Ornithological Applications, 2024, 126, 1–13
https://doi.org/10.1093/ornithapp/duae021
Advance access publication 29 May 2024
Research Article

AOS AMERICAN ORNITHOLOGICAL SOCIETY
Ornithological Applications
OXFORD

Songbird annual productivity declines with increasing soil lead contamination around nests

Frank R. Thompson III,[1,*] Thomas W. Bonnot,[2] Rebecka L. Brasso,[3] Melissa C. Roach,[4] Kathy Hixson,[5] and David E. Mosby[2]

[1]U.S.D.A. Forest Service Northern Research Station, Columbia, Missouri, USA
[2]U.S. Fish and Wildlife Service, Columbia, Missouri, USA
[3]Weber State University, Ogden, Utah, USA
[4]School of Natural Resources, University of Missouri, Columbia, Missouri, USA
[5]Southeast Missouri State University, Cape Girardeau, Missouri, USA

[*]Corresponding author: frank.r.thompson@usda.gov

ABSTRACT

Songbirds incidentally ingest soil contaminated with lead and several species in the Southeast Missouri Lead Mining District have a negative relationship between soil lead concentration and reproduction. We used an individual-based model (IBM) to simulate nesting processes throughout the breeding season to estimate annual productivity for 5 songbirds in relation to soil-lead concentration. We modeled daily nest survival and number fledged in relation to soil lead and incorporated these relationships into the IBM using a Bayesian approach that fully captured parameter uncertainty and process variation. The proportion of the posterior distribution for the effect of soil lead on daily nest survival was mostly negative for *Pipilo erythrophthalmus* (Eastern Towhee), *Passerina cyanea* (Indigo Bunting), *Cardinalis cardinalis* (Northern Cardinal), *Sialia sialis* (Eastern Bluebird; f = 0.972, 0.990, 0.741, 0.581, respectively), and slightly positive for *Spizella pusilla* (Field Sparrow; f = 0.680). The proportion of the posterior distribution for the effect of soil lead on the number fledged from successful nests was mostly negative for *S. pusilla*, *P. erythrophthalmus*, and *C. cardinalis* (f = 0.867, 0.585, 0.508, respectively) and positive for *P. cyanea* and *S. sialis* (f = 0.773, 0.744). Simulated annual productivity decreased by 0.04–1.47 young/female/year among species across the range of soil lead concentrations, with the greatest declines for *P. erythrophthalmus* and *P. cyanea*. The probability of fledging one or more young changed from 51% to 15% for *P. erythrophthalmus*, 57% to 23% for *P. cyanea*, 60% to 48% for *C. cardinalis*, 94% to 84% for *S. sialis*, and 57% to 64% for *S. pusilla* as soil-lead concentration around a nest increased from 20 to 4,000 ppm. Most nest failures were the result of predation; therefore, we suggest lead may have affected birds' behavior at the nest, or affected nest site quality, which resulted in higher nest predation.

Keywords: annual productivity, lead mining, Missouri, nest predation, soil lead contamination, songbirds

How to Cite

Thompson III, F. R., T. W. Bonnot, R. L. Brasso, M. C. Roach, K. Hixson, and D. E. Mosby (2024). Songbird annual productivity declines with increasing soil lead contamination around nests. Ornithological Applications 126:duae021.

LAY SUMMARY

- Songbirds incidentally consume soil contaminated with lead while foraging near mining operations. Previous research in the Southeast Missouri Lead Mining District found a negative relationship between soil lead concentration and some songbird reproductive parameters, such as nest survival and number of young fledged.
- We used data from this earlier study in an individual-based model to predict annual productivity by a female in a breeding season at increasing soil lead levels.
- Annual productivity decreased by 0.04–1.47 offspring/female/year and the probability of fledging one or more young changed from 51% to 15% for *Pipilo erythrophthalmus* (Eastern Towhee), 57% to 23% for *Passerina cyanea* (Indigo Bunting), 60% to 48% for *Cardinalis cardinalis* (Northern Cardinal), 94% to 84% for *Sialia sialis* (Eastern Bluebird), and 57% to 64% for *Spizella pusilla* (Field Sparrow) as soil-lead concentrations increased.
- Most nest failures were due to predation; therefore, we suggest possible explanations for the reduction in productivity are that lead affected birds' behavior and activity at the nest, or affected nest site quality, and resulted in higher nest predation.

La productividad anual de los pájaros cantores disminuye con el aumento de la contaminación por plomo del suelo alrededor de los nidos

Submission Date: September 6, 2023. Editorial Acceptance Date: May 14, 2024

RESUMEN

Las aves canoras ingieren incidentalmente suelo contaminado con plomo y varias especies en el Distrito Minero de Plomo del sureste de Missouri tienen una relación negativa entre la concentración de plomo en el suelo y la reproducción. Utilizamos un modelo basado en individuos (MBI) para simular los procesos de anidación a lo largo de la temporada reproductiva para estimar la productividad anual de cinco aves canoras en relación con la concentración de plomo en el suelo. Modelamos la supervivencia diaria del nido y el número de volantones en relación con el plomo en el suelo e incorporamos estas relaciones en el MBI usando un enfoque bayesiano que capturó completamente la incertidumbre de los parámetros y la variación del proceso. La proporción de la distribución posterior para el efecto del plomo en el suelo sobre la supervivencia diaria del nido fue mayormente negativa para *Pipilo erythrophthalmus*, *Passerina cyanea*, *Cardinalis cardinalis* y *Sialia sialis* (f = 0.972, 0.990, 0.741, 0.581, respectivamente) y ligeramente positiva para *Spizella pusilla* (f = 0.680). La proporción de la distribución posterior para el efecto del plomo en el suelo sobre el número de volantones de nidos exitosos fue mayormente negativa para *S. pusilla*, *P. erythrophthalmus* y *C. cardinalis* (f = 0.867, 0.585, 0.508, respectivamente) y positiva para *P. cyanea* y *S. sialis* (f = 0.773, 0.744). La productividad anual simulada disminuyó en 0.04–1.47 jóvenes/hembra/año entre las especies a lo largo del rango de concentraciones de plomo en el suelo, con las mayores disminuciones para *P. erythrophthalmus* y *P. cyanea.* La probabilidad de emplumar uno o más jóvenes cambió del 51% al 15% para *P. erythrophthalmus*, del 57% al 23% para *P. cyanea*, del 60% al 48% para *C. cardinalis*, del 94% al 84% para *S. sialis*, y del 57% al 64% para *S. pusilla* a medida que la concentración de plomo en el suelo alrededor de un nido aumentó de 20 a 4000 ppm. La mayoría de los fracasos de los nidos fueron resultado de la depredación; por lo tanto, sugerimos que el plomo puede haber afectado el comportamiento de las aves en el nido, o afectado la calidad del sitio del nido, lo que resultó en una mayor depredación de los nidos.

Palabras clave: aves canoras, contaminación de plomo en el suelo, depredación de nidos, minería de plomo, Missouri, productividad anual

INTRODUCTION

Lead exposure and uptake in over 120 species of birds results in both sublethal and lethal effects (Scheuhammer and Norris 1995, Haig et al. 2014 and references therein); such effects include mortality, lethargy, vascular damage, digestive tract dysfunction, anemia, emaciation, vision loss, neurological damage, and paralysis (Eisler 1988, Beyer et al. 1988, Douglas-Stroebel et al. 2004, Fisher et al. 2006, Pain 1996, Hoffman et al. 2000). Lead also affects reproductive parameters such as egg hatchability and the development and survival of young, reducing the lifetime fitness of birds (Edens and Garlich, 1983; Buerger et al. 1986; Burger, 1995; Burger and Gochfeld, 2000). Neurological damage resulting from lead poisoning can adversely affect avian behavior, such as food begging, feeding, depth perception, song learning, territorial aggression, and locomotion (Burger and Gochfeld, 1985, 2000, Janssens et al. 2003, Ecke et al. 2017, McClelland et al. 2019, Goodchild et al. 2021). Furthermore, lead poisoning might influence reproduction indirectly through its effects on behavior; for example, increased aggression can result in decreased provisioning of young or incubating females (Duckworth 2006) or result in lower nest success potentially due to reduced nest defense or elevated activity at the nest site resulting in increased predation (Brasso et al. 2023, Hitt et al. 2023).

Lead exposure in birds often occurs from ingestion of lead shot used for hunting and/or lead weights for fishing (Scheuhammer and Norris 1995); however, birds can also be exposed to lead in urban environments (Roux and Mara 2007, McClelland et al. 2019, Hitt et al. 2023) as well as in lead-mining areas (Blus et al. 1991, Beyer et al. 2004, Beyer et al. 2013). In the latter examples, birds are exposed to lead by ingesting contaminated vegetation, insects, and soil invertebrates (Price et al. 1974, Labare et al. 2004) and/or incidental ingestion of contaminated soil and dust while feeding, grooming, or other activities (Beyer et al. 1994, Vyas et al. 2000, Custer et al. 2003, De Francisco et al. 2003, Hansen et al. 2011, Beyer et al. 2013). There is increasing evidence that songbirds are exposed to lead from mining activities. For example, *Turdus migratorius* (American Robin), *Melospiza melodia* (Song Sparrow), and *Catharus ustulatus* (Swainson's Thrush) from contaminated areas in the Couer d'Alene mining district in northern Idaho, USA, had greater blood and liver lead concentrations than birds from uncontaminated sites and the concentration of lead in blood and in the liver was directly related to soil lead concentration (hereafter "soil lead"), suggesting that the ingestion of soil or prey contaminated with soil was the route of exposure (Hansen et al. 2011, Sample et al. 2011). Lead concentrations in *T. migratorius*, *Cardinalis cardinalis* (Northern Cardinal), *Riparia riparia* (Bank Swallow), *Stelgidopteryx ruficollis* (Southern Rough-winged Swallow), and *Toxostoma rufum* (Brown Thrasher) from contaminated sites in the Tri-State Mining District in southwestern Missouri, northeastern Oklahoma, and southeastern Kansas were 2.2–210 fold greater than birds from uncontaminated sites (Beyer et al. 2004). More recently, ground-foraging songbirds in the Southeast Missouri Lead Mining District had lead tissue concentrations in the blood, liver, and kidneys that were 8, 13, and 23 times greater, respectively, than in uncontaminated sites (Beyer et al. 2013). Therefore, while historically overlooked, songbirds can accumulate lead at significant concentrations that likely result in adverse effects.

