

Environmental lead reduces the resilience of bald eagle populations

Brenda J. Hanley¹ | André A. Dhondt² | María J. Forzán¹ |
 Elizabeth M. Bunting¹ | Mark A. Pokras³ | Kevin P. Hynes⁴ |
 Ernesto Dominguez-Villegas⁵ | Krysten L. Schuler¹

¹Wildlife Health Lab, Public and Ecosystem Health Department, College of Veterinary Medicine, Cornell University, 240 Farrier Road, Ithaca, NY 14853, USA

²Cornell Lab of Ornithology, Department of Ecology and Evolutionary Biology, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14853, USA

³Wildlife Clinic & Center for Conservation Medicine, Cummings School of Veterinary Medicine, Tufts University, 200 Westboro Road, North Grafton, MA 01536, USA

⁴New York State Department of Environmental Conservation, 108 Game Farm Road, Delmar, NY 12054, USA

⁵Wildlife Center of Virginia, 1800 South Delphine Avenue, Waynesboro, VA 22980, USA

Correspondence

Brenda Hanley, Cornell University, 240 Farrier Road, Ithaca, New York 14853, USA.

Email: bjh262@cornell.edu

Present address

María J. Forzán, Department of Veterinary Biomedical Sciences, College of Veterinary Medicine, Long Island University, 720 Northern Boulevard, Brookville, NY 11548, USA.

Ernesto Dominguez-Villegas, Private Wildlife Health Consultant, Richmond, VA, USA.

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Abstract

Bald eagles (*Haliaeetus leucocephalus*) are considered a recovery success in the United States after rebounding from near extirpation due to widespread use of the insecticide dichlorodiphenyltrichloroethane (DDT) in the twentieth century. Although abundances of bald eagles have increased since DDT was banned, other contaminants have remained in the environment with unknown influence on eagle population trends. Ingestion of spent lead (Pb) ammunition, the source of Pb most available to eagles and other scavengers in the United States, is known to kill individual eagles, but the influence of the contaminant on overall population dynamics remains unclear, resulting in longstanding controversy over the continued legality of the use of Pb in terrestrial hunting ammunition. We hypothesized that mortalities from the ingestion of Pb reduced the long-term growth rate and resiliency of bald eagles in the northeast United States over the last 3 decades. We used Holling's definition of resilience (the ability of a system to

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absorb changes of state variables, driving variables, and parameters and still persist) to quantify how reduction in survival from Pb-associated mortalities reduced the likelihood of population persistence. We used a population matrix model and necropsy records gathered between 1990 and 2018 from a 7-state area to compare population dynamics under current versus hypothetical Pb-reduced and Pb-free scenarios. Despite a robust increase in eagle abundances in the northeast United States over that period, we estimated that deaths arising from ingestion of Pb was associated with a 4.2% (females) and 6.3% (males) reduction in the asymptotic long-term growth rate (λ). Comparison between real (current) and counterfactual (Pb-reduced and Pb-free) population dynamics indicated that the deaths from acute Pb poisoning were additive because the mortality events were associated with marked reduction in annual survival performance of hatchlings and reproductive females. These shifts in survival performance were further associated with a reduction in resilience for hatchling (95.4%) and breeding (81.6%) female eagles. Counterintuitively, the current conditions produced an increase in resilience (68.9%) for immature and non-breeding female eagles over hypothetical Pb-free conditions, suggesting that the population of eagles in the northeast United States reorganized (in a population dynamics sense) to ensure population expansion despite additive mortalities associated with Pb. This study can be used by state and federal wildlife managers or non-governmental organizations to inform policy surrounding the use of lead ammunition or to educate hunters on the population-scale effects of their ammunition choices.

KEYWORDS

ammunition, bald eagle, combinatorial optimization algorithm, *Haliaeetus leucocephalus*, lead, long-term growth rate, northeast United States, Pb, population dynamics, population matrix model

Wildlife populations face mounting threats to long-term viability from anthropogenic activities. Among these threats are environmental contaminants that can reduce overall population potential (Pain et al. 2009, Franson and Russell 2014, Bruggeman et al. 2018). While not directly lethal, a prime example is the contaminant dichlorodiphenyltrichloroethane (DDT), which severely affected wildlife populations across the United States. Before it was banned in the United States in 1972, DDT reduced the reproduction of several species of raptors and precipitated the rapid decline in populations of the iconic bald eagle (*Haliaeetus leucocephalus*) in the United States and Canada (Grier 1982, Elliott and Harris 2002). Bald eagles were included in the United States Endangered



Species Act in 1973 (U.S. Fish and Wildlife Service [USFWS] 2007), and the species is now considered a model of Endangered Species Act success due to range-wide recovery and its formal delisting 2 decades later (USFWS 2007).

Despite the prohibition of DDT and the recovery of eagle abundances, eagles continue to succumb to environmental contaminants in the United States, including heavy metals (Katzner et al. 2018). One such contaminant is lead (Pb). Banned in the United States from paint in 1977, plumbing used for drinking water in 1986, and gasoline in 1996, Pb is still widely used in ammunition to hunt big game and predators in terrestrial habitats and in shot for small game and upland gamebirds (Kendall et al. 1996, Golden et al. 2016). In addition to unremediated relic deposits of Pb from once-legal (but now banned) anthropogenic activities (U.S. Geological Survey [USGS] 2005), Pb continues to be deposited into and remains in the environment through the practice of big game, pest, or predator hunting. A federal projectile ban to make the continued use of Pb ammunition illegal in terrestrial habitats does not currently exist (U.S. Department of the Interior [USDOI] 2017b).

Some terrestrial hunting practices involve discarding the carcass, parts, or viscera in the field for scavengers to consume (Pain et al. 2019). But Pb-based rifle bullets used for hunting expand when striking the target animal and can leave tens to hundreds of very small Pb fragments throughout the discarded tissues (Hunt et al. 2009). Indeed, the ingestion of Pb by scavenging wildlife has been reported for over a century, as have reports of mortalities of Pb toxicosis in non-target wildlife species wherever Pb ammunition is used (Rattner et al. 2008). As such, continued legal use of Pb ammunition in terrestrial habitats presents an ongoing hazard to non-target migratory birds and other scavenging species (Kendall et al. 1996, Golden et al. 2016).

Despite the Eagle Act rendering the direct take of a bald eagle illegal in the United States (USFWS 1940), veterinary records from necropsies on bald eagles collected in the wild by state wildlife agency biologists and their partners show that ingestion of discarded tissues containing spent Pb ammunition fragments is a widespread source of morbidity and mortality to eagles (Katzner et al. 2018). Ingestion of Pb fragments by wild scavenging eagles can cause acute or chronic morbidity and mortality, dependent on the quantity of Pb ingested in the contaminated tissues of the scavenged meal (Stansley and Murphy 2011, Franson and Russell 2014, Bruggeman et al. 2018). Despite the steady increase in eagle abundances in the northeast United States in recent years (USFWS 2007, Hanley et al. 2019), wildlife rehabilitators, veterinarians, and pathologists in the northeast United States continue to report eagle morbidities and mortalities from ingested Pb (Avian Haven Wild Bird Rehabilitation Center 2021, Cummings School of Veterinary Medicine 2021, University of New Hampshire 2021, USGS National Wildlife Health Center 2021, Wildlife Health Center of Virginia 2021), spawning regional and national controversy among wildlife managers, resource regulators, and the public on whether Pb ammunition should be banned outright (USDOI 2017a, b).

