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The impact of lead poisoning from ammunition sources on raptor populations in Europe

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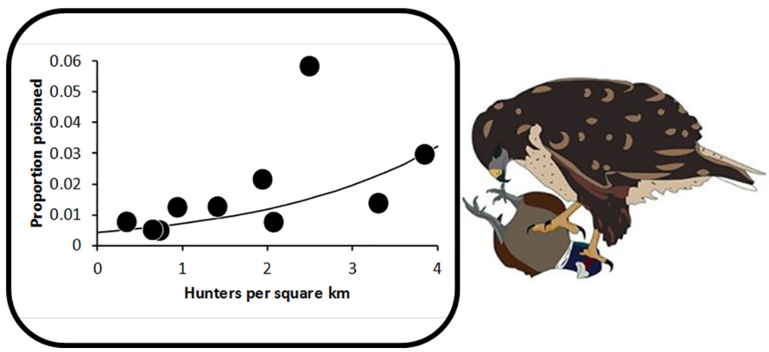
HIGHLIGHTS

- Lead poisoning causes deaths of some raptor species in Europe.
- Lead poisoning reduces population sizes of some raptor species in Europe.
- Prevalence of lead poisoning of raptors correlates with the density of hunters.

GRAPHICAL ABSTRACT



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ABSTRACT

Poisoning caused by ingestion of spent lead (Pb) ammunition in food items is a common cause of death of raptors. However, there has been no previous attempt to assess the impact of lead poisoning on populations of raptors throughout Europe or examine how this relates to the prevalence of hunting. We used measurements of lead concentration in the liver from over 3000 raptors of 22 species found dead or dying in the wild in 13 countries and a lead poisoning threshold of 20 ppm (dry weight) to assess the proportion of these in which lead poisoning caused or contributed to death. The prevalence of lead poisoning as a cause of death of raptors varied substantially among European countries and was positively correlated across countries with the reported number of hunters per unit area. Ten species had a non-zero proportion of individuals with concentrations exceeding the lead poisoning threshold ranging between 0.3% and 16.5%. The estimated annual conditional death rate from lead poisoning for these ten species averaged 0.44% (range 0.06–0.85%). Scavenging species feeding regularly on carcasses of game animals,tended to have a high annual probability of death from lead poisoning. So too did some predators which only sometimes scavenge, but prey on frequently hunted birds, such as gamebirds, waterfowl and pigeons, which may contain ingested or embedded lead shot. Small-bodied predators had a low annual probability of death from lead poisoning. Modelling indicated that European populations of adult raptors of the ten focal species averaged 6.0% smaller (range 0.2–14.4%) than they would be without the effects of lead poisoning. A given rate of lead poisoning mortality resulted in greater expected population reductions for species with high annual survival rate and late age at first breeding.

1. Introduction

Lead is a toxic metal with no known physiological functions in animals. It has negative effects on the functioning of most body systems in vertebrates. Once absorbed, largely through the gut or lungs after ingestion or

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inhalation, it passes into the bloodstream where its concentration then remains elevated for days or weeks, depending upon the intensity and duration of exposure (EFSA, 2010). From the blood, lead is transferred to soft tissues, especially the liver and kidney, and to bone. After an exposure event, soft tissue concentrations decline over a period of weeks, whereas much of lead deposited in bone remains there for the lifetime of the animal. No safe blood lead level has been found in humans (Paulson and Brown, 2019).

Lead occurs naturally in the environment, primarily in inorganic form, but its widespread distribution in the biosphere and the occurrence of elevated concentrations in the tissues of humans and animals mainly result from a long history of use by humans (Hernberg, 2000). As a result of the risks that lead poses to human health, most of its uses are now strongly regulated in Europe (EFSA, 2010) and most other developed countries. However, one of the remaining uses of lead with little or no regulation is the manufacture of ammunition projectiles (shotgun pellets, slugs, and rifle bullets). Even if a recent EU restriction on the use of lead gunshot for shooting in and around wetlands is fully effective, it is estimated that hunting elsewhere will still disperse approximately 14,000 t of lead annually into the bodies of game animals and the environment of the European Union in the form of spent projectiles and fragments thereof (ECHA, 2021). Exposure to this lead poses risks to humans and animals.

It has been recognised for more than a century that extensive mortality of waterfowl from lead poisoning can occur after ingestion of spent lead gunshot deposited in the environment by hunters (Wetmore, 1919). Embedded lead gunshot also increases the annual mortality rate of waterfowl that were struck but not killed by shot (Tavecchia et al., 2001). Lead poisoning of scavenging and predatory birds that ingest shot, bullets or ammunition fragments embedded in carrion or their prey is also long-established as a conservation problem (Krone, 2018). Poisoning of raptors by spent lead ammunition has also gained prominence as an environmental issue in the USA because it killed large numbers of the emblematic national bird, the bald eagle (*Haliaeetus leucocephalus*) (Cohn, 1985; Russell and Franson, 2014) and because of its role in causing declines of wild populations of the California condor (*Gymnogyps californianus*) (Finkelstein et al., 2012).

Evidence of the poisoning of waterfowl led to decades of piecemeal policy and regulatory change globally to replace lead gunshot with non-toxic alternatives (Stroud, 2015). Two examples of major initiatives are a nationwide ban on the use of lead gunshot for shooting waterfowl in the USA from 1991 (U.S. Department of the Interior, 1986) and a ban on the use of lead gunshot in and around wetlands throughout the European Union (EU) under EU REACH Regulations in January 2021 (EU, 2021). The latter ban followed limited implementation of a resolution under the African-Eurasian Waterbirds Agreement (AEWA, 1999) which was intended to phase out lead gunshot use in wetlands by 2000 (Stroud, 2015). There has been less regulatory action intended to reduce the incidence of poisoning of scavenging and predatory raptors and other terrestrial birds. However, the impacts of lead poisoning on the California condor and other predatory and scavenging birds led to a state-wide ban on the use of all lead ammunition for hunting in California from July 2019 (AB 711, 2013).