Brasso et al. (2023) investigated the relationship between mean soil lead surrounding nest sites and reproductive success of *Sialia sialis* (Eastern Bluebird), *Spizella pusilla* (Field Sparrow), *Pipilo erythrophthalmus* (Eastern Towhee), *C. cardinalis* and *Passerina cyanea* (Indigo Bunting) in the Southeast Missouri Lead Mining District. Blood lead concentrations of adult songbirds and their broods were significantly positively related to the mean soil lead surrounding their nests. Nest survival was strongly related to soil lead for *P. erythrophthalmus* and *P. cyanea* such that at high local lead concentrations, survival of nests to completion was < 2%; *C. cardinalis* and *S. sialis* also experienced negative effects, although these relationships were weaker and less supported. Small negative effects also existed for the number of young fledged (i.e., brood size) per successful nest for two species. These relationships suggest lead negatively affects songbird reproduction; however, annual productivity would more comprehensively measure the combined effects of these relationships on a species' reproduction. Ornithologists have cautioned that nest-survival may be a useful measure of pressures on a population such as nest predation but, estimates of annual productivity are needed for use in conservation strategies and to make inferences about population-level processes (Thompson et al. 2001, Jones et al. 2005). Annual productivity is the number of offspring produced by a female across all nesting attempts in a year and integrates all aspects of reproduction in a single measure that drives population growth.

Furthermore, even when individual elements of reproduction (e.g., clutch size, nest survival, and number of fledglings) have weakly supported relationships with environmental factors, their combined effects can be greater and compound over time such as nesting period or season. Annual productivity, however, is logistically difficult to measure in the field because it requires tracking all nesting attempts by uniquely marked birds through the entire breeding season. Alternatively, annual productivity can be estimated with individual-based models (IBMs) constructed from reproductive parameters more easily observed by monitoring a sample of nests (Pease and Gryzbowksi 1995, Powell et al. 1999, Mattsson et al. 2007, Bonnot et al. 2018).

Our objective was to determine the effects of soil lead contamination on annual productivity of *P. erythrophthalmus*, *P. cyanea*, *C. cardinalis*, *S. pusilla*, and *S. sialis* in the Southeast Missouri Lead Mining District. We incorporated data from Brasso et al. (2023) within generalized linear mixed models, fit using Bayesian methods, to estimate nest survival and number of fledglings per nest as a function of soil lead concentration around the nest. We integrated those results with other reproductive parameters in an IBM to simulate the effects of increasing levels of soil lead on annual productivity and the probability of fledging at least one young/year. We relied on the Bayesian treatment of uncertainty to account for both process variation and parameter uncertainty in our estimates.

METHODS

Study Area

Missouri was the top global producer of lead from the late 19th through the mid-20th century. Mining activities in the Southeast Missouri Lead Mining District have left a legacy of metal contamination in the region. Lead from smelting, tailings, and chat has contaminated soils, sediment, biota, and water, and wind, rain, and flooding events continue to release and remobilize lead (Besser et al. 2007, Seeger 2008, Allert et al. 2013, Beyer et al. 2018). Brasso et al. (2023) studied nesting songbirds on three contaminated sites (Anschutz Mine, Big River floodplain, and Magmont Vent) where mining, milling, and smelting processes released lead into the environment and soil lead was elevated (mean soil lead: 852–2,172 ppm, range: 21–35,967 ppm; Brasso et al. 2023) and two reference sites (Johnson's Shut-Ins State Park and Hawn State Park) for comparison that had no history of lead releases (mean soil lead: 21–31 ppm, range: < 14–38 ppm; Figure 1). Mean soil lead within a 60-m radius of the 579 bird nests found across all sites ranged 19–4,468 ppm (Brasso et al. 2023).

The 5 study sites were in or near the St. Francois Mountains, the topographic high point of the southeast Missouri Ozarks, and were underlain by Cambrian or Ordovician dolomites and sandstones. The Anschutz Mine site was a mix of pine (*Pinus* spp.) and oak (*Quercus* spp.) woodlands, old fields dominated by grasses, forbs, and eastern red cedar (*Juniperus virginiana*) saplings, and capped mine and mill wastes covered by grasses and forbs. The Magmont Vent site consisted of oak-hickory (*Carya* spp.) woodlands and forested uplands with scattered pines and was dissected by mowed power lines, a rail line, and a private road. The Big River floodplain site consisted of mowed fields, old fields, riparian forest, and upland oak-hickory forest on the slopes leading out of the river valley. The Hawn State Park site was an upland old field surrounded by oak-hickory and shortleaf-pine (*Pinus echinata*) woodland. Johnson's Shut-Ins State Park was comprised of old fields and mowed fields surrounded by oak-hickory forest with occasional pines.

Study Species

We studied *P. erythrophthalmus*, *P. cyanea*, *C. cardinalis*, *S. pusilla*, and *S. sialis* because they were the species monitored by Brasso et al. (2023) that had adequate sample sizes for our analysis. These were among a group of species selected for study because they foraged or nested on the ground and had the potential to incidentally ingest lead from soil and dust or by feeding on contaminated vegetation, insects, and soil invertebrates. Brasso et al. (2023) located and monitored from early April to late July in 2016, 2017, and 2018. *Sialis sialis* is a cavity and box nesting species (Gowaty and Plissner 2020), so nests were monitored by checking nest boxes that were erected for the study. The other 4 species were open-cup nesting species (Carey et al. 2020, Greenlaw 2020, Payne 2020, Halkin et al. 2021) and nests were found by systematic searching and observing bird behavior. Nests were monitored every 1–7 days and the number of eggs or nestlings and status of the nest recorded until the nest either failed or was successful.

Individual-based Model

Individual-based models are a framework for estimating population-level changes that result from individual-level ecological processes involving traits and behaviors (Grimm and Railsback 2013). They are used to model reproduction in songbirds and can account for variability among individuals in nesting behavior to achieve unbiased estimates of productivity (Powell et al. 1999, Mattsson et al. 2007, Bonnot et al. 2018). We used IBMs to estimate annual productivity of five species by simulating nesting activity of a female through the breeding season, incorporating estimates from empirical models of daily nest survival and number of fledglings per successful nest as a function of soil-lead concentration.

We defined annual productivity as the number fledged per female per year. We estimated annual productivity as a function of daily nest survival, number fledged per successful nest, length of the nesting season, length of the nesting cycle, probability of renesting following failure, number of days from failure to re-nest, probability of double brooding, and number of days from successful nest to double brood attempt (Table 1, Figure 2). We estimated daily nest survival and number fledged per successful nest as a function of soil lead (described below). The remaining parameters were based on species life history from Missouri studies and other sources (Cox et al. 2013, Roach et al. 2018). We only included the effects of soil lead on daily nest survival and number of fledglings per successful nest in our IBM based on findings by Brasso et al. (2023) that these may be important. There are less obvious hypotheses for effects of lead on the remaining species breeding parameters and insufficient data to consider these; therefore, we used the mean values for these parameters in Table 1. We implemented our model in Program R version 3.6.1 using JAGS via the *JagsUI* package (R Core Development Team 2021, Plummer 2003, Kellner 2019).