Population matrix models are used to link properties of individuals to population-scale processes (Tuljapurkar 1990, Caswell 2001), making them crucial analytical tools for translating the information contained in necropsy data sets to their corresponding effects at the population scale. A fundamental measure arising from a population matrix model is the long-term growth rate (λ), which is the summary of intrinsic performance and long-term viability of the population (Caswell 2001, Koons et al. 2007). This rate has been used to measure the population-scale consequences of a perturbation to the life cycle (de Kroon et al. 2000, Caswell 2001), making it key in summarizing the overall effects to the population from the presence of a contaminant. Alternatively, the stochastic growth rate measures population performance by merging intrinsic growth (or decline) with the net effects of gains or losses through dispersal (Tuljapurkar 1990), making this rate key in identifying whether dispersal has played a role in empirical population performance. In a long-lived species such as the bald eagle, the survival rates of the age classes and the age at first reproduction are influential factors to the long-term growth rate. Similarly, in an open population (one that experiences gains and losses through dispersal), net differences between emigration and immigration are influential to the stochastic growth rate. Both growth rates summarize (in different ways) the performance of the population and pinpoint the biological threshold differentiating a population that is expected to persist and one expected to decline.



Our objectives were to explore if documented mortalities of eagles from the ingestion of Pb altered the population scale dynamics of the wild eagle population in the northeast United States between 1990 and 2018, and if so, estimate the degree to which these mortalities altered growth rates, annual survival rates of eagles in each life stage, or the resilience of the population to absorb additional mortalities. We hypothesized that mortalities arising from the ingestion of Pb reduced the long-term growth rate and resiliency of bald eagles in the northeast United States between 1990 and 2018. We further hypothesized that average annual survival rates of eagles in the 3 life stages (hatchling, non-breeding, and breeding) were reduced as a result of mortalities associated with the ingestion of Pb.

STUDY AREA

The study area included Connecticut, Massachusetts, Maine, New Hampshire, New Jersey, New York, and Vermont, USA. Spanning 300,638 km² of land (USGS 1906), the area ranged in elevation from sea level to 1,916 m (Mt. Washington, NH), in minimum and maximum average (normal) temperature from -21°C to 31.5°C (Feb in ME and July in NJ, respectively; National Oceanic and Atmospheric Administration 2021), in human population/km² from 17.0 to 488 (ME to NJ, respectively; U.S. Census Bureau 2021), in forest cover of land area from 42% (NJ) to 89% (ME; U.S. Department of Agriculture Forest Service [USDA-FS] 2019), and in land use from urban (New York City) to wilderness (White Mountain National Forest Wilderness Areas; USDA-FS 2021). Our study spanned 29 consecutive calendar years from 1990–2018, which represented the period of population recovery when eagles in all 7 states exhibited expanding populations (Hanley et al. 2019). The study included the year 2007, when eagles were delisted from the Endangered Species Act (USFWS 2007).

METHODS

We based our study on population (annual counts and banding records) and veterinary (necropsy records) data that were gathered from regional sources for *post hoc* use. The population data consisted of the time series of bald eagles from the 7-state region as published in Hanley et al. (2019). These data included the pooled annual counts of breeding bald eagle pairs and active nests observed in each state during consecutive breeding periods (Jan–Jun). The banding records were collected by the USGS's Patuxent Bird Banding Laboratory and consisted of wild juvenile (eaglet) bald eagles that were banded and reencountered later. The veterinary data consisted of 1,232 records of necropsies on bald eagles sourced from regional universities, diagnostic laboratories, state wildlife agencies, and wildlife rehabilitators (Avian Haven Wild Bird Rehabilitation Center 2021, Cummings School of Veterinary Medicine 2021, University of New Hampshire 2021, USGS National Wildlife Health Center 2021, Wildlife Health Center of Virginia 2021; New York State Department of Environmental Conservation, Animal Health Diagnostic Center, unpublished data).

We did not alter the annual count data. Alterations to the banding data were limited to removal of unneeded variables and the reduction of records to include only eaglets that were confirmed to be banded in the nest. Alterations to the raw necropsy records were limited to the removal of unneeded variables; the standardization of remaining variables into a single, predetermined format; and the conversion of the units of measurement into standardized, predetermined units. Where necessary, we converted numerical Pb test values from their original value in dry weight (dw) into wet weight (ww) using the formula $dw/3.5 = ww$ (K. Bischoff, Cornell University, personal communication).

The decision whether to conduct a Pb test on any given eagle was made by the pathologist at the time of the necropsy and such decisions were completed prior to the transfer of records for use in this study. Because of this inconsistency in whether or how Pb tests were conducted across the regional necropsy data set, we added 1



variable *post hoc* to the veterinary data to quantitatively categorize each eagle record into a Pb category. We categorized eagles into Pb categories by comparing measured values in ≥ 1 of the postmortem samples (blood, liver, kidney, and bone) to the numerical Pb threshold values in Pain et al. (2019). We used numerical measurements in the veterinary records to categorize eagles into Pb groups rather than the pathologist's interpretation because the latter was not uniformly ascribed. The Pb groups included eagles with sufficiently high levels of Pb to cause clinical disease or death (Pb-toxicity) and eagles exposed to any level of Pb (Pb-exposure). Our categorization of Pb-toxicity assumed that because mortality, neurological dysfunction, immune suppression, and reproductive impairment are documented effects of exposure to Pb in birds (Kendall et al. 1996), levels associated with clinical signs would necessarily have resulted in decreased survival. Thus, eagles in the Pb-toxicity category surpassed one of the following Pb thresholds: blood ≥ 50 ug/dL (0.5 ppm), liver ≥ 6 ppm (ww), kidney ≥ 4 ppm (ww), or bone ≥ 20 ppm (dw; Pain et al. 2019). We assigned Pb-exposure to any eagle with >0 ppm Pb value in its blood, kidney, liver, or bone (Pain et al. 2019). For accounting purposes, we categorized necropsy records that indicated a Pb test had been conducted on the eagle, but the numeric result was an undetectable level of Pb (with detectable levels varying by the source facility) as Pb-none detected. We categorized eagles for which a Pb test was not conducted as Pb-no test conducted. We integrated only necropsy records of eagles with detectable, non-zero numerical Pb levels into our comparative models.