In 2021, the European Commission requested that the European Chemicals Agency (ECHA) produce a proposal to restrict the use of all lead ammunition for hunting across the EU to protect wild birds in terrestrial habitats, human health and the environment (ECHA, 2021). If accepted, the proposal will be adopted in 2023. Impacts on predatory and scavenging birds are an important part of the motivation for this restriction proposal and, as part of its assessment procedure, ECHA has presented estimates of the numbers of individual birds at risk of being killed by lead poisoning, and per capita annual mortality rates from this cause (ECHA, 2021; Table 1–55). These estimates are mostly based on the proportions of wild birds found dead with clinical signs of lead poisoning and/or tissue lead concentrations indicating lead poisoning as the likely cause of death. In birds, liver and kidney lead concentrations are frequently used to diagnose death from lead poisoning because they reflect exposure to lead in a few weeks before death (Franson and Pain, 2011).

Table 1
Numbers of raptors in Europe (N_s) for which the concentration of lead in the liver was reported and the number (N_c) and proportion (P_{Pb}) of these with concentrations exceeding the threshold for expected clinical effects. Species-specific values of P_{Pb} are given calculated from the raw data (crude) and also after adjustment for uneven sampling coverage of range countries using logistic regression Model 7 (see Table 2). Scientific names of species are given in Appendix A.

Species	N_s	N_c	Number of studies	Crude P_{Pb}	Adjusted P_{Pb}
Bearded vulture	54	2	5	0.037	0.038
Egyptian vulture	29	0	2	0.000	0.000
European honey buzzard	3	0	1	0.000	0.000
Griffon vulture	443	70	6	0.158	0.159
Cinereous vulture	52	0	2	0.000	0.000
Lesser spotted eagle	11	0	1	0.000	0.000
Spanish imperial eagle	51	0	2	0.000	0.000
Golden eagle	381	41	10	0.108	0.148
Bonelli'seagle	15	0	1	0.000	0.000
Eurasian sparrowhawk	297	1	7	0.003	0.002
Northern goshawk	102	5	6	0.049	0.046
Western marsh harrier	49	2	6	0.041	0.023
Hen harrier	16	0	3	0.000	0.000
Montagu's harrier	10	0	3	0.000	0.000
Red kite	289	12	7	0.042	0.028
Black kite	66	0	1	0.000	0.000
White-tailed eagle	436	72	14	0.165	0.173
Common buzzard	619	11	12	0.018	0.010
Common kestrel	67	0	5	0.000	0.000
Merlin	66	0	3	0.000	0.000
Eurasian hobby	11	0	2	0.000	0.000
Peregrine falcon	34	1	6	0.029	0.018
Total	3101	217	105	0.070	–

Until recently, there were insufficient data on concentrations of lead in the tissues of raptors in Europe to evaluate the likely population-level impacts of lead poisoning, but an increase in the number of published studies stimulated a wide-ranging recent review by Monclús et al. (2020). However, although that review documented tissue lead concentrations, it did not attempt to assess the numbers and proportions of raptors killed by lead poisoning throughout Europe or its possible effects on their population size in Europe. In this paper, we compile updated information on levels of lead poisoning in raptors across Europe and use them to estimate population-level impacts for all raptor species for which we found evidence of high-level exposure. We compare conclusions drawn from these population-level impacts with those from estimates of death rates. On its own, our analysis of the prevalence and population impact of lead poisoning in Europe does not identify the probable source or sources of lead in raptors with tissue lead concentrations indicating lead poisoning as the likely cause of death. Attribution of high lead levels to potential sources has been attempted for some raptor species in some countries using data on stable isotopes of lead (e.g. Mateo-Tomás et al., 2016; Taggart et al., 2020), but data availability is currently insufficient to apply this approach at a Europe-wide level. We therefore test the hypothesis that variation among species and European countries in the prevalence of lead poisoning is correlated with variation in exposure to spent lead ammunition from hunting using two alternative approaches. First, we compare the proportion of raptors in Denmark with tissue lead concentrations indicating lead poisoning before and after a ban on the use of lead shotgun ammunition for all hunting. Second, we test for a correlation across European countries between the proportion of raptors with tissue lead concentrations indicating lead poisoning and a country-specific proxy measure of the intensity of hunting.

2. Materials and methods

2.1. Collation of data on the concentration of lead in the liver

Our initial objective was to collate all data available on the proportion of individual diurnal raptors (families Accipitridae and Falconidae) found dead or moribund in the wild in Europe which had concentrations of lead in their tissues consistent with clinical effects of exposure. Our study region, which we refer to henceforth as "Europe", comprised the 27 countries constituting the European Union (EU) in 2021, together with the United Kingdom (UK), which was a member of the EU until 2020 and Switzerland, which is surrounded by EU countries. There are 37 raptor species which breed regularly in the study region, comprising a combined total of about 3.9 million adult individuals (27 Accipitridae species and 10 Falconidae; see Supplementary Table A1). We checked all of the references presented in the supplementary information of the review paper (doi:10.1016/j.scitotenv.2020.141437) on lead contamination in raptors in Europe by Monclús et al. (2020). This compilation included results published up to February 2019. For the subsequent period from 2019 to June 2021 we used similar search terms to those used by Monclús et al., (2020) in Google Scholar to identify more recently published papers and supplemented these with an unpublished dataset provided by O. Krone, data from a draft PhD thesis by G. Peniche-Peyron and accepted papers pre- publication which were brought to our attention.