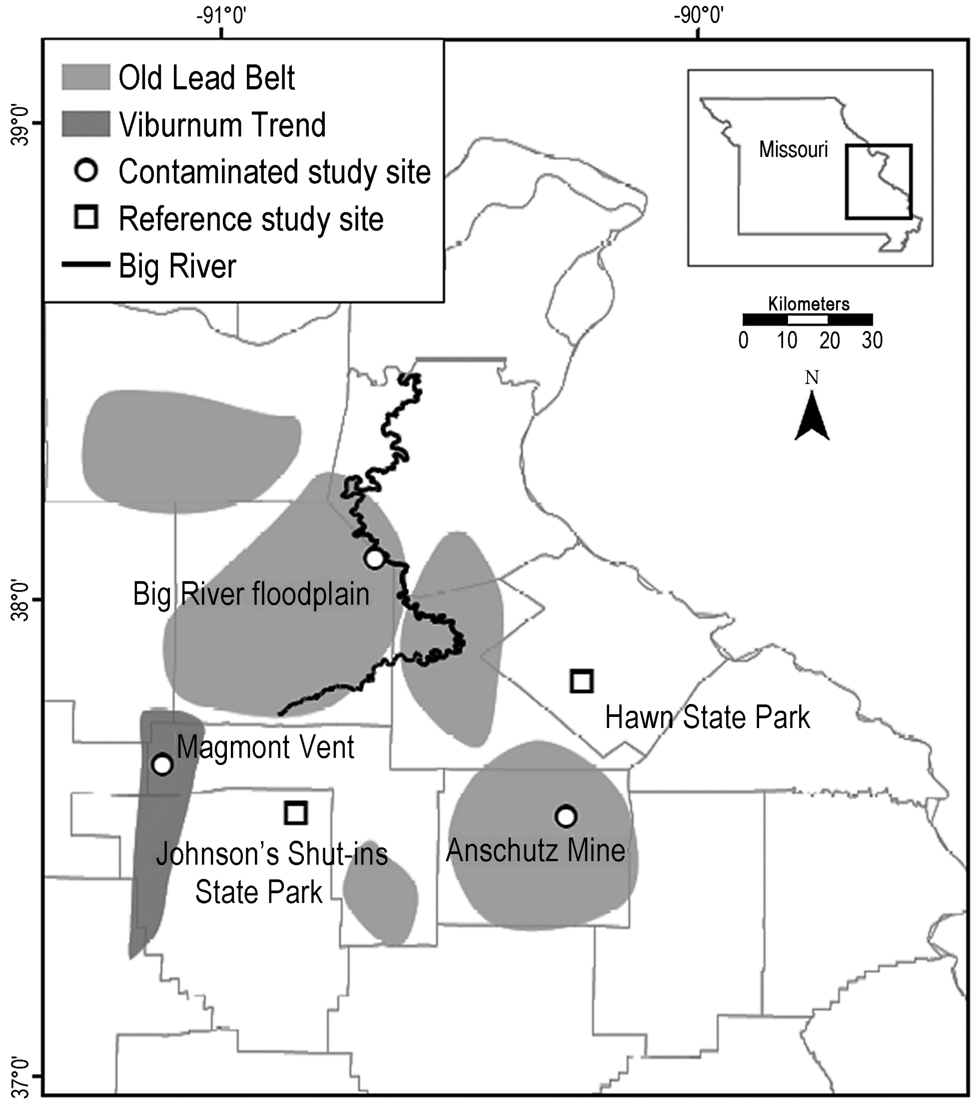

FIGURE 1. Location of study sites at which songbird reproductive success was monitored by Brasso et al. (2023) to relate to soil lead concentrations in Missouri, 2016–2018. We used data from Brasso et al. (2023) in an individual-based model to estimate annual productivity as a function of soil lead concentration.

TABLE 1. Species reproductive parameters used in an individual-based model to estimate annual productivity of 5 songbirds in Southeast Missouri, 2016–2018.

Parameter	*Spizella pusilla*	*Pipilo erythrophthalmus*	*Passerina cyanea*	*Cardinalis cardinalis*	*Sialia sialis*
Length of breeding season (days)	103	105	81	106	143
Length of nest cycle	23	27	26	25	36
Probability of renesting following failure	0.9	0.9	0.9	0.9	0.9
Number of days from failure to re-nest	5	9	3	5.5	14
Probability of double brooding	0.3	0.3	0.2	0.3	0.4
Number of days from successful nest to double brood attempt	13	15	19	16	15
Maximum clutch size	5	5	4	4	5

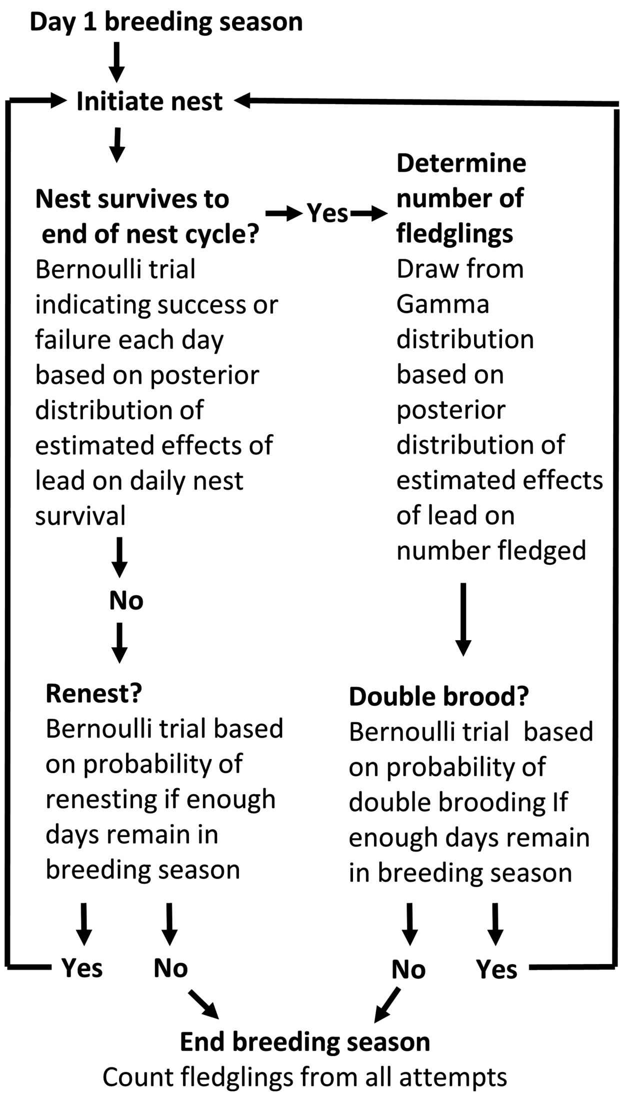

FIGURE 2. Flow diagram depicting the individual-based model used to estimate breeding season productivity in relation to soil lead concentrations in Missouri, 2016–2018. We conducted 100 replicate simulations for each species at each of 9 soil lead concentrations. The simulation began with a nest initiated on day 1 of the breeding season. The estimated effects of soil lead on daily nest survival and number fledged came from empirical models fit with nest observation data from Brasso et al. (2023). We determined if a species renested or double brooded based on remaining days in the breeding season and the probability of renesting or double brooding, the number of days between renesting or double brooding, and nest cycle length; these values were constants derived from published studies.

Nest survival and number fledged

We fit generalized linear mixed models (GLMMs) to estimate daily nest survival and number fledged from a successful nest as a function of species and soil lead within our IBM. We used data from Brasso et al. (2023) consisting of observations of nest survival and number of fledglings from 2,658 nest checks of 95, 52, 155, 184, and 93 nests of *S. sialis*, *P. erythrophthalmus*, *S. pusilla*, *P. cyanea*, and *C. cardinalis*, respectively. Nests were checked every 1 to 7 days (dependent on nest age), until the nest fledged or failed. The mean soil lead was calculated within a 60-m radius of each nest based on maps of soil lead estimated from over 1,000 soil samples in the surrounding area and $\log_{10}$ transformed and then converted to standardized *Z*-scores (see Brasso et al. 2023 for additional details).

We treated daily nest survival as a probability (0–1) and modeled it within the generalized linear model using a Bernoulli distribution. We modified the logit link function for the daily nest survival as an exponential function of the length of each nest-check interval (Shaffer 2004, Brasso et al. 2023). We modeled the number fledged from successful nests with a gamma distribution to match the structure of our nest data, where considering only successful nests precluded zero values by default. We tried other distributions considered more suitable for discrete data, but the gamma distribution had the best fit followed by a negative binomial, a Poisson distribution after transforming the data by subtracting 1 to shift the data to include zeros, and a Poisson with non-transformed data; we evaluated fit by the overdispersion parameter, Bayesian *P*-value, and leave-one-out cross-validation (described below), and visual inspection of histograms. Although the gamma distribution is continuous, continuous distributions have been shown to outperform discrete distributions such as Poisson and multinomial when modeling small counts such as number fledged (McDonald and White 2010). Models included random effects for site and year because species responses may be conditional within a site or year and to control for factors that varied by site or year that were not accounted for.

We fit two models across all species. We modeled *S. sialis* separately from the 4 open-cup nesting species because nest survival and fledging could be substantially different for an artificial cavity-nesting species. For open-cup nesters, we modeled the interaction of species and soil-lead concentration to account for differences in species responses. We assigned a categorical variable representing 4 species and set *S. pusilla* as the reference category because preliminary analyses indicated it had the smallest effect for soil lead concentration. Thus, this interaction represented how the effect of soil lead concentration differed for each species from the reference species, *S. pusilla*. We calculated the overall effect of lead on each species by summing the soil lead concentration effect and the interaction effect for that species (Brambor et al. 2006).

We fit models using a Bayesian approach and Markov chain Monte Carlo analysis in the JAGS package *jagsUI* 1.5.0 in R version 3.6.0 (R Core Team 2021). Estimates were based on 3 chains of 20,000 iterations, a burn-in of 5,000 iterations, a thinning rate of 5, and a posterior sample of 9,000. We specified uninformative priors with normal distribution of mean of zero for regression parameters and a uniform distribution for standard deviation parameters. We evaluated model convergence using the Gelman-Rubin statistic, requiring values < 1.1 for all model parameters, and inspected trace plots to check that Markov chains were well mixed (Link and Barker 2010). We assessed goodness-of-fit through posterior predictive checks and leave-one-out cross-validation (LOO) in the *loo* R package (Plummer 2003, Kéry and Royle 2016, Vehtari et al. 2016, 2017). We retained the full posterior distribution for each estimated parameter in both models for use in the IBM.

Simulation trials

We developed species-specific IBMs that simulated daily nesting activity and bird behavior throughout a general breeding season. We simulated 100 replicates of each species at each lead concentration. For each replicate a nest was initiated (start of nest cycle) on day one of the breeding season. We simulated nest fate each day of the nest cycle as a Bernoulli trial (binary outcome, success or failure) based on the 9,000 posterior samples of the effects of soil lead concentration on daily nest survival. We used the overall population mean estimates for site and year random effects, allowing us to generalize our predictions across sites and years. We repeated this process for each day up to the number of days in the nest cycle (length of nest cycle; Table 1). If a nest consecutively survived each day to the end of the nest cycle and was considered successful, we estimated the number of young fledged by drawing from a gamma distribution based on the 9,000 posterior samples from the empirical model for the effect of soil lead concentration on number of young fledged for a species at a soil lead concentration and rounding up to the nearest integer value, assuming population levels of site and year. If a nest failed, we assumed a 90% probability of renesting if there were enough days left in the season when allowing for the number of days from failure to re-nest (Table 1) and the length of nest cycle; if there were not enough days left in the breeding season the breeding season was over. Grzybowsk and Pease (2005) determined that limiting nest attempts by length of the breeding season and nesting cycle produced results more concordant with observational data than assuming a maximum number of attempts. We used a combination approach and let the length of the breeding season and length of the nest cycle be the primary factor determining nest attempts but also set a fixed limit of 8 attempts because otherwise at very low-nest survival values the number of attempts could be simulated to be unrealistically high. We used essentially the same process used for renesting to simulate double-brooding or renesting following a successful nest based on the probability of double brooding and number of days from successful nest to double brood attempt (Table 1). Uncertainty was captured in our estimation of daily nest survival and number fledged from successful nests by conducting simulations for all 9,000 posterior values of these parameters but for the remaining parameters in we used the values in Table 1 which represented population means.