The explanatory variables used in our comparative models included the eagle's 1) age by year (0, 1, 2, ...) converted into hatchling (<1 yr), immature and of breeding age but unreproductive (non-breeding; 1–5 yr), and breeding stages (>5 yr); 2) sex (male or female); 3) location of residency (by state) during the breeding period (Jan–Jun) of each calendar year (1990, 1991, ..., 2018); 4) numeric value of the Pb level (in ppm); 5) tissue in which the numeric Pb level was measured (blood, kidney, liver, or bone); 6) year of removal from the wild (1990, 1991, ..., 2018); and 7) assigned Pb group as determined by the numerical Pb level (Pb-no test conducted, Pb-none detected, Pb-exposed, Pb-toxicity). The response variables used in our model included the long-term growth rate, calculated by solving for the dominant root of the population matrix model; the stochastic growth rate, calculated using the time series of breeding eagles; and the annual survival rates of each life stage, calculated by multiplying the stage-wise survival rates in the population matrix model across consecutive breeding and non-breeding periods (Caswell 2001).

We used the Pb determinations to create the time series for 3 comparative groups of eagles: the unaltered control (current or factual) group, a Pb-reduced hypothetical (counterfactual) group, and a Pb-free hypothetical (counterfactual) group. The control group was simply the empirical time series data for breeding pairs of bald eagles in the northeast United States from 1990–2018 (Hanley et al. 2019). The Pb-reduced group consisted of the hypothetical population of eagles in the northeast United States that was identical to the unaltered control group, except this group did not experience the losses of eagles shown by our records to have died from Pb-toxicity. The Pb-free group consisted of the hypothetical population of eagles in the northeast United States that was identical to the unaltered control group, except this group did not experience the losses of eagles shown by our records to have died with any level of Pb in their tissues.

We created the Pb-reduced time series for each sex by adding the known mortalities of adult eagles of each sex with Pb-toxicity back into the control time series in the years of their observed removal from the wild. We created the hypothetical Pb-free time series for each sex by adding the known mortalities of adult eagles of each sex with detectable levels of Pb back into the control time series in the years of their removal from the wild. The 2 Pb-free time series (male time series and female time series) therefore contained eagles that had non-zero levels of Pb in their tissues but perhaps died for other primary reasons (e.g., vehicle trauma, conspecific trauma, electrocution). We did not add back eagles of either sex in the Pb-none detected and Pb-no test conducted categories into either hypothetical time series. We also omitted eagles of unknown sex from the hypothetical time series. Additional details used to craft the hypothetical time series are available online in the Supporting Information.

A typical procedure to employ a population matrix model for viability and perturbation analyses is to generate field data to estimate vital rates, input those rates into the matrix that is representative of the life history, then use



matrix mathematics to project abundances and compute other population-scale properties (Caswell 2001). We reversed this process. We used a combinatorial optimization algorithm (Korte and Vygen 2018) with sequences of abundances (the time series counts of breeding pairs) within a symbolic matrix framework to estimate the combinatorial magnitude of the vital rates that would have needed to exist in the matrix to produce the empirical abundances of eagles in the northeast United States (Hanley et al. 2019). We gave the combinatorial optimization algorithm the empirical time series and the symbolic mathematical structure representing the eagle life history, then instructed the computer to search for the combinatorial sets of vital rate values (fertility, annual survival rates of hatchling, non-breeding, and breeding birds) that could have existed between 1990 and 2018 to produce the sequence of breeding pair abundances that was observed by agency officials throughout the region during that time. Additional details of the algorithm are in Hanley et al. (2019).

We used 3 identical algorithms to estimate the vital rates from the time series of the control group, the Pb-reduced group, and the Pb-free groups. The 3 algorithms were programmed identically in the boundaries of the initial conditions, the starting seed, the life history (symbolic population matrix model), the number of probabilistic trials to be completed during the search, technical settings of the search patterns, the storage criteria of candidate sets discovered during the search, search instructions (decision rules regarding which candidate sets to retain and which to discard), and mathematical formulas to compute the population properties from the resulting matrix sets of vital rates. We executed the 3 algorithms on the same computer under the same software and with the same package versions in R (R Core Team 2020). The 3 algorithms differed only in their inputs (the time series), which were themselves identical except for the inclusion of the observed eagle mortalities confirmed by regional wildlife veterinarians and rehabilitation professionals to have existed in the study area during the study timeframe. Comparisons of the population properties arising from the 3 algorithms constituted our analysis to study differences in control (current or factual), Pb-reduced (counterfactual), and Pb-free (counterfactual) groups of eagles in the northeast United States.

The 3 algorithms estimated vital rates for eagles in each of the 3 groups. We then used these estimates in conjunction with traditional matrix equations (Caswell 2001) to compute the population properties for each group. Population properties included the median and interquartile range of the long-term growth rate, stochastic growth rate, annual probability of survival for hatchling eagles, annual probability of survival for non-breeding eagles, and annual probability of survival for breeding eagles. We then used the vital rate estimates to project the median, maximum, and minimum abundances of hatchlings, non-breeders, and breeders of each group over the 3-decade (1990–2018) time span. For completeness of the population viability analysis, we further used the vital rate estimates to compute additional asymptotic (long-term) and transient (short-term) population-scale properties (Caswell 2001, Stott et al. 2012).

An algorithm did not return a single set of vital rates that could have produced the time series. Rather, it returned multiple plausible sets of vital rates that could have produced the time series. Because each plausible set arose when the machine searched the parameter space at random, we declared each plausible set to be a datum, and the collection of data to be the random sample for that group taken from all possible samples. From that random sample, we calculated traditional summary statistics including the median and interquartile range of the response variables. We evaluated statistical differences among the 3 eagle groups using the group medians. We deemed this the counterfactual population analysis, or CounterPOPd analysis.

We did not presume that the samples would meet the distributional criteria necessary to conduct a parametric comparison. We therefore decided *a priori* to compare group medians using the non-parametric Kruskal Wallis test (Conover 1999). Should group medians differ, we decided *a priori* to determine the directionality of differences using pairwise Dunn tests (Conover 1999). We predetermined our experiment-wise Type I error rate (α) to be 0.05 and downgraded the critical value for each hypothesis test (α') according to the Bonferroni correction (Conover 1999). The critical value for each hypothesis test was $\alpha' = \frac{0.05}{(2 \times 36)} = 0.00069 = 6.9 \times 10^{-4}$. We used the margin of error (3%) and the estimate of variance of the long-term growth rate (Hanley et al. 2019) to compute the sample size needed for each eagle group ($n \geq 33$).



A biological threshold exists at the long-term growth rate value of 1. A growth rate ≥ 1 means the population is viable, whereas a growth rate < 1 means the population is inviable (Caswell 2001). This biological threshold may be rewritten in terms of minimum annual survival of each stage (marginal thresholds) or the minimum combinatorial annual survival among stages (a joint threshold). Our analysis adapted Holling's (1973) definition of resilience (the ability of a system to absorb changes of state variables, driving variables, and parameters, and still persist) to be the straight-line (marginal) distance between median annual survival of each life stage in an uncontaminated environment (i.e., the Pb-free group) and the minimum annual survival necessary in that stage to sustain the overall population (growth rate ≥ 1). We computed the resilience of female hatchlings, female non-breeders, and female breeders. We then computed the proportion of the resilience used under current (control) conditions by mortalities associated with Pb.

