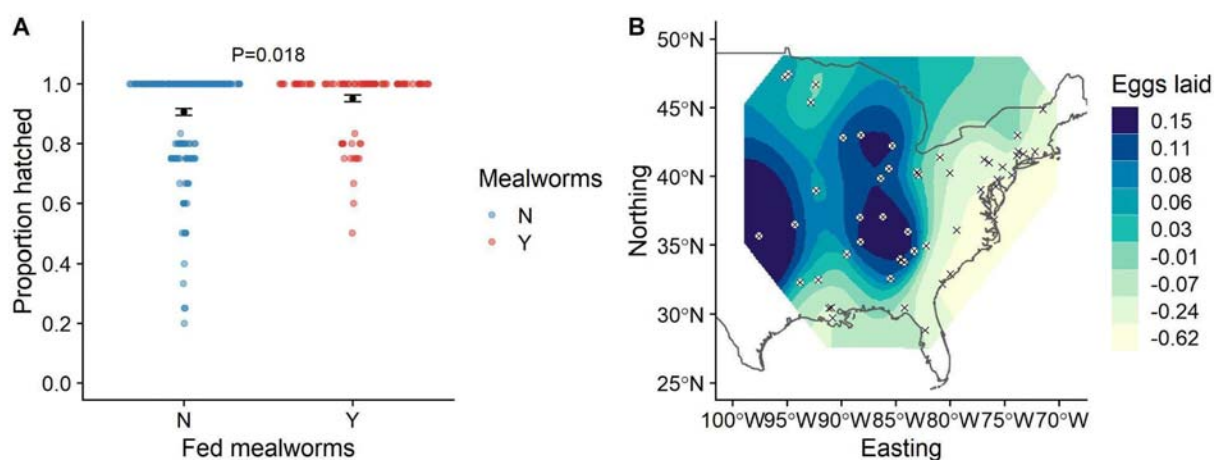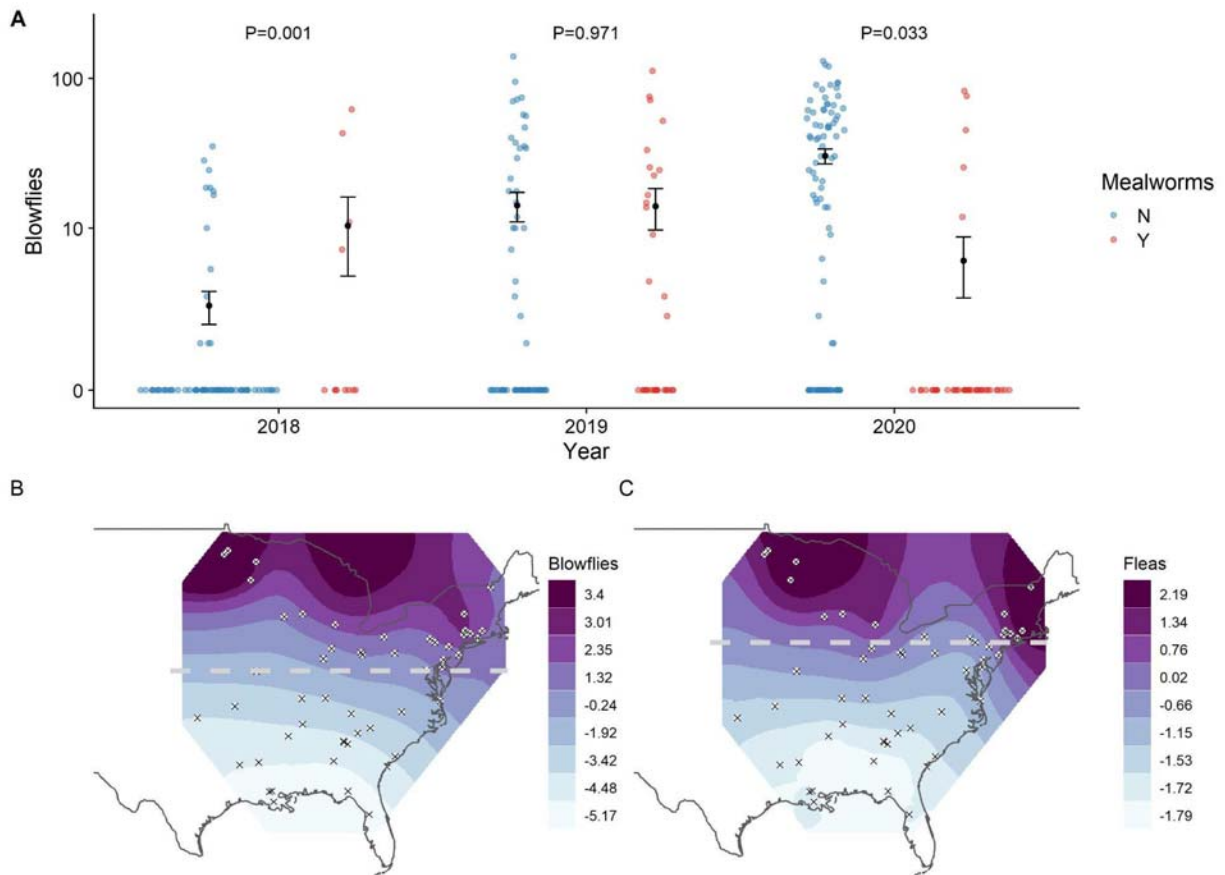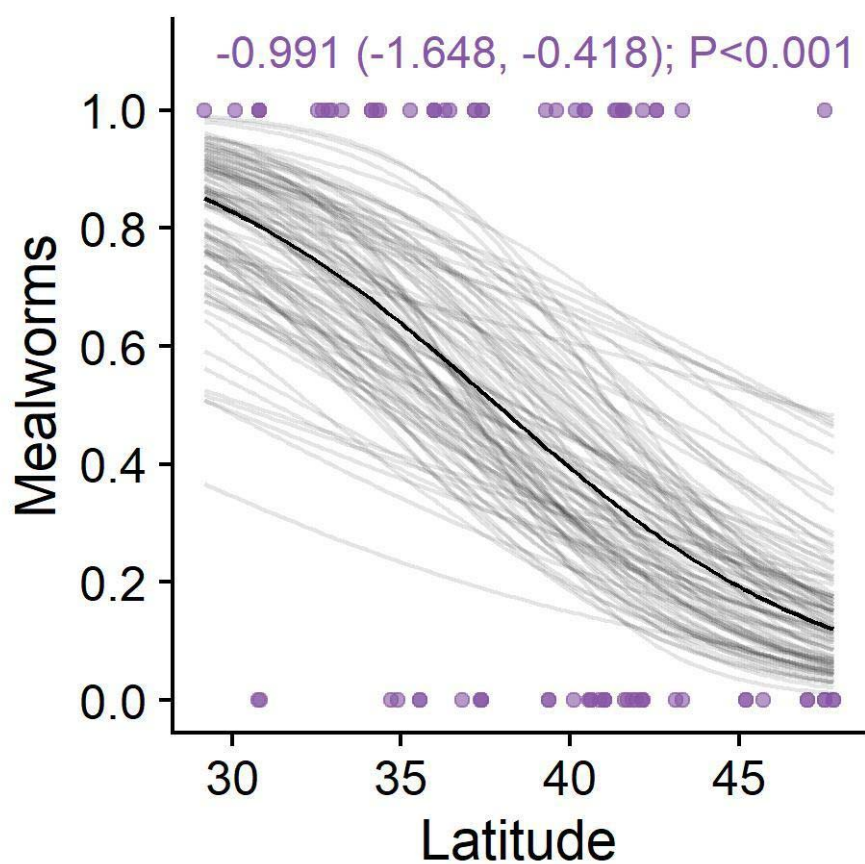595 of the posterior. The estimate, 95% credibility intervals, and P-value are displayed at the top.

596

597 **Figure 1.**

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600   **Figure 2.**

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605   **Figure 3.**

-0.991 (-1.648, -0.418); P<0.001

606