We included data from tissue analyses of birds collected within our study region which were found dead in the wild or found moribund and which died in captivity shortly afterwards (within two weeks). Samples from nestlings and birds brought into captivity for longer periods were excluded. We excluded data from studies which focussed specifically on potential exposure to lead from a point source such as a mining area or smelter. Data were excluded when they were thought to replicate results from other papers that we included. Eligible datasets used in our analyses are given in Supplementary Table A2.

We analysed data on the concentration of lead in the liver, which reflects the level of exposure within a few weeks prior to death (Franson and Pain, 2011). We classified each liver lead concentration using widely-used threshold concentrations for clinical exposure in raptor tissues of 6 ppm (wet weight) and 20 ppm (dry weight) (Franson and Pain, 2011). Liver concentrations of lead above these clinical thresholds are the minimum levels generally used to confirm a diagnosis of lead poisoning mortality. Some of the birds with lead concentrations above the threshold might not have died only from lead poisoning, though many of the birds in the clinical poisoning category had tissue concentrations many times in excess of the threshold. Conversely, birds may die from lead poisoning with liver lead concentrations lower than the threshold. Birds with lead concentrations below the clinical threshold category would be expected to have experienced less severe health impacts from lead, but these may nonetheless have been a contributory cause of death, either directly or indirectly by affecting behaviour or the immune system.

An important objective of our study was to make estimates of the proportions of raptors with levels of lead in the liver indicating recent clinical exposure for all European countries with a breeding population of each species. An obstacle to doing that was that data on liver lead concentrations were not available for all such countries. There were no eligible data on liver lead concentration in any raptor species for 16 of the 29 countries in our study region (compare Supplementary Tables A1 and A2). To overcome this problem we fitted statistical models to describe the relationship between the proportion of sampled birds with clinical levels of lead in the liver and independent covariates. The purpose of these models was to allow the calculation of expected proportions of birds with clinical exposure for countries where data on liver lead concentration were lacking, but where values for the covariates were available. We therefore also obtained from the published papers and reports, the species of raptor, the country or countries from which the birds were collected, the range of years in which birds were collected, whether or not a ban on all use of lead shotgun ammunition for hunting was in force at the time and country-specific information on hunting.

2.2. Logistic regression model of the proportion of raptors with levels of lead in the liver indicating recent clinical exposure

We modelled the proportion of sampled birds with levels of lead in the liver indicating recent clinical exposure P_{Pb} from each study of each species in relation to potential independent covariates. P_{Pb} is the number of birds with liver lead concentration exceeding the clinical threshold N_c divided by the number of birds sampled N_s. Data for those species with $N_c = 0$ in every country do not contribute information to the estimation of the coefficients representing the effects of the other covariates, so we fitted regression models only to data for the species for which the grand total of the number of clinical cases across all countries exceeded zero. We modelled the effect of species identity as a categorical variable (factor) with a number of levels equal to the number of species with eligible data. We modelled the effect of the country of collection as a set of binary dummy variables which took the value 1 if a country contributed data to a study of a given species and was otherwise zero. We adopted this approach because 6% (6/105) of the species-study combinations reported data from more than one country, but it was not possible to attribute lead concentrations of individual birds to each country. Dummy variable values for an arbitrary reference country (UK) were all coded zero. We used the same dummy variable approach to code the timing of sample collection. We assigned a binary dummy variable to each of the decades, 1980s, 1990s, 2000s, 2010s and 2020s and scored these as having the value 1 if some samples were collected in that decade and as zero if none were. Dummy variable values for the earliest reference decade (1970s) were arbitrarily coded zero. We considered that modelling the effect of time period as a categorical variable in this way was preferable to modelling its effect as a continuous variable because we had no *a priori* reason to expect a sustained increase or decrease over time.

We wished to examine the possible effect on P_{Pb} of regulation intended to prevent exposure of raptors and other wildlife to spent lead shotgun ammunition used in hunting. We therefore compared results for countries in which the use of such ammunition is allowed by law with those for countries where lead shotgun ammunition is banned and where there is compliance with the law. Within our study region and study period, the use of lead shotgun ammunition for all hunting has been banned only in Denmark (from 1996) and the Netherlands (from 1993). In Europe there was partial regulation by 2018 of lead shotgun ammunition in 18 of the other EU27 countries and also in Norway, Switzerland and the UK (Mateo and Kanstrup, 2019). This regulation usually applied only to certain quarry species, especially waterfowl, and/or to wetland habitats, and compliance with these partial regulations has mostly been incomplete or has not been measured (Mateo and Kanstrup, 2019; Green et al., 2021). In any case, most quarry killed using lead shotgun ammunition are of species not covered by the partial regulations or which are shot in other habitats. Hence, most quarry animals are likely to be killed using lead shotgun ammunition in all European countries except the Netherlands and Denmark. We found no eligible data on liver lead concentrations in raptors for the Netherlands, but there were two eligible studies for Denmark. Clausen and Wolstrup (1979) reported liver lead concentration for 48 raptors of four species sampled in Denmark in 1976–1977, which is more than 19 years before the use of lead shotgun ammunition was banned there. In addition, Kanstrup et al. (2019) reported liver lead concentrations for 124 raptors of ten species sampled in Denmark in 2013–2016, at least seven years after the ban. We fitted logistic regression models to a dataset which included the results from Denmark of Clausen and Wolstrup (1979) and all other countries, but not those from Kanstrup et al. (2019). This set of results is uniform in that it comes from countries where the use of lead shotgun ammunition for hunting is allowed by law (Mateo and Kanstrup, 2019) and where the majority of such ammunition used is composed of lead (Kanstrup and Thomas, 2019). We then used the logistic regression model fitted to this dataset to calculate the numbers of raptors with clinical levels of lead in the liver in the samples of Kanstrup et al., 2019 obtained after lead shotgun ammunition was banned in Denmark which would have been expected there if the ban had not occurred. Based upon surveys of ammunition types used to kill pheasants and mallards in 2016–2018, most Danish hunters complied with the ban (Kanstrup and Balsby, 2019). Hence, this comparison is a test of the hypothesis that regulation to prevent the use of lead shotgun ammunition for all hunting affects the proportion of raptors with clinical lead levels in the liver.