We used an additional set of algorithms to verify that the ecological assumptions made in our CounterPOPd analysis did not inappropriately influence our conclusions. Given the time series of breeding eagles in the northeast from 1990–2018, the early period of recovery contained low abundances of breeding eagles, where suitable nesting territories were largely vacant. Alternatively, the recent period of recovery contained higher abundances of breeding eagles where suitable nesting territories experienced comparatively higher occupancy. The population density analysis (the DensiPOPd analysis) controlled for differences in densities by comparing the 3 eagle groups under low densities relative to those in the CounterPOPd analysis and high densities relative to those in the CounterPOPd analysis. We further verified that the dispersal assumptions made in the CounterPOPd analysis did not inappropriately influence our conclusions. The counterfactual and geographically closed population analysis (ClosedCounterPOPd analysis) compared the same 3 eagle groups in CounterPOPd but assumed no dispersal. Finally, the counterfactual and geographically closed population density analysis (ClosedDensiPOPd analysis) compared the 3 eagle groups under no dispersal and low densities, and no dispersal and high densities.

We used USGS eaglet banding and encounter data to examine whether the dynamics predicted by the CounterPOPd analyses existed in an independent data set. We tabulated the number of eaglets that were banded in the nest and then relocated as breeding adults into or out of the northeast United States as suggested by their observed locations during subsequent breeding periods (the BandingPOPd analysis).

RESULTS

The recorded number of breeding pairs of eagles in the northeast United States rose over the past 3 decades from 147 (1990) to 1,497 (2018; Hanley et al. 2019). During the same period, at least 1,232 dead or dying eagles were collected from the wild in the study area and taken to rehabilitation or diagnostic centers; 30.6% (377/1,232) of these eagles were reported to have non-zero levels of Pb in their tissues at the time of their death and 11.3% (139/1,232) had Pb measurements that surpassed the criteria for Pb-toxicity (Table 1). A Pb test had been conducted by the pathologist on an additional 109 birds, but the result was an undetectable level of Pb, while the remaining 746 birds in the data set were not tested for Pb.

Statistical comparisons in the CounterPOPd analysis supported our hypothesis that differences in the long-term growth rates existed between eagle groups. Lead-toxicity deaths were associated with a reduction in the median long-term growth rate for female eagles ($\chi^2 = 28.09$, $P = 7.9 \times 10^{-7} < \alpha'$). The difference in the long-term growth rate between the Pb-reduced group (0.934) and the control group (0.892) for female eagles was 0.042, or equivalently, the long-term growth rate of the Pb-reduced group was 4.2% higher than the long-term growth rate of the control group (Tables 2–3). This 0.042 discrepancy in the long-term growth rate did not, however, result in outright biological discrepancies in female abundances among factual and counterfactual scenarios (Figure 1). Lead-toxicity deaths were also associated with a reduction in the median long-term growth rate for male eagles ($\chi^2 = 52.64$, $P = 3.7 \times 10^{-12} < \alpha'$). The difference in the long-term growth rate between the Pb-reduced group (0.955) and the growth rate of the control group (0.892) for male eagles was 0.063, or equivalently, the long-term



TABLE 1 Veterinary data from necropsies on bald eagles in the northeast United States, 1990–2018, tabulated by sex, stage, and lead (Pb) category. The hatchling stage represents birds <1 year old, the non-breeder stage represents any non-reproductive bird in its second year of life (or older, so long as it is not reproductive), and the breeder stage represents any reproductive bird. The Pb-exposure category includes any eagle with >0 ppm Pb value in any tissue. Birds in the Pb-toxicity category surpassed one of the following Pb thresholds: blood ≥ 50 ug/dL (0.5 ppm), liver ≥ 6 ppm (wet weight), kidney ≥ 4 ppm (wet weight), or bone ≥ 20 ppm (dry weight; Pain et al. 2019). Records that indicated a Pb test had been conducted at the time of necropsy but the result was an undetectable level of Pb were categorized as Pb-none detected, with limits of detection varying depending on the source facility. The Pb-toxicity group is a subset of the Pb-exposure group, so Pb-exposure, Pb-none, and no test add to the total

Sex	Stage	Pb-toxicity	Pb-exposure	Pb-none	No test	Total
Female	Hatchling	2	20	11	44	75
	Non-breeder	7	17	7	47	71
	Breeder	18	42	10	73	125
Male	Hatchling	2	10	23	18	51
	Non-breeder	8	23	7	42	72
	Breeder	13	31	9	63	103
Unknown	Hatchling	6	43	21	103	167
	Non-breeder	11	43	3	61	107
	Breeder	56	96	8	157	261
	Unknown	16	52	10	138	200

growth rate of the Pb-reduced group was 6.3% higher than the long-term growth rate of the control group. We found no evidence that the median long-term growth rates differed among control and Pb-free groups for eagles of either sex ($P > \alpha'$). We further found no evidence that the median stochastic growth rates differed among groups for eagles of either sex ($P > \alpha'$).

Statistical comparisons in the CounterPOPd analysis supported our hypothesis that differences in the annual survival existed between eagle groups. Lead was associated with a decrease in the median annual survival for female and male hatchlings (females: $\chi^2_2 = 72.94$, $P = 2.2 \times 10^{-16} < \alpha'$, males: $\chi^2_2 = 63.49$, $P = 1.6 \times 10^{-14} < \alpha'$) and a decrease in median annual survival for female and male breeders (females: $\chi^2_2 = 38.72$, $P = 3.8 \times 10^{-09} < \alpha'$; males: $\chi^2_2 = 51.89$, $P = 5.3 \times 10^{-12}$) but an increase in median annual survival for female and male non-breeders (females: $\chi^2_2 = 53.84$, $P = 2.0 \times 10^{-12} < \alpha'$, males: $\chi^2_2 = 45.68$, $P = 1.2 \times 10^{-10} < \alpha'$; Tables 2–3; Figure 2). An increase in median survival refers to the average survival shared by all members of that segment and not to the realized survival of any given individual in the physiological sense.

Mortality due to Pb was associated with a decrease in resilience for female hatchlings and female breeders but an increase in resilience for female non-breeders. Hypothetical populations of eagles that live in a Pb-free habitat can maintain population viability despite an annual survival probability as low as 75% (or mortality up to 25%) for female hatchlings, an annual survival probability as low as 80% (or mortality up to 20%) for female non-breeders, or an annual survival probability as low as 83% (or mortality up to 17%) for female breeders (Table 4). The hypothetical resilience of female hatchlings in a Pb-free habitat is 0.131; the median annual survival of female hatchlings in a Pb-free environment is 0.881 (Table 3), but the population as a whole can persist when median annual survival is 0.750 (Table 4), giving a baseline female hatchling resilience of $0.881 - 0.750 = 0.131$. Under current (control) conditions, the resilience of female hatchlings is 0.006; the median annual survival in a contaminated environment is 0.756 (Table 3), but the population can persist when median annual survival is 0.750 (Table 4), giving a female hatchling resilience of $0.756 - 0.75 = 0.006$. The proportion of resilience remaining for female hatchling eagles after removal