We conducted simulation trials with the IBM for each species at soil lead concentrations of 25, 50, 100, 200, 400, 800, 1,600, 3,200, and 4,000 ppm. We simulated this range of soil lead because it approximated the range of mean soil lead around nests found across all 5 sites (19–4,468 ppm) and we included more concentrations at the lower end of this range because of the logarithmic nature of the relationship between nest survival and soil lead (Brasso et al. 2023). We replicated each soil lead concentration trial 100 times using the 9,000 predictions from the full posterior samples for nest survival and number fledged. We modeled a reasonable number of discrete values of soil lead to capture the nature of the relationship across the range of soil lead while keeping model processing time reasonable.

Multiple sources of variation or uncertainty can be considered in decision making concerning risks to species population viability (McGowan et al. 2011, Bonnot et al. 2018); therefore, we summarized results multiple ways to show these sources of variation. First, we accounted for all sources of uncertainty by summarizing predicted annual productivity across the full posterior distribution of estimated effects of lead on nest survival and number fledged ($n = 9{,}000$) and also the 100 replicate IBM simulations, resulting in a posterior distribution of 900,000 estimates. The first source of variation represents parameter uncertainty in the effects of lead on nest survival and number fledged. The second source of variation can be thought of as process variation resulting from the 100 simulation trials or ecological variation among individuals. However, simulation models are often based on mean effect sizes to exclude parameter uncertainty and focus on process variation. Therefore, we also focused on the process variation by averaging estimated annual productivity across 9,000 samples for effects of lead on nest survival and number fledged and calculated the mean and full distribution of the 100 replicates of each trial. Some applications of these results might require estimates of young produced at finer resolutions of soil lead concentrations than the nine discrete levels we simulated so we used spline regression (*splines* package, Program R version 3.6.1) to estimate the mean offspring/female/year for each species across a more continuous range of soil lead from 25 to 4,000 ppm.

Finally, we also considered a risk-based metric, the probability of fledging one or more young based on soil lead. We calculated this metric as the proportion of predictions with an annual productivity of ≥ 1 across all 100 replicates and their 9,000 samples. This summarization more comprehensively depicts risk and potential injury across soil lead concentrations by considering both process variation and parameter uncertainty in a single estimate and is analogous to the way risk is often presented in population viability analyses (Goldwasser et al. 2000, Possingham et al. 2002, McGowan et al. 2011).

RESULTS

We used data from 95, 52, 155, 184, and 93 nests of *S. sialis*, *P. erythrophthalmus*, *S. pusilla*, *P. cyanea*, and *C. cardinalis*, respectively, monitored by Brasso et al. (2023). Mean soil lead concentration in a 60-m radius around nests ranged from 18 to 4,381 ppm with values well distributed across this range for all 5 species (Figure 3). Fifteen *S. sialis* nests failed due to abandonment, 5 to predation, and 2 to weather related events. Thirty-four open-cup nests failed due to abandonment, 283 to predation, and 3 to weather-related events. We ran models for nest survival and number fledged and models converged for all species. Model diagnostics indicated models for nest survival and number fledged fit the data; Bayesian *p*-values were between 0.3 and 0.8, c-hat ($\hat{c}$) values were close to 1; and Pareto *k* diagnostic values were predominately good (Table 2).

The effects of lead on nest survival and number fledged varied by species from strong to weak (Figure 4, Supplementary Material Table 1). Posterior samples for the effects of soil lead indicated varying negative effects on daily nest survival and rates of certainty; there was a 0.99, 0.97, 0.74, and 0.58 probability of a negative effect on *P. cyanea*, *P. erythrophthalmus*, *C. cardinalis*, and *S. sialis*, respectively. We observed a marginal, positive effect of soil lead on *S. pusilla* (0.68 probability). The 95% credible intervals for the mean effect did not overlap zero for *P. cyanea*, but did for the other 4 species.

Models for the number fledged showed mixed uncertainty for negative effects of soil lead across species. *S. pusilla*, *P. erythrophthalmus*, and *C. cardinalis* had a 0.87, 0.59, and 0.51 probability of a negative effect, respectively; whereas *S. sialis* and *P. cyanea* had a 0.77 and 0.74 probability of a positive effect, respectively (Figure 4, Supplementary Material Table 1). Irrespective of whether credible intervals for the mean effects of soil lead on a species overlapped zero, we used

TABLE 2. Goodness-of-fit measures for models relating nest survival and number fledged to soil lead concentrations around the nest in Southeast Missouri, 2016–2018.

Species	Response	Bayesian *P*-value	C-hat	Percent pareto *k* diagnostics < 0.5 (good)
Open-cup nesters	Nest survival	0.40	1.02	100.0
Open-cup nesters	Number fledged	0.70	0.92	97.1
Sialia sialis	Nest survival	0.40	1.17	99.3
Sialia sialis	Number fledged	0.78	0.84	97.3

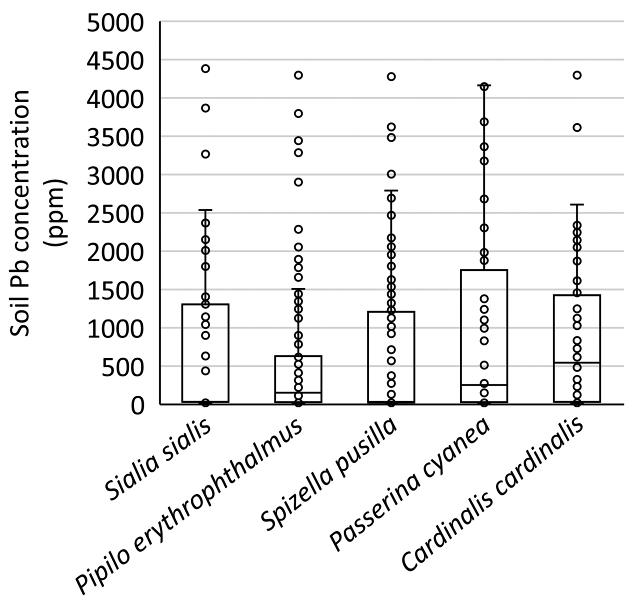

FIGURE 3. Boxplot of the mean soil lead concentrations in a 60-m radius around songbird nests in the Southeast Missouri Lead Mining District, 2016–2018. The bottom and top of the box are the first and third quartiles, the horizontal line in the box is the median, the whiskers are the range of non-outlier values defined by 1.5 times the distance between the first and third quartile, and dots are outliers.

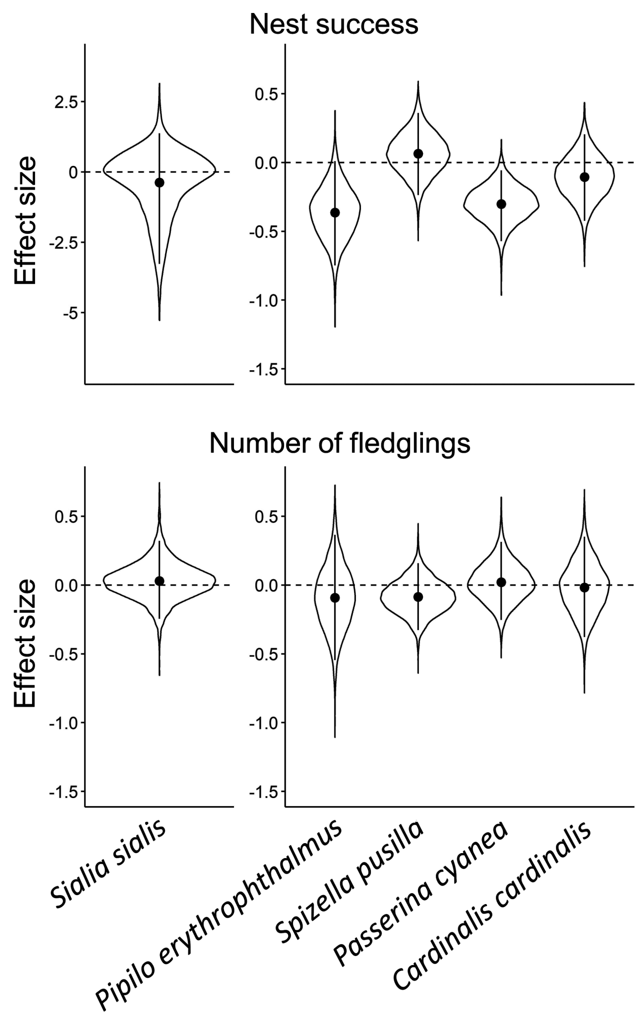

FIGURE 4. Posterior distributions (in white) of effect sizes of soil-lead concentration on fledglings/successful nest and nest survival. The horizontal line at 0 represents no effect, the black dot is the mean, and the vertical line is the 95% credible interval of the posteriors. The proportion of the posterior distribution above or below zero represents the weight of evidence or probability of a positive or negative effect, respectively.

the estimated effects for nest survival and number fledged in the simulation of annual productivity because the overall model fit the data and we included the full posterior distributions of the estimated effects to appropriately display variation and uncertainty.