There were no eligible data on liver lead concentration for many species-country combinations and no data for any raptor species for over half of the countries in our study region (Supplementary Tables A1 and A2). Therefore, to allow the estimation of approximate values of P_{Pb} for countries with missing values, we assessed the use of a variable as a proxy for the variation among countries in P_{Pb}. We hypothesised that the proxy variable might correlate with variation among countries in the exposure of raptors to lead derived from ammunition used for hunting and allow us to estimate P_{Pb} for countries with no data on raptor liver lead. The potential proxy we assessed was the number of hunters in the country divided by its surface area. Numbers of hunters in each country in 2010 were obtained from FACE (2010) and are tabulated, together with country land surface areas in Supplementary Table A3. We called this independent variable "hunter density" and modelled its effect on P_{Pb} as a continuous covariate. We recognise that the methods used to obtain data on the number of hunters are not defined in detail in this source and that exposure of raptors to spent lead ammunition will be influenced by many factors in addition to hunter density, such as the mean number of shots fired per hunter per year and the principal quarry species. Nonetheless, we consider this to be the best proxy variable currently available.

We fitted logistic regression models with the number of clinical cases N_c of each species in each study in relation to the number of birds sampled N_s as a binomial dependent variable. We used models with a logit link function and a binomial error term. Potential effects on P_{Pb} of species, country, decades represented and hunter density were modelled as independent covariates with a logistic link function. We modelled all covariates as having fixed effects rather than random effects because we did not think it reasonable to assume that differences among categories were normally distributed. Our approach assumes that logit(P_{Pb}) = log$_e$(P_{Pb}/(1-P_{Pb})) is a linear function of the independent variables. We fitted models with all possible combinations of main effects of the four covariates, except that we avoided including country and hunter density together in the same model because these two variables are confounded with one another. We compared the performance of models using Akaike's Information Criterion for small samples (AIC$_c$) (Burnham and Anderson, 2002). For the global model (i.e. that with the most fitted parameters), the degree of overdispersion (ratio of residual deviance to residual degrees of freedom) was 1.46, which we took to indicate only marginal overdispersion. Hence, so we considered it unnecessary to use a quasi-binomial, rather than binomial, error term.

2.3. Calculation of the additional annual mortality of raptors from lead poisoning from the proportion of deaths attributed to lead poisoning

For simulation modelling of effects of lead poisoning on population size we needed to know the additional annual mortality rate M_{Pb} caused by lead poisoning, where M_{Pb} = (1–S_{Pb}) and S_{Pb} is the conditional probability of surviving for one year without dying from lead poisoning, given that the bird does not die from any other cause. We assumed that the proportion P_{Pb} of dead and dying raptors found with clinical levels of lead in the liver is equivalent to the proportion of deaths in the sampled populationattributable to lead poisoning. Using an estimate of the observed annual adult survival rate S_{obs} under current conditions, taken from the scientific literature (Supplementary Table A4), the additional annual mortality rate of adults caused by lead can be calculated as

$$M_{Pb} = 1 - \exp\left(P_{Pb}\ \log_e(S_{obs})\right) \quad (1)$$

which is equivalent to

$$S_{Pb} = \exp\left(P_{Pb}\ \log_e(S_{obs})\right) \quad (2)$$

The expected annual survival rate of adults in the absence of lead poisoning S_0 is then given by

$$S_0 = S_{obs}/(1 - M_{Pb}) \quad (3)$$

Using published values for S_{obs} from Supplementary Table A4 and values of P_{Pb} from the logistic regression model described above, we were then able to calculate values of M_{Pb}, S_{Pb} and $S_0$for each of the ten species with observed $P_{Pb} > 0$. We used a version of the model which included the proxy variable hunter density (see above) to calculate M_{Pb} and S_{Pb} for each country with a breeding population of a given species and then took the weighted mean of these estimates across all countries, using the proportion of the European breeding population in each country from Supplementary Table A1 as weights.

We used expected country-specific values of M_{Pb} and S_0 derived from the same regression model to calculate the expected annual number of deaths D of breeding age adults from lead poisoning in each country as

$$D = VS_0M_{Pb} \quad (4)$$

where$V$ is the national population of breeding adults. We then summed D across countries to obtain an estimate of the total annual number of deaths of each species in Europe.

2.4. Simulation modelling of the effect of lead poisoning on the population size of raptors

Having built a statistical model of the proportion of dead and dying raptors with evidence that lead poisoning was the cause of death or contributed to death, we next wished to assess the effect of additional mortality caused by lead poisoning on raptor population size. We did this by using the simulation model described in Appendix B. The model uses assumptions about the compensatory effects of density dependence to calculate the extent to which the additional mortality caused by lead poisoning, as estimated from P_{Pb}, is likely to reduce the size of the adult population. We assumed that per capita recruitment was negatively related to adult population size by an exponential function and that other demographic rates were not density-dependent, as appears to be the case for most raptor species studied (Newton, 1979). We calculated the maximum value of per capita recruitment, which occurs at low adult density, using the Demographic Invariants method of Niel and Lebreton (2005).