TABLE 2 The shift in the medians of long-term growth rates (lambdas) and annual survival rates among sex, life stage, and group (control, Pb-reduced, and Pb-free) for bald eagles in the northeast United States from 1990–2018. The hatchling stage represents birds <1 year old, the non-breeder stage represents any non-reproductive bird in its second year of life (or older), and the breeder stage represents any reproductive bird. The control group represents the (unaltered) empirical group of bald eagles, the Pb-reduced group represents the hypothetical group of bald eagles that did not experience deaths from Pb toxicity, and the Pb-free group represents the hypothetical group of eagles that did not experience deaths that were associated with any level of Pb. The last column specifies whether the estimated shift in the median values was substantiated when the data were analyzed in a system hypothetically closed to dispersal. Estimates for the long-term growth rates using the combinatorial optimization algorithm are known to be biased low (Hanley et al. 2019)

Parameter	Segment	Shift in median	Parameter value	Substantiated in a closed system?
Long-term growth rate	Females	Pb-reduced > control	0.934 > 0.892	No
	Males	Pb-reduced > control	0.955 > 0.892	No
Annual survival	Hatchling females	Pb-reduced > control	0.837 > 0.756	Yes
		Pb-free > control	0.881 > 0.756	Yes
	Hatchling males	Pb-reduced > control	0.847 > 0.756	No
		Pb-free > control	0.885 > 0.756	No
	Non-breeding females	Pb-free < control	0.887 < 0.947	No
	Non-breeding males	Pb-free < control	0.885 < 0.947	No
	Breeding females	Pb-free > control	0.928 > 0.848	Yes
	Breeding males	Pb-reduced > control	0.957 > 0.848	No
Pb-free > control		0.977 > 0.848	No	

of Pb-associated mortality is 4.6% ($0.006/0.131 = 4.6\%$). Thus, the reduction in resilience for female hatchlings when an environment shifts from uncontaminated (Pb-free) to contaminated (control) is 95.4% ($(0.131 - 0.006) / 0.131 = 95.4\%$).

The hypothetical resilience of female non-breeding eagles in a Pb-free habitat is 0.087; the median annual survival of female non-breeders in an uncontaminated environment is 0.887 (Table 3), but the population can persist when median annual survival is 0.80 (Table 4), giving a baseline female non-breeder resilience of $0.887 - 0.80 = 0.087$. Under current (control) conditions, the resilience of female non-breeders is 0.147; the median annual survival in a contaminated environment is 0.947 (Table 3), but the population can persist when median annual survival is 0.80 (Table 4), giving a female non-breeder resilience of $0.947 - 0.80 = 0.147$. The proportion of resilience remaining for female non-breeding eagles after removal of Pb-associated mortality is 168.9% ($0.147/0.087 = 168.9\%$). The increase in resilience for female non-breeders when an environment shifts from uncontaminated (Pb-free) to contaminated (control) is 68.9% ($(0.087 - 0.147)/0.087 = 68.9\%$).

The hypothetical resilience of female breeding eagles in a Pb-free habitat is 0.098; the median annual survival of female breeders in an uncontaminated environment is 0.928 (Table 3), but the population can persist when median annual survival is 0.83 (Table 4), giving a baseline female breeder resilience of $0.928 - 0.83 = 0.098$. Under current (control) conditions, the resilience of female breeders is 0.018; the median annual survival in a contaminated environment is 0.848 (Table 3), but the population can persist when median annual survival is 0.83 (Table 4), giving a female breeder resilience of $0.848 - 0.83 = 0.018$. The proportion of resilience remaining for female breeding eagles after removal of Pb-associated mortality is 18.3% ($0.018/0.098 = 18.3\%$). The decrease in



TABLE 3 Comparisons of the interquartile ranges (IQR) of the long-term population growth and annual survival rates among sex, stage, and group (control, Pb-reduced, and Pb-free) for bald eagles in the northeast United States from 1990–2018. The hatchling stage represents birds <1 year old, the non-breeder stage represents any non-reproductive bird in its second year of life (or older), and the breeder stage represents any reproductive bird. The control group represents the (unaltered) empirical group of bald eagles, the Pb-reduced group represents the hypothetical group of bald eagles that did not experience deaths from Pb toxicity, and the Pb-free group represents the hypothetical group of eagles that did not experience deaths that were associated with any level of Pb. The long-term growth rates are known to be biased low (Hanley et al. 2019)

Parameter	Segment	Scenario	Sample size	IQR				
				Min.	First quartile	Median	Third quartile	Max.
Long-term growth rate	Females	Pb-reduced	70	0.912	0.919	0.934	0.968	0.983
		Pb-free	89	0.869	0.892	0.919	0.957	0.981
		control	40	0.892	0.892	0.892	0.972	0.976
	Males	Pb-reduced	284	0.807	0.923	0.955	0.976	0.976
		Pb-free	70	0.876	0.876	0.876	0.912	1.006
		control	40	0.892	0.892	0.892	0.972	0.976
Annual survival	Hatchling females	Pb-reduced	70	0.807	0.807	0.837	0.874	0.918
		Pb-free	89	0.755	0.881	0.881	0.886	0.916
		control	40	0.756	0.756	0.756	0.848	0.848
	Hatchling males	Pb-reduced	284	0.743	0.799	0.847	0.865	0.970
		Pb-free	70	0.733	0.817	0.885	0.885	0.897
		control	40	0.756	0.756	0.756	0.848	0.848
	Immature and non-breeding females	Pb-reduced	70	0.831	0.855	0.911	0.979	0.979
		Pb-free	89	0.805	0.852	0.887	0.887	0.949
		control	40	0.871	0.947	0.947	0.954	0.954
	Immature and non-breeding males	Pb-reduced	284	0.813	0.900	0.911	0.980	0.980
		Pb-free	70	0.855	0.855	0.855	0.913	0.978
		control	40	0.871	0.947	0.947	0.954	0.954
	Breeding females	Pb-reduced	70	0.720	0.865	0.869	0.947	0.998
		Pb-free	89	0.832	0.888	0.928	0.996	0.996
		control	40	0.848	0.848	0.848	0.922	0.942
	Breeding males	Pb-reduced	284	0.783	0.885	0.957	0.966	0.995
		Pb-free	70	0.848	0.883	0.977	0.977	0.977
		control	40	0.848	0.848	0.848	0.922	0.942

resilience for female breeders when an environment shifts from uncontaminated (Pb-free) to contaminated (control) is 81.6% ($(0.098 - 0.018)/0.098 = 81.6\%$).