Patterns in simulated nest attempts, daily and period nest survival, and number fledged suggested the IBM was performing realistically and verified the IBM was performing as designed. The number of nest attempts was greater for species with lower nest survival and greater at higher soil lead levels for species with a negative relationship between nest survival and soil lead (Supplementary Material Figure 1). Simulated daily and period nest survival declined with increasing soil lead for all species, except *S. pusilla* (Supplementary Material Figure 2), and reflected the effect sizes for soil lead on nest survival. Patterns in number fledged per female reflected the effect of soil lead on nest survival and number fledged per successful nest (Supplementary Material Figure 3). Individuals fledged 0 young, indicating nest failures, 1–4 or 5 young, where 4 or 5 was the maximum brood size, and in some cases up to 10 young, indicating double brooding. Species with the strongest negative effect of lead on nest survival showed more nest failures with 0 fledged at 4,000 ppm lead and more young fledged at 25 ppm lead because of greater nest success.

The combined effects of nest survival and number fledged in the IBM were small to large decreases in annual productivity, depending on species, as soil lead increased (Figures 5 and 6; Supplementary Material Table 2). When including parameter uncertainty from the empirical models, the declines in productivity are present, but less certain, as seen in the broad

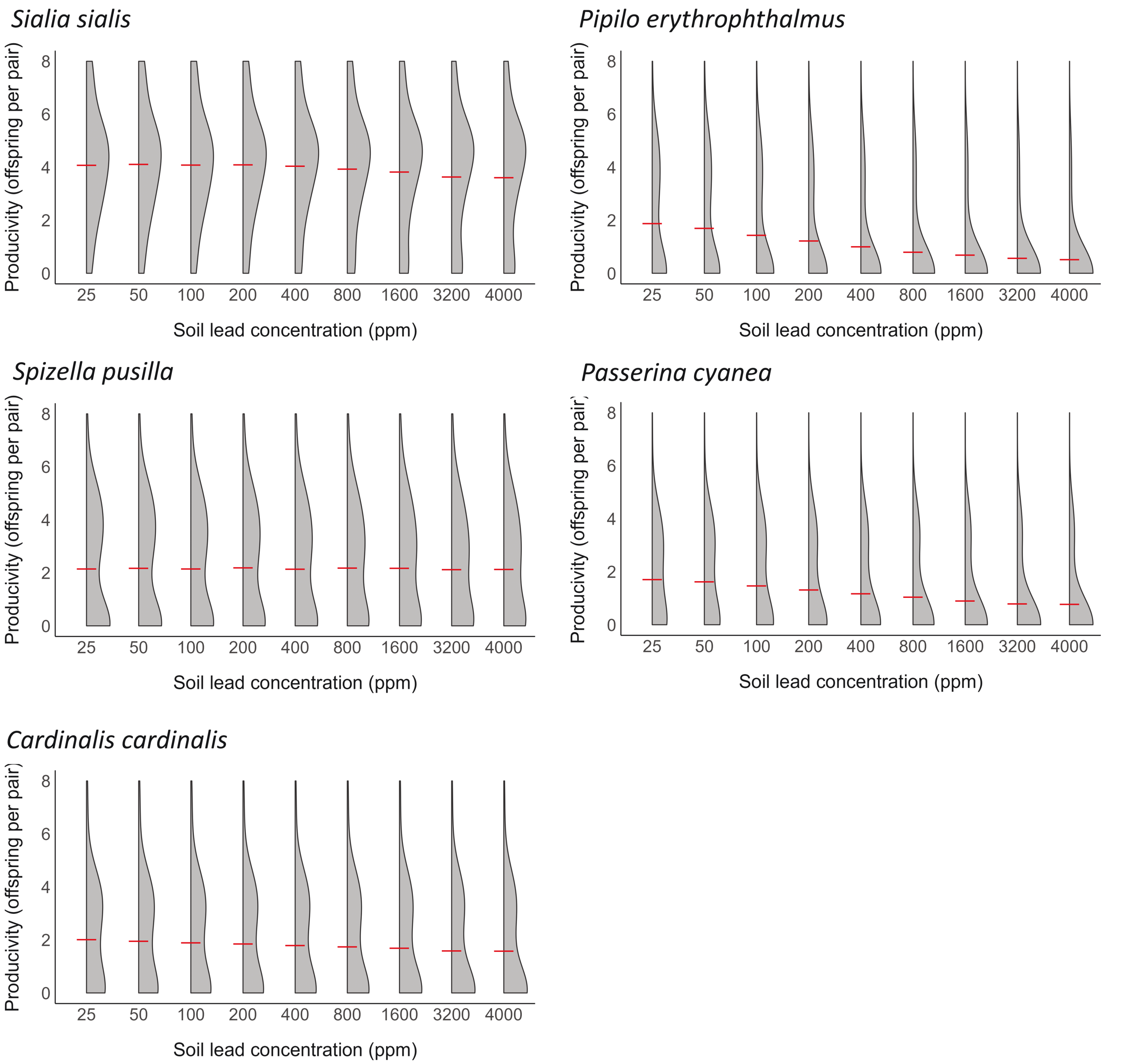

FIGURE 5. Mean (horizontal line) and posterior predictive distribution of annual songbird productivity at different lead concentrations based on 100 replicate simulations (i.e., process variation) and 9,000 posterior samples for the effect of soil lead on nest survival and number fledged (i.e., parameter uncertainty) from an individual-based model that simulated nest activity through a breeding season.

predictive distributions (Figure 5). The reduction in annual productivity is more apparent when focusing on process variation; however, the means are the same in either approach (Figure 6). Mean annual productivity decreased from 2.28 to 2.24 for *S. pusilla*, 2.02 to 0.56 for *P. erythrophthalmus*, 1.70 to 0.76, for *P. cyanea*, 2.03 to 1.59 for *C. cardinalis*, and 4.69 to 4.51 for *S. sialis*. The decreases in annual productivity for *S. pusilla* was small and not unidirectional because of a small positive effect of lead on nest survival and a slightly larger negative effect on number fledged (Figure 6; Supplementary Material Table 2). The pattern in annual productivity for *S. sialis* was also small and not unidirectional but because of a small negative effect of lead on nest survival and a positive effect on number fledged (Figure 6; Supplementary Material Table 1). The probability of fledging one or more young changed from 51% to 15% for *P. erythrophthalmus*, 57% to 23% for *P. cyanea*, 60% to 48% for *C. cardinalis*, 94% to 84% for *S. sialis*, and 57% to 64% for *S. pusilla* as soil-lead concentration around a nest increased from 25 to 4,000 ppm (Figure 7).

DISCUSSION

Results from our IBM approach highlight a risk of soil lead contamination on annual productivity of a group of breeding songbirds in Missouri. Consistent with Brasso et al. (2023), both sets of empirical models identified influence of soil lead on nest survival and number fledged that ranged from strong

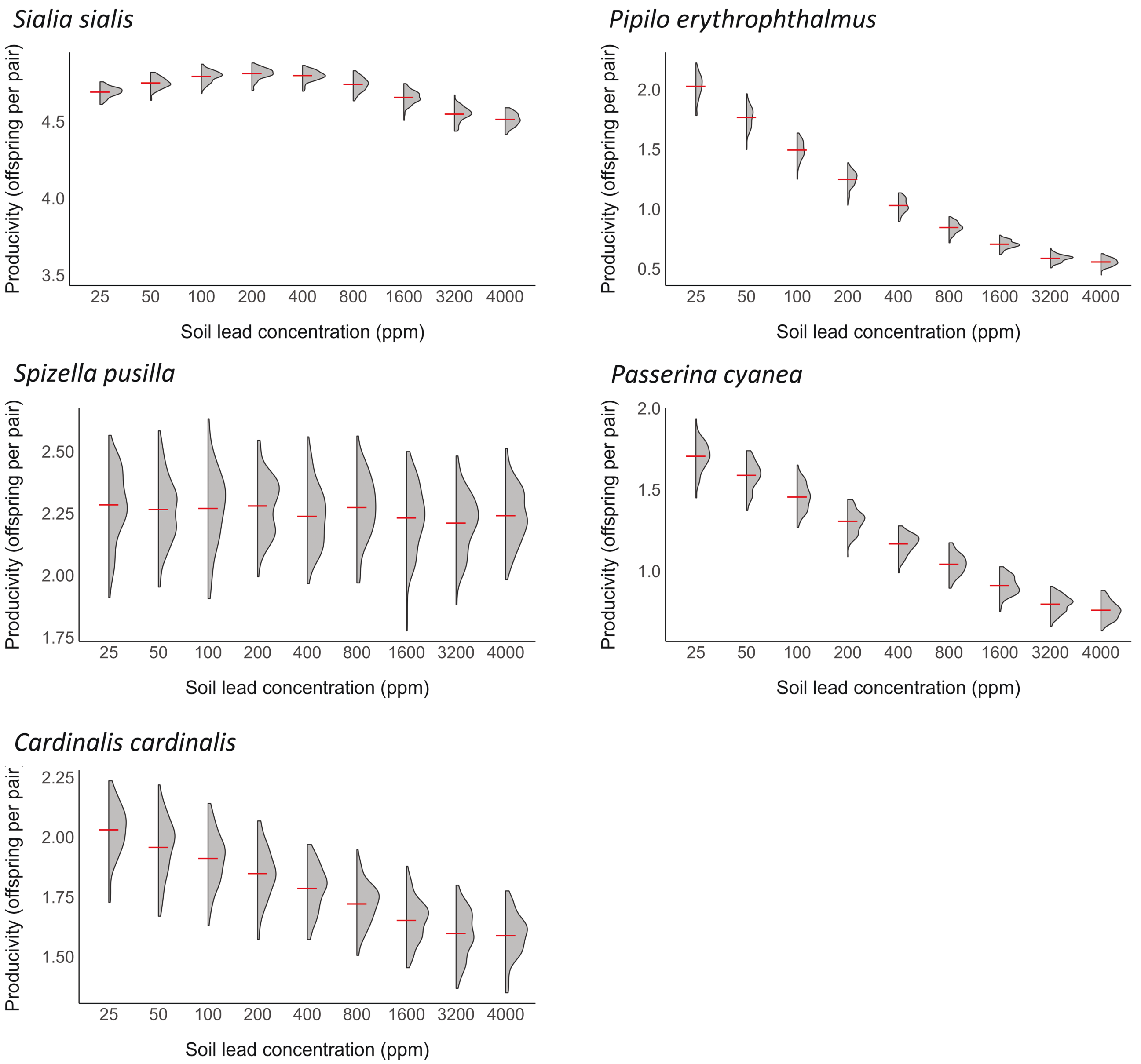

FIGURE 6. Mean and posterior predictive distribution of annual songbird productivity at different lead concentrations based on 100 replicate simulations (i.e., process variation) and the mean effect size for the effect of soil lead on nest survival and number fledged (i.e., no parameter uncertainty) from an individual-based model that simulated nest activity through a breeding season.