We ran the simulation model for each raptor species using appropriate species-specific values of the unimpacted annual survival rate of adults S_0, calculated as described in Section 2.3, and mean age at first breeding, as given in Supplementary Table A.5. Each simulation began with an assumed population of 500 adults and a carrying capacity 1000 adults. We ran the model with one-year time steps for 100 years with no lead poisoning (M_{Pb} = 0) and then ran it for a further 200 years with lead poisoning set using values of M_{Pb} calculated for each European species as described in Section 2.3. During the period with no lead poisoning, the population rapidly increased to carrying capacity and stabilised there. Using our calculated expected values of M_{Pb} for European raptors, the simulated population then declined, for all species, to a stable level during the 200-year period with lead poisoning. We took the proportion by which the stable level was lower than the carrying capacityto be the expected proportion by which the European population of each species would be reduced. This is equivalent to the counterfactual of population size (CPS) approach of Green et al. (2016a).

3. Results

3.1. Proportion of raptors with concentrations of lead in the liver exceeding the threshold for clinical effects

We found studies of lead concentrations in raptor liver samples meeting our criteria which covered 13 countries and 22 species. Excluding the post-ban results for Denmark from Kanstrup et al. (2019) (see above), there were 105 eligible species-study combinations that we used in our logistic regression models (Supplementary Table A2). Overall, 7.0% (217/3101) of the birds covered by these studies had liver concentrations that exceeded the clinical threshold indicating lead poisoning as a cause of death. Ten of the

22 species (45%) had at least one case above the clinical threshold and the crude species-specific proportions exceeding the clinical threshold P_{Pb} of these ten species ranged from 0.3% to 16.5% (Table 1). Sample sizes were less than 30 individuals for seven of the 12 species (58%) with no clinical cases detected and exceeded 30 for all ten of the species for which clinical cases were detected. Hence, it seems likely that increased sample sizes would increase the number of raptor species in Europe for which at least some birds with clinical levels of lead are detected.

3.2. Factors affecting the proportion of raptors with clinical concentrations of lead in the liver

Logistic regression modelling indicated that the proportion of raptors with lethal concentrations of lead in the liver differed among species and countries. A model with these two effects (Model 5) had by far the lowest value of AIC_c of models with all combinations of main effects of the four candidate covariates (Table 2). Within the set of 12 models we fitted, the relative importance (Burnham and Anderson, 2002) of species was highest (1.000), followed closely by country (0.980), with the relative importance of decade (0.049) and hunter density (0.016) being much lower. We used the fitted parameters of Model 5 to generate the estimated effects of country on logit(P_{Pb}), which were estimated differences in logit(P_{Pb}) between the value for a given country and that of the reference country (UK). This approach would be rendered invalid if there were substantial differences among species in the effects of country on logit(P_{Pb}) or differences among countries in the effect of species on logit (P_{Pb}). We tested for this possibility by adding a two-way species-country interaction term to Model 5. There was no indication of a statistically significant interaction ($F_{42,29} = 1.10$; $P = 0.402$). We therefore consider it acceptable to use the main-effect terms for country from Model 5 as a country-specific measure of exposure of raptors to lead poisoning. These country effects were significantly positively correlated with the density of hunters in the country. The correlation was significant regardless of whether results for three countries whose regression coefficients were not expected to be reliably estimated because of small samples of birds ($N_s < 30$) were included (Spearman rank correlation coefficient $r_S = 0.797$; two-tailed $P = 0.001$) or excluded ($r_S = 0.733$; two-tailed $P = 0.016$). This correlation provides support for our hypothesis that differences among countries in P_{Pb} were positively correlated with hunter density. We illustrate this relationship by a graph of the expected country-specific values of P_{Pb} for common buzzard (*Buteo buteo*) from Model 5 plotted against hunter density (Fig. 1). We used the logistic regression model in which P_{Pb} was related only to species and hunter density (Model 7) to calculate expected values of P_{Pb} for common buzzard using data for all raptor species. The expected relationship from Model 7 fits the points calculated from Model 5 reasonably well (Fig. 1). However, the substantial difference in AIC_c between Models 5 and 7 indicates that there are significant differences in P_{Pb} between countries beyond those explained by the relationship with hunter density. The logistic regression coefficient from Model 7, which represents the expected increase in logit(P_{Pb}) with each increase of one hunter per square kilometre, was 0.509. This is equivalent to an increase of 66% in the odds of clinical exposure to lead for each additional hunter per square kilometre. The 95% confidence interval for the regression coefficient did not overlap zero (0.206–0.812).

Table 2
Comparison of logistic regression models of the proportion (P_{Pb}) of raptors with concentrations of lead in the liver exceeding the threshold for clinical effects. Independent covariates whose effects were included (1) or excluded (0) from each model are shown by the four model specification columns. The model with the lowest AIC_c and highest AIC_c weight (Model 5) is indicated in bold.