While not tested statistically, results in the ClosedCounterPOPd analysis corroborated results in the CounterPOPd analysis that Pb was associated with a decrease in the median annual survival for female hatchlings and a decrease in the median annual survival for female breeders but an increase in the median annual survival for female

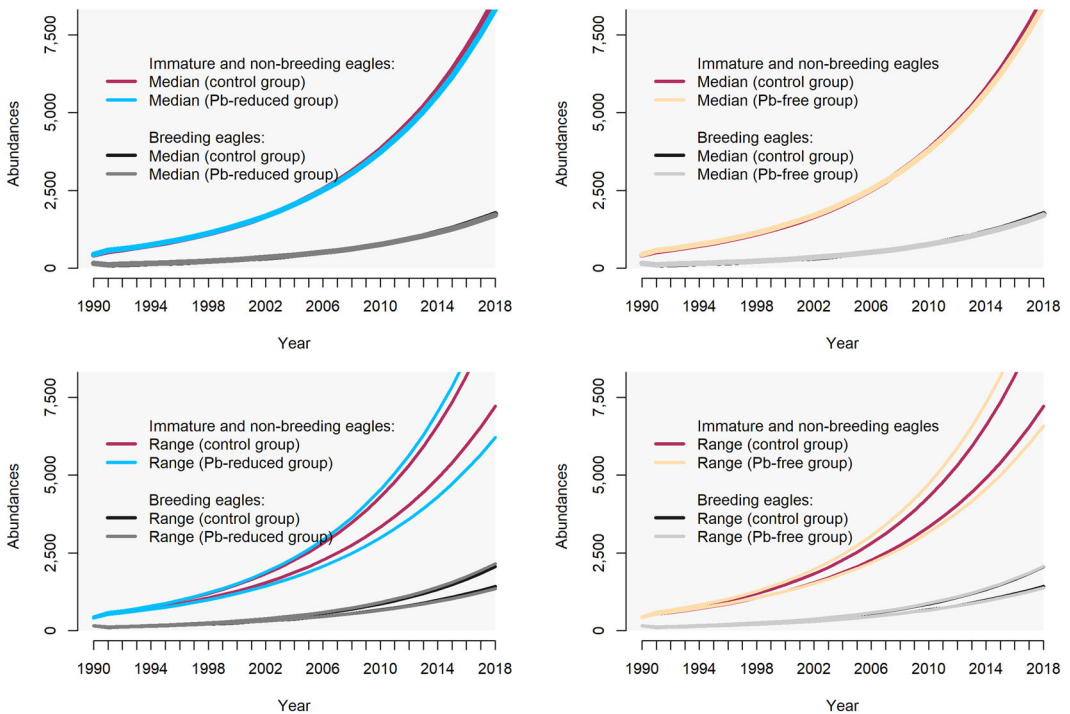


FIGURE 1 Despite an estimated 4.2% (female) to 6.3% (male) difference in the long-term growth rate among eagle groups, differences in abundances between groups during the 3-decade timeframe were biologically negligible. Abundances of eagles as assessed using the CounterPOPd analysis are depicted by medians (top row) and transient envelopes (minimums and maximums; bottom row). The control group represents the (unaltered) empirical time series of bald eagles in the northeast United States from 1990–2018 that were exposed to lead (Pb). The Pb-reduced group represents the counterfactual time series of bald eagles that did not experience deaths from Pb toxicity. The Pb-free group represents the counterfactual time series of eagles that did not experience deaths associated with any level of Pb

non-breeders (last column of Table 2). The results in the DensiPOPd and ClosedDensiPOPd analyses failed to corroborate the results of the CounterPOPd and ClosedCounterPOPd analyses (see the Supporting Information).

The eaglet banding and encounter data set revealed that from 1990–2018, eagles in the northeast United States disproportionately traded nesting territories with eagles from other populations along the Atlantic and Mississippi flyways. The study area gained 2 more eagles of immediate breeding age (4–6 yr) from immigration than it lost from emigration prior to 1990 but lost 27 more eagles of immediate breeding age through emigration than it gained through immigration after 1990. Similarly, the study area gained 14 more eagles approaching breeding age (1–3 yr) from immigration than it lost from emigration prior to 1990 but lost 41 more eagles approaching breeding age through emigration than it gained through immigration after 1990.

DISCUSSION

Due in part to the modeling complexities surrounding the life history of eagles and the contextual situation of population recovery in the study area (Franson et al. 2003, Scheuhammer et al. 2003, Keyfitz and Caswell 2005, Koons et al. 2006), the population-scale consequences to bald eagles through the continued deposition of Pb into uplands has long constituted a critical information gap for wildlife managers in the northeast United States.

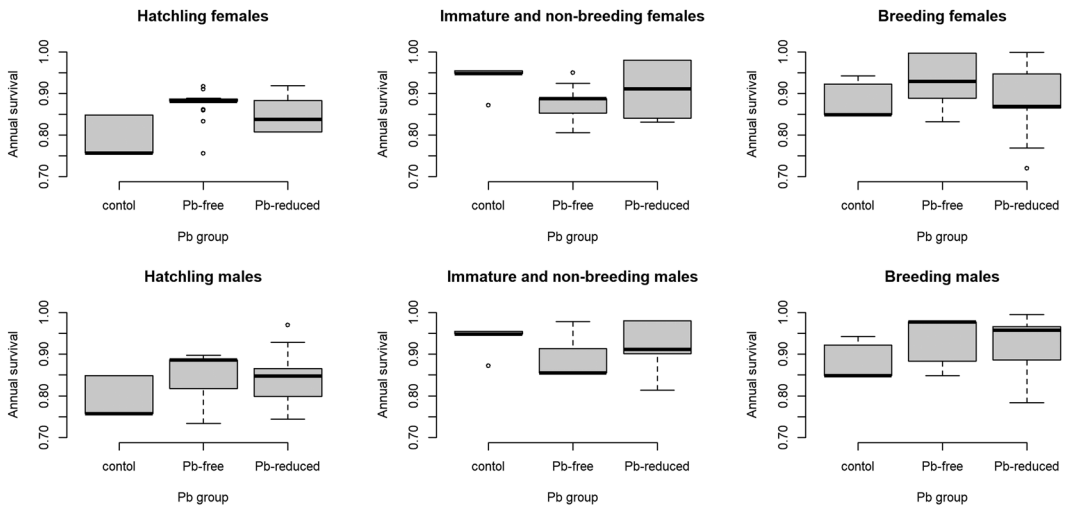


FIGURE 2 Comparisons in the median annual survival among groups for hatchling, non-breeding, and breeding bald eagles in the northeast United States, 1990–2018 as assessed using the CounterPOPd analysis show that the negative impact on average survival by mortality associated with lead (Pb) is especially large for hatchlings. The control group represents the unaltered empirical time series of bald eagles that were exposed to Pb. The Pb-reduced group represents the counterfactual time series of bald eagles that did not experience deaths from Pb toxicity. The Pb-free group represents the counterfactual time series of eagles that did not experience deaths associated with any level of Pb. The boxplots represent the interquartile range (IQR) of parameter estimates. Boxplots display the 25th percentile (first quartile; Q1), 50th percentile (second quartile; Q2), and 75th percentile (third quartile; Q3), and are connected by dashed lines to the error bars. Error bars include the relative minimum ($Q1 - 1.5 \times IQR$) and maximum ($Q3 + 1.5 \times IQR$) values of the parameter estimates. Circles represent outliers

TABLE 4 The independent (marginal) minimums in the annual survival rates necessary to sustain a viable population differentiated by sex, stage, and group (control, Pb-reduced, and Pb-free) for bald eagles in the northeast United States from 1990–2018. The hatchling stage represents birds <1 year old, the non-breeder stage represents any non-reproductive bird in its second year of life (or older), and the breeder stage represents any reproductive bird. The control group represents the (unaltered) empirical group of bald eagles, the Pb-reduced group represents the hypothetical group of bald eagles that did not experience deaths from Pb toxicity, and Pb-free group represents the hypothetical group of eagles that did not experience deaths that were associated with any level of Pb

	Hatchling		Non-breeding		Breeding	
	Female	Male	Female	Male	Female	Male
Pb-reduced	0.75	0.84	0.83	0.91	0.72	0.95
Pb-free	0.75	0.78	0.80	0.85	0.83	0.97
Control	0.80	0.86	0.87	0.94	0.84	0.84

Two versions of data-informed CounterPOPd analysis suggested the same conclusion: mortality events of wild eagles that arose from the ingestion of Pb interacted with expanding population dynamics in a manner that depressed the long-term growth rate of the population. We estimated the depression of this growth rate to be 4.2% in female eagles and 6.3% in male eagles.