to weak negative effects, and in 3 cases slightly positive effects, and all with varying levels of uncertainty. On their own, results from these models paint a less certain and only partial picture of the threat that elevated soil lead may pose to songbird breeding. However, when these processes are combined and their effects are accumulated over multiple nest attempts across a breeding season, as done with our IBM, the overall negative impacts of soil lead contamination become more evident. The potential to overlook such a threat is common and stems from the difficulty in extrapolating such individual-level and local-scale processes to a more realized context (e.g., annual productivity; Evans et al. 2016, Bonnot et al. 2018). However, there are increasing examples demonstrating how the integration of seemingly intricate and minor environmental effects (even when those effects contradict) can result in meaningful impacts on demography and populations (Tanner et al. 2017, Bonnot et al. 2018). For example, the positive but weak effect of soil lead on nest survival for *S. pusilla* was offset by a slightly stronger negative effect on the number fledged, ultimately resulting in a decline (albeit small) in annual productivity. Similarly, a weak negative effect of lead on nest survival for *S. sialis* interacted with a small positive effect on number fledged that results in a small decline in productivity. Given these complexities, IBM and probabilistic approaches can help decision makers understand the true risk from threats such as soil lead contamination. Even though mean productivity was predicted to decrease with increasing soil lead concentration for all 5 species, we remind readers that only 2 of our 5 species had strong support for an effect of lead concentration on nest survival and they should be cognizant of the levels of uncertainty and magnitude of changes predicted by our IBM.

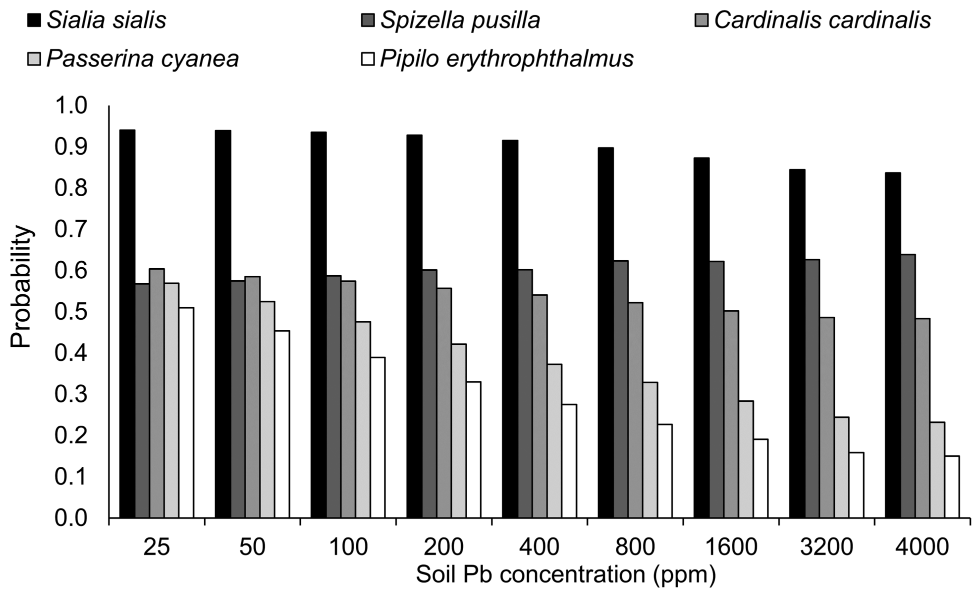

FIGURE 7. Probability of fledging one or more young at various mean soil lead concentrations surrounding a nest. The probabilities are based on the full posterior distributions of estimated effects and therefore account for both process variation and parameter uncertainty.

It is important to quantify potential impacts in species risk assessments in ways that acknowledge the full range of uncertainty and still facilitate decisions. Direct estimates of the soil lead effects in the empirical GLMMs were often uncertain, as demonstrated by posterior distributions that overlapped 0 to varying degrees (Figure 4). Integrating the full Bayesian posterior samples within the IBM allowed a more comprehensive assessment of the impacts while still including the full range of empirical uncertainty. However, the discrete nature of the process we were simulating (annual productivity) and the limited distribution it was allowed to take (a gamma distribution capped at the maximum clutch size for each species; Table 1), resulted in a great deal of uncertainty in the final predicted distributions across replications and posterior samples, complicating interpretation (Figure 5). We addressed this issue by isolating and summarizing the point estimates of annual productivity to more clearly show the process variation for effects (Figure 6). However, risk-based metrics can be more useful to decision makers because they condense the estimated effects and their uncertainty into a single risk probability that is both more intuitive and more fundamental to the assessment (Figure 7). This approach is also consistent with the National Research Academy's recommendation to report results related to exposure to hazardous pollutants as distributions of estimates and to present realistic estimates of risk as a range of probabilities (National Research Council 1994), and subsequent guidance by the U.S. Environmental Protection Agency on risk assessment for Superfund (United States Environmental Protection Agency 2001). By expressing uncertainty as the probability of fledging young, we demonstrated a decline in annual productivity that biologists and decision makers may consider unacceptable, and in some cases, unsuitable for sustaining breeding bird populations.

Nest predation was responsible for driving the patterns in productivity for open-cup-nesting species. Two-hundred and eighty-three of 286 failures of open-cup nests were due to predation, whereas only 5 of 22 failures of *S. sialis* nests resulted from predation. *Sialis sialis* nested in man-made nest boxes with predator guards that significantly limited predation and overall bluebirds had much greater productivity than open-cup nesters. These results are consistent with the well-established pattern of greater nest site safety from predation for cavity nesters compared to open-cup nesters (Lack 1948, Nice 1957, Martin 1995). We suggest a possible explanation for this pattern is our results are indicative of a predation-mediated effect of soil-lead concentration on productivity. Most nest failures were due to predation and nest survival was generally more strongly related to soil lead for open-cup nesters than bluebirds. However, even for *S. sialis*, of the 5 nests that failed to predation, 4 occurred on contaminated sites with soil lead around the nest > 1,389 ppm.

Increased parental activity at the nest can increase the likelihood that predators will discover and depredate a nest (Conway and Martin 2000, Martin et al. 2000). Birds have evolved strategies to reduce activity at their nest in response to nest predation or perceived predation risk. Birds increase the rate they feed nestlings and that males feed incubating females under reduced predation risk (Fontaine and Martin 2006). Birds synchronize parental feeding trips to the nest, which significantly decreases parental activity at the nest and increases nest survival (Bebbington and Hatchwell 2016, Leniowski and Węgrzyn 2018). Given these complex behavioral responses to predation, we speculate that a possible explanation for lower productivity at higher soil lead is that behavior by adults or nestlings is affected in a way that results in greater nest predation. Neurological damage resulting from lead poisoning adversely affects a wide range of behaviors in birds that include food begging, feeding, depth perception, song learning, territorial aggression, and locomotion (Burger and Gochfeld 1985, Burger and Gochfeld 2000, Janssens et al. 2003, Ecke et al. 2017, McClelland et al. 2019, Goodchild et al. 2021). Hitt et al. 2023 observed lower nest survival of mockingbirds associated with lead contamination in urban areas and speculated altered behaviors such as heightened aggression (McClelland et al. 2019) could result in more investment in territory defense at the expense time spent provisioning young or incubating females (Duckworth 2006) or nest defense (Dunn et al. 2003) and result in lower nest survival.

In addition to bird activity at the nest, variation in nest site quality and vegetation structure can also affect nest predation (Martin et al. 2000, Thompson 2007, Roach et al. 2018). Perhaps high soil lead impacted vegetation and affected nest-site quality, or effected birds behavior such that they selected less suitable nest sites. However, Brasso et al. (2023) did not find support for adding habitat effects (e.g., nest concealment, percent ground cover, percent shrub cover, woody stem densities) to nest survival models that included a soil lead effect. Nests on contaminated sites tended to have less ground cover and more small woody stems than nests on reference sites, but confidence intervals for the means overlapped (Brasso et al. 2023). This suggests to us that there were not strong nest site effects on nest survival or at least none that were not already accounted for by soil lead. It is possible that soil lead affected nest predation through some combination of effects on bird behavior or nest-site quality and that soil lead was a better proxy for nest quality effects than the vegetation features we measured.

Potential Future Research

We demonstrated potential impacts of soil lead contamination on songbird productivity in five species of songbirds. Mechanisms affecting nest predation and its relationship to soil lead could be further investigated by monitoring nests with video cameras to record bird and predator behavior (Thompson et al. 1999, Ribic et al. 2012) and determine if there were differences in behavior related to lead concentration that affected nest predation. Alternatively, experimentally manipulating bird blood lead concentrations and monitoring bird behavior and productivity and separating lead effects on behavior from nest-site quality effects may be informative.