Model	Model specification				Number of parameters	ΔAIC_c	AIC_c weight
	Species	Country	Decade	Hunter density			
0	0	0	0	0	1	211.28	<0.001
1	1	0	0	0	22	24.91	<0.001
2	0	1	0	0	13	109.61	<0.001
3	0	0	1	0	6	168.61	<0.001
4	0	0	0	1	2	160.57	<0.001
5	**1**	**1**	**0**	**0**	**34**	**0.00**	**0.951**
6	1	0	1	0	27	11.34	0.003
7	1	0	0	1	23	16.33	<0.001
8	0	1	1	0	18	93.94	<0.001
9	0	0	1	1	7	142.20	<0.001
10	1	1	1	0	39	6.96	0.029
11	1	0	1	1	28	8.15	0.016

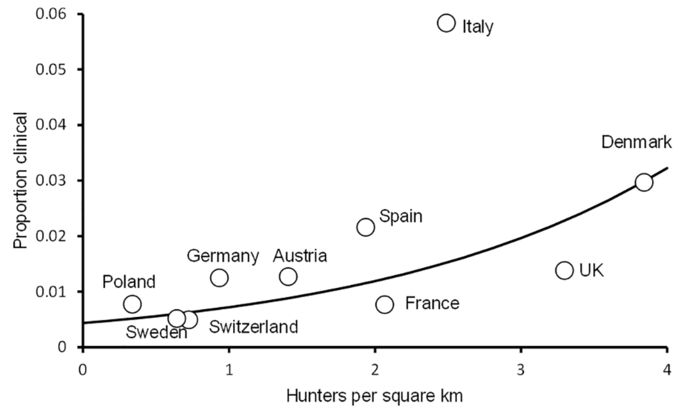

Fig. 1. Proportions of common buzzards in ten European countries expected to have concentrations of lead in the liver exceeding the threshold for clinical effects in relation to the density of hunters in each country (number per square km). Plotted points are expected proportions from Model 5 (see Table 2) and are based upon data for all raptor species.Points representing results for three countries with small samples (N_s<30) of raptors sampled are omitted, but the relationship remains significant if these are included.The curve shows the expected relationship for common buzzard from Model 7, which relates P_{Pb} to species identity and hunter density, with no effect of country.

We used Model 7 and hunter densities for all European countries to calculate expected species-specific values of P_{Pb}, which were adjusted to allow for the fact that liver lead data were not available for some countries with breeding populations of a species. We made this adjustment by using Model 7 and hunter densities from Table S3 to calculate expected P_{Pb} values for every country with a breeding population of the species. We selected Model 7 for this purpose only because we required a proxy variable to substitute for the main effect of country in Model 5, which our multi-model comparison (Table 2) showed to be almost as important as the effect of species. We considered replacement of the effect of country by its proxy variable hunter density (Model 7) to be the simplest approach available and to be reasonable because of the strong correlation of hunter density with the country effects from Model 5. We also considered the use of Model 11 for these calculations. Model 11 includes effects of decade in addition to species and hunter density and its AIC_cvalue was lower than that of Model 7 (Table 2). However, we preferred Model 7 over Model 11 because it was simpler and avoided the use of an addition variable with low relative importance (decade). However, we note that the expected values of logit(P_{Pb}) from Model 11 and Model 7 were very closely correlated with each other ($r = 0.996$). Hence, we concluded that results obtained using our preferred Model 7 would in any case be similar to those obtained using Model 11. We used Model 7 to obtain the weighted mean of expected P_{Pb} across all countries with breeding populations, using the proportions of the European breeding population in each country from Supplementary Table A1 as weights. Most of these adjusted values of P_{Pb} were similar to the crude values (Table 1). Adjusted P_{Pb} was strongly correlated with crude P_{Pb} (Pearson $r = 0.983$) across species, but the adjustment altered the ranking of P_{Pb} for a few species (Table 1).

3.3. Comparison of the post-ban proportion of raptors with clinical concentrations of lead in the liver in Denmark with expected values based upon the logistic model of data from countries without a complete ban

We used Model 5, which includes data on liver levels of lead from countries without a ban on the use of lead shotgun ammunition for all hunting,

Table 3
Numbers of raptors in Denmark (N_s) for which the concentration of lead in the liver was reported and the number (N_c) of these with concentrations exceeding the threshold for expected clinical effects. Data are from the study by Kanstrup et al. (2019) which was based upon birds collected after a ban on the use of lead shotgun ammunition for hunting. Also shown are numbers of birds from this sample expected to have clinical levels of liver lead based upon a logistic regression model (Model 5) fitted only to data collected in countries where lead shotgun ammunition was not banned, including data from Denmark collected before the ban.

Species	N_s	N_c	Model 5 expected N_c
Golden eagle	2	0	0.23
Eurasian sparrowhawk	5	0	0.01
Northern goshawk	5	0	0.16
Western marsh harrier	1	0	0.02
Hen harrier	2	0	0.00
Red kite	8	0	0.20
White-tailed eagle	12	0	2.67
Common buzzard	48	0	0.43
Common kestrel	38	0	0.00
Peregrine falcon	3	0	0.05
All species	124	0	3.77

to calculate expected values of P_{Pb} for Denmark for the 124 raptors of ten species sampled there by Kanstrup et al. (2019) after use of lead shotgun ammunition for hunting was banned in Denmark. Kanstrup et al. (2019) found that liver lead did not exceed the threshold for clinical effects in any of the birds sampled. The number of clinical cases expected from this sample, based upon Model 5 fitted to data from countries without a ban, was 3.77 cases (Table 3). The Poisson probability of observing no clinical cases if the expected number is 3.77 is 0.023. Hence, this result indicates that the prevalence of clinical levels of lead in the livers of raptors in Denmark after the ban was lower than that expected from the regression model of prevalences in countries without such a ban, including results from Denmark before the ban.

3.4. Additional annual mortality of raptors attributed to lead poisoning

We calculated expected values for the conditional additional mortality rate due to lead poisoning M_{Pb}, the annual survival rate of adults in the absence of lead poisoning S_0 and the annual number of deaths of breeding adults caused by lead poisoning using the procedure described in Section 2.3. For the ten raptor species for which $P_{Pb} > 0$, M_{Pb} varied 14-fold, ranging between 0.0006 (Eurasian sparrowhawk *Accipiter nisus*) and 0.0085 (northern goshawk *Accipiter gentilis*) (Table 4). The modelled total annual number of deaths of adults ranged between 1 (bearded vulture *Gypaetus barbatus*) and 2597 (common buzzard), with the total annual number of deaths of all ten species combined being 5,498 birds.