Once the population settles into the stable state, the asymptotic property of the long-term growth rate will have sole influence over population density, growth, and structure (Stott et al. 2011), rendering the depression in



the long-term growth rate the key inference of this study. But such long-term properties do not consider transient phenomena such as exogenous disturbances to stable stage structure (Stott et al. 2010), which constitute the second key inference of this study: despite the depression in the long-term growth rate, the difference in abundances of eagles between groups during the 3-decade timeframe was biologically negligible (Figure 1). Transient processes that coalesce into abundance manifestations vary among 2 axes—time and population density—both of which depend on initial conditions (Stott et al. 2011). Within an eagle group, differences in starting stage abundances or momentary perturbations to stable stage proportions can influence abundances in the short term, via temporary peaks and valleys in abundances known as amplification or attenuation, respectively, or in the long term, where abundance projections settle into a fixed ratio higher or lower than would be expected in the same group under stable status (inertia; Stott et al. 2011). Negligible differences in abundances among eagle groups is explained by these transient mechanisms acting on the stage distributions in each time step. While it is impossible to use our data to infer the true stable distribution of bald eagles in the northeast (and thus control the effects of transient influences on abundance projections), we attempted to control this factor by initiating all 3 algorithms with identical boundary parameters on initial conditions. Accordingly, differences in initial stage abundances among hatchlings and non-breeding eagles produced 3 abundance projection envelopes (Stott et al. 2011), in which the realized projection of abundances in each group could lie anywhere (Figure 1). Because stage structure was unknown, the comparison of bounds on plausible abundances (i.e., maximal or minimal) may be most appropriate (Stott et al. 2011). In consideration of the unknown initial abundances of hatchlings and non-breeding eagles in the year 1990, the envelopes of possible abundances reveal that the Pb-reduced and Pb-free conditions produced higher possible maximal abundances over the past 3 decades (Figure 1). The same argument does not apply for the median long-term growth rate, as the Strong Ergodic Theorem of Demography states that if the age-specific fertility and mortality patterns of a population remain unchanged over time, its (st)age composition will converge to a fixed form, regardless of initial shape (Arthur 1982).

Our analysis further suggested that current conditions harbored a community of eagles with fewer surviving hatchlings but more surviving non-breeders than would have been present had the community been free of Pb-related mortalities. Non-breeding eagles achieve breeding status around 4–6 years of age, so the excess survival enjoyed by non-breeders under current conditions in the northeast United States could explain the observed exodus of non-breeding and breeding eagles seen in the independent USGS banding data. Indeed, these independent USGS data corroborated the modeling interpretations that the study area under current (control) conditions may not be as desirable as other areas to nest and raise chicks.

Our analysis produced the counterintuitive result that mortalities from Pb increased non-breeder resilience by 68.9%, which deserves detailed discussion. Our interpretation of this result is mathematically technical and it follows from the literature of population dynamics, which states that a population that experiences unpredictable disturbance may need to change to be resistant to these disturbances by having smaller transient population dynamics, such smaller near-term oscillations in abundances, as an insurance against population decline (Stott et al. 2011). We offer 3 pieces of supporting technical evidence that supports this interpretation in eagles. First, comparisons of estimated stable stage distributions (SSD; the distribution of individuals in each life stage when the population is growing at the asymptotic growth rate; Caswell 2001) for female eagles revealed that stability existed under Pb-free conditions when 83% of the females were non-breeders and 17% of the females were breeders. In the matrix model, the hatchling stage is shorter in length than 1 year, so hatchlings and non-breeders share the non-reproductive life stage when population properties are computed (Hanley et al. 2019). Under control conditions, SSD was achieved when 81% of the females were non-breeders and 19% of the females were breeders. Thus, the death of a single female breeder under Pb-free conditions would distort the SSD more readily than the same perturbation under control conditions ($1/17 > 1/19$). Because transients arise whenever the population is not in SSD (Stott et al. 2011), the smaller relative perturbation arising from a mortality under the control conditions implies that the contaminated population reorganized to resist the effects of disturbance by producing smaller near-term transient oscillations in abundance.



Secondly, asymptotic dominant elasticities (e ; the relative importance of each vital rate to the dominant eigenvalue; de Kroon et al. 2000, Caswell 2001) of female eagles revealed that in all 3 eagle groups, stasis in the non-breeding stage (a_{22}) had the highest rank of influence on the long-term growth rate. But comparison of the elasticity of a_{22} ($e_{a_{22}}$) across eagle groups revealed that contamination by Pb further increased the influence of this rate on the long-term growth rate (control conditions: $e_{a_{22}} = 61\%$; Pb-reduced conditions: $e_{a_{22}} = 52\%$; Pb-free conditions: $e_{a_{22}} = 49\%$). The total elasticity allocated to non-breeders ($e_{a_{2,}}$, where a_{32} represented the transition to breeder and $e_{a_{2,}} = e_{a_{22}} + e_{a_{32}}$) revealed that the influence of non-breeder performance (successful survival and transition into the breeding stage) on the long-term growth rate increased from $e_{a_{2,}} = 73\%$ in the Pb-free environment to $e_{a_{2,}} = 80\%$ under current (contaminated) conditions. In the face of disturbance, reorganization to place higher emphasis on the life stage with the highest performance may have further ensured against population decline.

Finally, reproductive values (v ; the reproductive contribution to the future population by individuals in each life stage when the population is growing at the asymptotic growth rate; Caswell 2001) of female eagles revealed that in all 3 eagle groups, individuals that occupied the breeding stage made the largest relative contribution to the future population. But comparison of v in breeding eagles across the 3 groups revealed that breeders that lived in contaminated conditions ($v = 53\%$) made comparatively less reproductive contribution to future generations than breeders that lived in hypothetical Pb-reduced conditions ($v = 62\%$) or Pb-free conditions ($v = 64\%$). In the face of disturbance, reorganization to place higher emphasis on the fittest life stage while simultaneously increasing their reproductive value may have further ensured against overall population decline. Such a reorganization would have ensured that highly desirable nesting territories made vacant from the sudden death of a breeder were promptly refilled by increasingly fit, important, and reproductively valuable individuals. While we did not test whether territories were immediately refilled, we interpreted the increase in non-breeder resilience as a population-scale signature of this reorganization. In summary, we interpret the counterintuitive result that mortalities from Pb increased non-breeder resilience by 68.9% not to mean that Pb is any way beneficial to eagles but rather as evidence that the population dynamics of eagles responded to additive mortalities in a manner that ensured population persistence.