Management Implications

We found evidence of small to large declines in annual productivity of 5 species of songbirds as soil lead concentration increased. The probability of fledging one or more young ranged from 15–64% at a mean soil lead concentration of 4,000 ppm for the 5 species studied. Mean annual productivity decreased from 2% to 73%, depending on species, across a range of soil lead concentrations typical of non-contaminated sites (25 ppm) to highly contaminated sites (4,000 ppm). Annual productivity at the upper end of observed soil lead concentrations were likely too small for at least two species to sustain local populations and these species are likely either declining on these sites or functioning as population sinks (Donovan and Thompson 2001). Effective restoration of local songbird abundance in the Southeast Missouri Lead Mining District will likely require measures to improve and/or increase songbird habitat. Techniques that reduce exposure of birds to lead such as treating soil with amendments that reduce lead toxicity or creating or restoring habitat in uncontaminated areas through forest, woodland, savanna, or old field restoration distant from soil lead contamination could be implemented to reduce or offset losses in birds.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

Acknowledgments

We thank D. M. Cleveland, B. A. Rattner, N. K. Karouna-Renier, and J. S. Lankton for their contributions to the original study (Brasso et al. 2023) that provided data for this analysis. We thank A. Horner-Hanley, K. E. Skrabbis, P. Lee, J. L. Reidy, 2 anonymous reviewers, and the Associate Editor and Editor for review of the manuscript. Logistical assistance during data collection for R. L. Brasso and K. Hixson was provided by Southeast Missouri State University.

Funding statement

The U.S. Department of the Interior (DOI) Office of Restoration and Damage Assessment funded this study (award # F21AC01388), and the U.S. Department of Agriculture Forest Service Northern Research Station provided in-kind support.

Ethics statement

This was a modeling study based on published data; see Brasso et al. (2023) for details on data collection and animal use protocols and permits for the original study that provided the data.

Conflict of interest statement

We have no conflicts of interest.

Author contributions

F.R.T., T.W.B., R.L.B., and D.E.M. conceived the idea and formulated the research question. R.L.B, K.H. M.C.R., F.R.T., and D.E.M. contributed data and T.W.B and F.R.T. analyzed the data. F.R.T. and T.W.B. wrote the paper with input and review by D.E.M., R.L.B, K.H., and M.C.R.

Data availability

The data and program code used to fit the models presented in this study are available at Thompson (2023).

LITERATURE CITED

Allert, A. L., R. J. DiStefano, J. F. Fairchild, C. J. Schmitt, M. J. McKee, J. A. Girondo, W. G. Brumbaugh, and T. W. May (2013). Effects of historical lead-zinc mining on riffle-dwelling benthic fish and crayfish in the Big River of southeastern Missouri, USA. *Ecotoxicology* 22:506–521.

Bebbington, K., and B. J. Hatchwell (2016). Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. *Behavioral Ecology* 27:652–659.

Besser, J. M., W. G. Brumbaugh, T. W. May, and C. J. Schmitt (2007). Biomonitoring of lead, zinc, and cadmium in streams draining lead-mining and non-mining areas, Southeast Missouri, USA. *Environmental Monitoring and Assessment* 129:227–241.

Beyer, W. N., J. W. Spann, L. Sileo, and J. C. Franson (1988). Lead poisoning in six captive avian species. *Archives of Environmental Contamination and Toxicology* 17:121–130.

Beyer, W. N., E. E. Connor, and S. Gerould (1994). Estimates of soil ingestion by wildlife. *The Journal of Wildlife Management* 58:375–382.

Beyer, W. N., S. W. Casteel, K. R. Friederichs, E. Gramlich, R. A. Houseright, J. R. Nichols, N. K. Karouna-Renier, D. Y. Kim, K.

I. Rangen, B. A. Rattner, and S. L. Schultz (2018). Biomarker responses of *Peromyscus leucopus* exposed to lead and cadmium in the Southeast Missouri Lead Mining District. *Environmental Monitoring and Assessment* 190, article 104.

Beyer, W. N., J. Dalgarn, S. Dudding, J. B. French, R. Mateo, J. Miesner, L. Sileo, and J. Spann (2004). Zinc and lead poisoning in wild birds in the Tri-State Mining District (Oklahoma, Kansas, and Missouri). *Archives of Environmental Contamination and Toxicology* 48:108–117.

Beyer, W. N., J. C. Franson, J. B. French, T. May, B. A. Rattner, V. I. Shearn-Bochsler, S. E. Warner, J. Weber, and D. Mosby (2013). Toxic exposure of songbirds to lead in the Southeast Missouri Lead Mining District. *Archives of Environmental Contamination and Toxicology* 65:598–610.

Blus, L. J., C. J. Henny, D. J. Hoffman, and R. A. Grove (1991). Lead toxicosis in Tundra Swans near a mining and smelting complex in northern Idaho. *Archives of Environmental Contamination and Toxicology* 21:549–555.

Bonnot, T. W., W. A. Cox, F. R. Thompson III, and J. J. Millspaugh (2018). Threat of climate change on a songbird population through its impacts on breeding. *Nature Climate Change* 8:718–722.

Brambor, T., W. R. Clark, and M. Golder (2006). Understanding interaction models: Improving empirical analyses. *Political Analysis* 14:63–82.

Brasso, R., D. Cleveland, F. R. Thompson III, D. E. Mosby, K. Hixson, M. Roach, B. A. Rattner, N. K. Karouna-Renier, and J. S. Lankton (2023). *Effects of lead exposure on birds breeding in the Southeast Missouri Lead Mining District*. U.S. Geological Survey Scientific Investigations Report 2023–5032, U.S. Geological Survey, Columbia, MO, USA. https://doi.org/10.3133/sir20235032.

Buerger, T. T., M. E. Carrington, R. E. Mirarchi, and M. E. Lisano (1986). Effects of lead shot ingestion on captive Mourning Dove survivability and reproduction. *The Journal of Wildlife Management* 50:1–8.

Burger, J. (1995). A risk assessment for lead in birds. *Journal of Toxicology and Environmental Health* 45:101–28.

Burger, J., and M. Gochfeld (1985). Early postnatal lead exposure: Behavioral effects in Common Tern chicks (*Sterna hirundo*). *Journal of Toxicology and Environmental Health* 16:869–886.

Burger, J., and M. Gochfeld (2000). Effects of lead on birds (Laridae): A review of laboratory and field studies. *Journal of Toxicology and Environmental Health, Part B, Critical Reviews* 3:59–78.

Carey, M., D. E. Burhans, and D. A. Nelson (2020). Field Sparrow (*Spizella pusilla*), version 1.0. In *Birds of the World* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.fiespa.01

Conway, C. J., and T. E. Martin (2000). Evolution of avian incubation behavior: Influence of food, temperature, and nest predation. *Evolution* 54:670–685.

Cox, W. A., F. R. Thompson III, J. L. Reidy, and J. Faaborg (2013). Temperature can interact with landscape factors to affect songbird productivity. *Global Change Biology* 19:1064–1074.

Custer, C., T. Custer, A. Archuleta, L. Coppock, C. Swartz, and J. Bickham (2003). A mining impacted stream—Exposure and effects of lead and other trace elements on Tree Swallows (*Tachycineta bicolor*) nesting in the upper Arkansas River Basin, Colorado. In *Handbook of Ecotoxicology*, second edition (D. J. Hoffman, B. A. Rattner, G. A. Burton Jr., and J. Carins Jr., Editors). Lewis Publishers, Boca Raton, FL, USA. p. 787–812.

De Francisco, N., J. D. Ruiz Troya, and E. I. Agüera (2003). Lead and lead toxicity in domestic and free living birds. *Avian Pathology* 32:3–13.

Donovan, T. M., and F. R. Thompson III (2001). Modeling the ecological trap hypothesis: A habitat and demographic analysis for migrant songbirds. *Ecological Applications* 11:871–882.

Douglas-Stroebel, E., D. J. Hoffman, G. L. Brewer, and L. Sileo (2004). Effects of lead-contaminated sediment and nutrition on Mallard duckling brain growth and biochemistry. *Environmental Pollution* 131:215–222.

Duckworth, R. A. (2006). Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology* 17:1011–1019.

Dunn, M., M. Copelston, and L. Workman (2003). Trade-offs and seasonal variation in territorial defence and predator evasion in the European Robin *Erithacus rubecula*. *Ibis* 146:77–84.

Ecke, F., N. J. Singh, J. M. Arnemo, A. Bignert, B. Helander, Å. M. M. Berglund, H. Borg, C. Bröjer, K. Holm, M. Lanzone, T. Miller, Å. Nordström, J. Räikkönen, I. Rodushkin, E. Ågren, and B. Hörnfeldt (2017). Sublethal lead exposure alters movement behavior in free-ranging Golden Eagles. *Environmental Science and Technology* 51:5729–5736.

Edens, F. W., and J. D. Garlich (1983). Lead-induced egg production decrease in leghorn and Japanese quail hens: *Poultry Science* 62:1757–1763.

Eisler, R. (1988). *Lead Hazards to Fish, Wildlife, and Invertebrates: A Synoptic Review.* U.S. Department of Interior, Fish and Wildlife Service, Biological Report 85 (1.14), Contaminant Hazard Reviews Report Number 14, Patuxent Wildlife Research Center Laurel, MD, USA.

Evans, M. E. K., C. Merow, S. Record, S. M. McMahon, and B. J. Enquist (2016). Towards process-based range modeling of many species. *Trends in Ecology & Evolution* 31:860–871.

Fisher, I. J., D. J. Pain, and V. G. Thomas (2006). A review of lead poisoning from ammunition sources in terrestrial birds. *Biological Conservation* 131:421–432.

Fontaine, J. J., and T. E. Martin (2006). Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecological Letters* 9(4):428–34.

Goldwasser, L., S. Ferson, and L. Ginzburg (2000). Variability and measurement error in extinction risk analysis: The Northern Spotted Owl on the Olympic Peninsula. In *Quantitative Methods for Conservation Biology* (S. Ferson and M. Burgman, Editors). Springer-Verlag, New York, NY, USA. pp. 169–187.

Goodchild, C. G., M. L. Beck, I. VanDiest, F. N. Czesak, S. J. Lane, and K. B. Sewall (2021). Male Zebra Finches exposed to lead (Pb) during development have reduced volume of song nuclei, altered sexual traits, and received less attention from females as adults. *Ecotoxicology and Environmental Safety* 210, Article 111850.