3.5. Reduction of adult population size attributed to the effects of lead poisoning

Modelled percentage reductions in adult population size (Table 4) ranged between 0.2% (Eurasian sparrowhawk) and 14.4% (white-tailed eagle *Haliaeetus albicilla*),with a tendency for larger reductions in population size to occur in species with high additional mortality rate (Fig. 2). The total number of adults by which the expected total European equilibrium population, summed across all ten species, was reduced was about 55,000 birds, which represents 2.2% of the combined total numbers of adults of these ten species expected in the absence of lead poisoning.

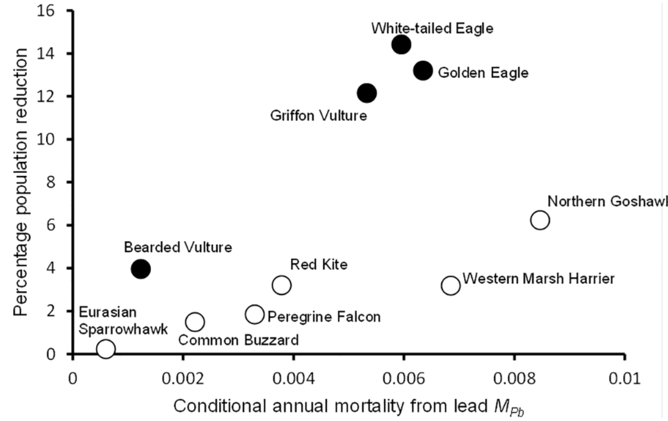

Fig. 2. Relationship between the modelled percentage reduction in stable adult population size of ten European raptor species and the conditional annual mortality attributed to lead poisoning M_{Pb}. Results are shown separately for four species with low maximum population multiplication rate λ_{max} (λ_{max}< 1.1; filled circles) and six species with high maximum population multiplication rate (λ_{max}> 1.1; open circles).

4. Discussion

4.1. Interspecific variation in the conditional annual mortality attributed to lead poisoning

Our estimates of the conditional annual mortality attributed to lead poisoning were substantial for some raptor species and varied considerably among species. We suggest that the annual conditional probability of a bird dying from lead poisoning M_{Pb} is the best measure of interspecific variation in this risk because, unlike the proportion of deaths attributed to lead poisoning P_{Pb}, it is independent of annual rates of mortality from other causes. Obligate scavengers, such as vultures, and facultative scavengers, such as golden eagle *Aquila chrysaetos*, white-tailed eagle and common buzzard, have been found to be among the species with the highest tissue concentrations of lead (Monclús et al., 2020). Our results for M_{Pb} showed a similar pattern. Two species of vulture (bearded and griffon) and four other species which often obtain a substantial proportion of their food by scavenging (white-tailed eagle, golden eagle, common buzzard, red kite) were among the nine species of the 22 species we studied with M_{Pb} > 0.001. An association of high M_{Pb} with scavenging is consistent with the hypothesis that raptors are exposed to high levels of lead principally

Table 4
Parameter values used to calculate the number of deaths of adult raptors caused by lead poisoning and the modelled effect of lead poisoning on stable adult population size in Europe.

Species	Observed adult survival S_{obs}	M_{Pb}	Unimpacted adult survival S_0	Maximum population multiplication rate λ_{max}	Modelled annual adult deaths	% adult population reduction	Number of adults by which population reduced
Bearded vulture	0.968	0.0012	0.969	1.044	1	4.0	20
Griffon vulture	0.967	0.0053	0.972	1.080	376	12.1	10,035
Golden eagle	0.958	0.0063	0.964	1.076	74	13.2	1848
Eurasian sparrowhawk	0.688	0.0006	0.688	1.382	219	0.2	1187
Northern goshawk	0.830	0.0085	0.837	1.180	1073	6.2	10,033
Western marsh harrier	0.740	0.0068	0.745	1.296	791	3.2	5081
Red kite	0.875	0.0038	0.878	1.168	234	3.2	2328
White-tailed eagle	0.966	0.0060	0.972	1.069	64	14.4	1856
Common buzzard	0.808	0.0022	0.809	1.196	2597	1.5	21,796
Peregrine falcon	0.830	0.0033	0.833	1.279	69	1.8	470

when they feed on carrion containing spent lead ammunition derived from hunted game animals. No individuals with liver lead concentration exceeding the clinical threshold were found in some species which obtain much of their food by scavenging, such as Egyptian vulture *Neophron percnopterus* and black kite *Milvus migrans*. However, the number of studies and the total number of individuals sampled for these species were small (Table 1), so failure to detect evidence of lead poisoning should not be taken to be evidence of the absence of poisoning of these species. Three raptor species which feed predominantly on live prey had $M_{Pb} > 0.001$ (northern goshawk, peregrine falcon *Falco peregrinus* and western marsh harrier *Circus aeruginosus*, the last also being a facultative scavenger). We suggest that these raptor species, which usually scavenge infrequently, may be exposed to the lead ammunition ingested by or embedded in the bodies of their prey. Mean body weights of northern goshawk, western marsh harrier and peregrine falcon all exceed 500 g and their prey includes manyfrequently-hunted bird species, such as waterfowl, gamebirds and pigeons (Cramp and Simmons, 1980; delHoyo et al., 1994). The bodies of live birds of these species frequently contain embedded or ingested lead shotgun pellets (Pain et al., 2015). M_{Pb} was less than 0.001 in all of the six smaller-bodied (<500 g) raptors for which we had data (merlin *Falco columbarius*, common kestrel *Falco tinnunculus*, Eurasian sparrowhawk, Eurasian hobby *Falco subbuteo*, Montagu's harrier *Circus pygargus*, hen harrier *Circus cyaneus*). These species take predominantly live prey and feed on insects, small rodents and small birds and only rarely take larger-bodied prey species. They are therefore less likely to feed on frequently-hunted species and hence to be exposed to ammunition-derived lead in their prey.