Lead-related deaths of wild raptors are known to occur and have long been recorded in the veterinary literature despite robust overall wild populations. For example, Elliott et al. (2011) reported a stable or growing bald eagle population in British Columbia, Canada despite Elliott et al. (1992) finding that 14% of the eagles found dead in the same area and during the same time period carried elevated tissue burdens of Pb. Despite the obvious bald eagle recovery in the northeast United States, our novel use of a combinatorial optimization algorithm was the first of its kind to put empirical mortalities of individual eagles into the context of the population dynamics of wild eagles. We were able to use this novel computational approach to compare growth and survival rates among eagle groups, and to reveal the presence of a functional reorganization of population dynamics to accommodate a loss of resilience.

Even with powerful modeling tools, however, the dynamics of wildlife populations are notoriously difficult to predict (Caswell 2001, Stott et al. 2010) and are further complicated when human-induced mortality is considered (Lebreton 2005, Stott et al. 2011). Our modeling endeavor was further challenging because veterinary evidence was limited to observational data. We mitigated this complication by employing a traditional analytical model as the foundational framework of our comparison, and then used matching (of the environment in which both groups operate) to regulate the effects of unmeasured variables among the comparative groups (Dohoo et al. 2012). We further scrutinized the objectivity of our modeling by comparing results against those from analyses conducted under differing biological and ecological assumptions. Finally, we compared our results against an independent data set. Our diligence in the process makes us confident that our results accurately estimate the differences in population dynamics between control, Pb-reduced, and Pb-free groups as supported by our data, and that our inferences were robust to our modeling assumptions and decisions.

Our study was a *post hoc* analysis of historical demographic and veterinary data that had been collected by several independent sources for other initial purposes. Thus, there existed considerable statistical difficulties that we could mitigate, but not fully rectify. First, the veterinary data were opportunistic, observational, and potentially



spatially and temporally biased. The records were likely non-random and the information contained in each record was not necessarily representative of the entire wild population of eagles. Accordingly, we could not defensibly consider our raw necropsy data to be a statistically representative sample of all bald eagles that were harmed or killed by the ingestion of Pb in the northeast United States. We instead created the hypothetical time series using tabulations of known mortalities only. Because we made no attempt to infer that additional eagles had been killed by Pb (and instead treated our data as if all eagles killed by Pb in the northeast were contained in our veterinary data set), our analysis was conservative. In other words, we put the burden of evidential proof on the existence and shareability of the veterinary records, which biased our results toward a Type II error (declaring insignificance when significance indeed exists; Conover 1999). If additional eagles died of Pb toxicosis in the wild and remained *in situ*, if additional eagles died of Pb toxicosis and the cause of death were recorded by pathologists but the records did not appear in this study, or if a Pb test (with a non-zero result) had been recorded for every eagle record present in this study, the true consequences of Pb on eagles in the northeast United States could differ from those results reported here.

Second, we categorized the veterinary records *post hoc* according to the quantitative Pb severity classes contained in Pain et al. (2019). We acknowledge that the use of different cutoff values to tabulate Pb-toxicosis, Pb-exposure, or Pb-none may alter the categorization of eagles into Pb groups, which may in turn alter the hypothetical time series, and therefore, the results. Similarly, classification of eagles by a pathologist interpretation (instead of a strictly quantitative approach) could alter the categorization of eagles into Pb groups. Indeed, any difference in the conventions or definitions used to construct the counterfactual time series could alter the nature of the hypothetical time series, which in turn could propagate differences through the algorithm to influence conclusions.

Third, while the long-established use of population matrix models is to compare wildlife scenarios under differing management regimes (Caswell 2001), we were not able to directly apply this tool in the traditional manner to compare vital rates (and corresponding population-scale consequences) of Pb-contaminated and Pb-free populations using field-generated data. Rather, we compared dynamics between Pb-contaminated (control) and hypothetical Pb-free populations that arose from matrix proxies (differences in time series projections), which were themselves estimated using novel computational approach designed to intake observational veterinary data. Our evidence could therefore support associative interpretations of differences among eagle groups but could not support causative conclusions.

Additive mortality occurs when the disease mortality summed with other sources of mortality equates to an increase in total mortality (Kistner and Belovsky 2014). Lower survival (higher mortality) in the control group than in the Pb-reduced group suggests that deaths associated with Pb-toxicosis are an additive source of mortality for eagles in the Northeast.

MANAGEMENT IMPLICATIONS

Lead is a toxic contaminant, so some countries have passed legislation to restrict additional anthropogenic deposition or taken steps to remediate previous depositions. Despite a patchwork of Pb regulation by states in the United States, some Pb-based ammunition remains unregulated at the federal level. This study shows that while abundances have increased, ingested Pb has a negative effect on eagle populations in the northeast United States. Although current levels of Pb contamination in the northeast United States have not caused a region-wide decline of eagles, these conditions have stressed the resilience of this population. The reduction of eagle mortality from Pb toxicosis can alleviate survival pressure of female hatchlings and breeders, and may return the eagle populations to dynamics that contain robust resilience. The results of this study can be used in efforts by state and federal wildlife managers or non-governmental organizations to educate hunters of the consequences of their ammunition choices or to inform policy surrounding the use of lead ammunition.



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CONFLICT OF INTERESTS

Mark A. Pokras has previously published, consulted, and given expert testimony on Pb toxicity in wildlife species. The remaining authors declare no conflicts.

ETHICS STATEMENT

Necropsies were conducted at the facility of origin, where the gross pathology professionals adhered to sound ethical and animal welfare principles, including compliance with all applicable federal, state, and local regulations. The digital veterinary records were not used in the conduct of any experimental procedures on a live animal nor did this study collect, euthanize, and donate the specimen to a museum collection. Thus, the analysis did not require an Institutional Animal Care and Use Committee protocol.

DATA AVAILABILITY STATEMENT

The time series data are at <https://doi.org/10.1002/ecs2.2963>. The veterinary data are at <https://doi.org/10.7298/qg9d-9p17>, <https://doi.org/10.7298/6by1-j636>, <https://doi.org/10.7298/jn80-e080>, <https://doi.org/10.7298/m8yz-1r93>, <https://doi.org/10.7298/hyyc-ws65>, <https://doi.org/10.7298/3p9p-j249>, and by contacting the New York State Department of Conservation (wildlife@dec.ny.gov). The software is at <https://doi.org/10.7298/0v1k-wq39.2>, <https://doi.org/10.7298/7rxf-ee77>, <https://doi.org/10.7298/6yb8-5c25.2>, <https://doi.org/10.7298/q4t7-1y54.2>, <https://doi.org/10.7298/n2x8-6p10.2>, and <https://doi.org/10.7298/1n7f-xs53>. Access dates for data and software is 27 July 2021. In the software, the control group is denoted Northeast, the Pb-reduced group is denoted Exper.I, and the Pb-free group is denoted Exper.II.

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SUPPORTING INFORMATION

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