Gowaty, P. A., and J. H. Plissner (2020). Eastern Bluebird (*Sialia sialis*), version 1.0. In *Birds of the World* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.easblu.01

Greenlaw, J. S. (2020). Eastern Towhee (*Pipilo erythrophthalmus*), version 1.0. In *Birds of the World* (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.eastow.01

Grimm V., and S. F. Railsback (2013). *Individual-based Modeling and Ecology*. Princeton University Press, Princeton, NJ, USA.

Grzybowski, J. A., and C. M. Pease (2005). Renesting determines seasonal fecundity in songbirds: What do we know? What should we assume? *The Auk* 122:280–91.

Haig, S.M., J. D'Elia, C. Eagles-Smith, J. M. Fair, J. Gervais, G. Herring, J. W. Rivers, and J. H. Schulz (2014). The persistent problem of lead poisoning in birds from ammunition and fishing tackle. *The Condor: Ornithological Applications* 116:408–428.

Halkin, S. L., D. P. Shustack, M. S. DeVries, J. M. Jawor, and S. U. Linville (2021). Northern Cardinal (*Cardinalis cardinalis*), version 2.0. In *Birds of the World* (P. G. Rodewald and B. K. Keeney, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.norcar.02

Hansen, J. A., D. Audet, B. L. Spears, K. A. Healy, R. E. Brazzle, D. J. Hoffman, A. Daily, and W. N. Beyer (2011). Lead exposure and poisoning of songbirds using the Coeur d'Alene River Basin, Idaho, USA. *Integrated Environmental Assessment and Management* 7:587–595.

Hitt, L. G., S. Khalil, A. Blanchette, M. E. Finkelstein, E. K. Iverson, S. C. McClelland, R. D. Ribeiro, J. Karubian (2023). Lead exposure is correlated with reduced nesting success of an urban songbird. *Environmental Research* 227:115711.

Hoffman, D. J., G. H. Heinz, L. Sileo, D. J. Audet, J. K. Campbell, and H. H. Obrecht III (2000). Developmental toxicity of lead-contaminated sediment in Canada Geese (*Branta canadensis*). *Journal of Toxicology and Environmental Health, Part A* 59:235–252.

Janssens, E., T. Dauwe, E. Van Duyse, J. Beernaert, R. Pinxten and M. Eens (2003). Effects of heavy metal exposure on aggressive behavior in a small territorial songbird. *Archives of Environmental Contamination and Toxicology* 45:121–127.

Jones, J., P. J. Doran, L. R. Nagy, and R. T. Holmes (2005). Relationship between Mayfield nest-survival estimates and seasonal fecundity: A cautionary note. *The Auk* 122:306–312.

Kellner K. (2019). jagsUI: A wrapper around “rjags” to streamline “JAGS” analyses. R package version 1.5.1. https://CRAN.R-project.org/package=jagsUI

Kéry, M., and J. A. Royle (2016). *Applied Hierarchical Modeling in Ecology*, volume 1. Academic Press, London, UK.

Labare, M. P., M. A. Butkus, D. Riegner, N. Schommer, and J. Atkinson (2004). Evaluation of lead movement from the abiotic to biotic at a small-arms firing range. *Environmental Geology* 46:750–754.

Lack, D. (1948). The significance of clutch size. Part 3. Some interspecific comparisons. *Ibis* 90:25–45.

Leniowski, K., and E. Węgrzyn (2018). Synchronisation of parental behaviours reduces the risk of nest predation in a socially monogamous passerine bird. *Scientific Reports* 8:7385.

Link, W. A., and R. J. Barker (2010). *Bayesian Inference with Ecological Applications*. Academic Press, London, UK.

McDonald, T. L., and G. C. White (2010). A comparison of regression models for small counts. *The Journal of Wildlife Management* 74:514–521.

Martin, T. E. (1995). Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101–127.

Martin, T. E., J. Scott, and C. Menge (2000). Nest predation increases with parental activity: Separating nest site and parental activity effects: *Proceedings of the Royal Society B: Biological Sciences* 267:2287–2293.

Mattsson B. J., R. J. Cooper, and C. Handel (2007). Which life-history components determine breeding productivity for individual songbirds? A case study of the Louisiana Waterthrush (*Seiurus motacilla*). *The Auk* 124:1186–1200.

McClelland, S. C., R. Durães Ribeiro, H. W. Mielke, M. E. Finkelstein, C. R. Gonzales, J. A. Jones, J. Komdeur, E. Derryberry, E. B. Saltzberg, and J. Karubian (2019). Sub-lethal exposure to lead is associated with heightened aggression in an urban songbird. *Science of the Total Environment* 654:593–603.

McGowan, C. P., M. C. Runge, and M. A. Larson (2011). Incorporating parametric uncertainty into population viability analysis models. *Biological Conservation* 144:1400–1408.

National Research Council (1994). *Science and Judgment in Risk Assessment*. The National Academies Press, Washington, D.C., USA.

Nice, M. M. (1957). Studies in the life history of the Song Sparrow. *Transactions of the Linnean Society, New York* 4:1–247.

Pain, D. J. (1996). Lead in waterfowl. *In Environmental Contaminants in Wildlife: Interpreting Tissue Concentrations* (W. N. Beyer, G. H. Heinz, and A. W. Redmon-Norwood, Editors). Lewis Publishers, Boca Raton, FL, USA. pp. 251–264.

Payne, R. B. (2020). Indigo Bunting (*Passerina cyanea*), version 1.0. In *Birds of the World* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.indbun.01

Pease, C. M., and J. A. Grzybowski (1995). Assessing the consequences of brood parasitism and nest predation on seasonal fecundity in passerine birds. *The Auk* 112:343–363.

Plummer, M. (2003). *JAGS: A program for analysis of Bayesian graphical models using Gibbs Sampling*. Third International Workshop on Distributed Statistical Computing (DSC 2003), Vienna, Austria.

Possingham, H. P., D. B Lindenmayer, and G. N Tuck (2002). Decision theory for population viability analysis. In *Population Viability Analysis*. University of Chicago Press, Chicago, IL, USA. pp. 470–489.

Powell, L. A., M. J. Conroy, D. G. Krementz, and J. D. Lang (1999). A model to predict breeding-season productivity for multibrooded songbirds. *The Auk* 116:1001–1008.

Price P. W., B. J. Rathcke, and D. A. Gentry (1974). Lead in terrestrial arthropods: Evidence for biological concentration. *Environmental Entomology* 3:370–372.

R Core Team (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Ribic, C. A., F. R. Thompson III, and P. J. Pietz (Editors) (2012). *Video Surveillance of Nesting Birds*. University of California Press, Berkeley, California, USA.

Roach, M. C., F. R. Thompson III, and T. Jones-Farrand (2018). Songbird nest success is positively related to restoration of pine–oak savanna and woodland in the Ozark Highlands, Missouri, USA. *The Condor: Ornithological Applications* 120:543–556.

Roux, K. E., and P. P. Marra (2007). The presence and impact of environmental lead in passerine birds along an urban to rural land use gradient. *Archives of Environmental Contamination and Toxicology* 53:261–268.

Sample, B., J. Hansen, A. Dailey, and B. Duncan (2011). Assessment of risks to riparian songbirds from lead in the Coeur d’Alene Basin, Idaho. *Integrated Environmental Assessment and Management* 7:596–611.

Scheuhammer, A. M., and S. L. Norris (1995). *A review of the environmental impacts of lead shotshell ammunition and lead fishing weights in Canada.* Occasional Paper 88 of the Canadian Wildlife Service, Ottawa, Ontario, Canada.

Seeger, C. M. (2008). History of mining in the Southeast Missouri Lead District and description of mine processes, regulatory controls, environmental effects, and mine facilities in the Viburnum Trend subdistrict. In *Hydrologic Investigations Concerning Lead Mining Issues in Southeastern Missouri* (M. J. Kleeschulte, Editor). U.S. Geological Survey Scientific Investigations Report 2008-5140, U.S. Geological Survey, Reston, VA, USA.

Shaffer, T. A. (2004). A unified approach to analyzing nest success. *The Auk* 121:526–540.

Tanner, E. P., R. D. Elmore, S. D. Fuhlendorf, C. A. Davis, D. K. Dahlgren, and J. P. Orange (2017). Extreme climatic events constrain space use and survival of a ground-nesting bird. *Global Change Biology* 23:1832–1846.

Thompson, F. (2023). *Songbird Annual productivity is negatively related to soil lead contamination around nests (data set)*. U. S. Fish and Wildlife Service. https://doi.org/10.7944/9T82-H585.

Thompson, B. C., G. E. Knadle, D. L. Brubaker, and K. S. Brubaker (2001). Nest success is not an adequate comparative estimate of avian reproduction. *The Journal of Field Ornithology* 72:527–536.

Thompson, F. R., III (2007). Factors affecting nest predation on forest birds in North America. *Ibis* 148:98–109.

Thompson III, F. R., W. D. Dijak, and D. E. Burhans (1999). Video identification of predators at songbird nests in old fields. *The Auk* 116:259–264.

United States Environmental Protection Agency (2001). *Risk Assessment Guidance for Superfund: Volume III - Part A, Process for Conducting Probabilistic Risk Assessment*. Office of Emergency and Remedial Response, United States Environmental Protection Agency, EPA 540-R-02-002, Washington, D.C., USA.

Vehtari, A., A. Gelman, and J. Gabry (2017). Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Statistics and Computing* 27:1413–1432.

Vehtari, A., A. Gelman, and J. Gabry (2016). loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models. R package version 0.1.6. https://github.com/stan-dev/loo

Vyas, N. B., J. W. Spann, G. H. Heinz, W. N. Beyer, J. A. Jaquette, and J. M. Mengelkoch (2000). Lead poisoning of passerines at a trap and skeet range. *Environmental Pollution* 107:159–166.