4.2. Suitability of alternative metrics for assessing the impact of lead poisoning on raptor populations in Europe

In the Introduction, we noted that ECHA has used estimates of the numbers of birds at risk of being killed by lead poisoning, and annual mortality from this cause as part of its assessment procedure for the restriction proposal on the use of lead ammunition for hunting in terrestrial habitats (ECHA, 2021). Our results enable us to supplement this approach for raptors in a conservation-relevant way. A striking finding of our study is that that the numbers and proportions by which we expect adult populations to be reduced by lead poisoning can be surprisingly large, even when the numbers of birds we estimate to be killed by lead poisoning annually are low. For example, the modelled reduction in adult population size attributed to lead poisoning for all raptor species in Europe combined (55,000) is about ten times larger than the annual number of adult deaths estimated to occur from this cause. A graphical illustration of this result is shown in Fig. 2, where the modelled percentage reduction in adult population is plotted against the estimated conditional annual mortality rate from lead poisoning M_{Pb} for individual species. It can be seen that adult population reductions of more than 10% are expected for some species in which less than 1% of adults are expected to die from lead proportion during a year of exposure to it. This apparent discrepancy is especially large for those species with low maximum population multiplication rate λ_{max}. These are species with high annual adult survival and late age at first breeding (Table 4). Although surprising at first sight, these results are in accord with studies of the effects of other causes of additional mortality on populations of long-lived and late-maturing animals, such as albatrosses (*Diomedea* sp. and *Phoebastria* sp.) and marine mammals (Weimerskirch et al., 1997; Niel and Lebreton, 2005; Wade, 1998). We suggest that the expected impact of lead poisoning on adult population size is a more appropriate metric for assessment of its importance than are additional mortality rates because it takes into account differences among species in the sensitivity of their population size to a given level of additional mortality. These differences sensitivity are attributable, to a large extent, to differences in life-history parameters, especially the annual survival rate and mean age at first breeding.

We note that lead poisoning of raptors and other birds is not a new phenomenon. Raptors in Europe have been exposed to substantial amounts of dietary lead derived from shotgun and rifle ammunition used in hunting for well over a century and all other exposure pathways also have a history spanning at least decades. For this reason, we suggest that the reductions in population size of European raptors estimated here have already occurred. Populations are likely to have begun to impacted by lead poisoning long ago and to have continued to be reduced, relative to their expected unimpacted state, for many decades. Population sizes are unlikely to be declining at present because of lead poisoning, because they have stabilised in the past at reduced levels through the operation of density-dependent processes. However, we would expect populations of the species currently most impacted by lead poisoning to be substantially larger if exposure to dietary lead could be reduced to a low level.

4.3. Association of geographical and temporal variation in the proportion of raptor deaths attributed to lead poisoning with exposure to spent lead ammunition from hunting

The hypothesis that lead poisoning of raptors is related to ammunition-derived lead from hunting receives some support from the possible relationship of interspecific variation in lead poisoning risk with diet differences described above. However, stronger evidence is provided by the significant positive correlation we found between variation among countries in estimates of the proportion of raptor deaths attributed to lead poisoning P_{Pb} and the mean number of hunters per unit area of the country. This hypothesis was also supported by finding that $P_{Pb}$was lower (zero) after the complete ban on lead shotgun ammunition was introduced in Denmark than expected from our regression model based upon data from countries without a complete ban (including pre-ban Denmark).

Although some raptors in Europe are likely to die from lead poisoning in circumstances where the principal source of lead to which they were exposed was something other than spent ammunition, we suggest that the proportion of such cases is likely to be small. This is supported by our analysis of variation among countries in P_{Pb} in relation to the country-specific density of hunters which indicates that the proportion of raptor deaths associated with clinical levels of lead in the liver would be expected to be very small in a hypothetical country with no hunters (see Fig. 1). In addition, a study found that about 90% of the lead in livers of common buzzards found dead in the UK with clinical liver concentrations had isotopic characteristics resembling those of lead from widely-used types of shotgun ammunition (Taggart et al., 2020).

4.4. Potential sources of bias in our assessment of the impact of lead poisoning

Our findings concerning the prevalence of lead poisoning as a cause of death of raptors might be biased by failure of either or both of our two principal assumptions: (1) that all raptors with liver lead levels above the clinical threshold are likely to have died from lead poisoning, but none of those below this threshold did so, and (2) that sampled raptors were representative of all deaths of wild birds of each species. We suggest that there are two reasons why our crude method of assigning all dead birds with liver lead levels above the threshold as lead poisoned and all of those with levels below the threshold as dying from something other than lead poisoning is likely to bias the estimate of the prevalence of lead poisoning downwards, making our estimates conservative. Firstly, it is likely that a proportion of birds with lead levels below the threshold died entirely or partly because of their exposure to lead. It is known that exposure to lead at levels below the threshold affects the immune system, which is likely to increase susceptibility to infectious disease, and alters locomotory behaviour, which might reduce ability to forage and increase the risk of flying accidents (e.g. Franson and Pain, 2011; Ecke et al., 2017; Kelly and Kelly, 2005; Vallverdú-Coll et al., 2015a, 2015b). It has long been known that some physiological effects of lead can occur at very low levels of exposure. For example, inhibition of the haem-biosynthetic enzyme delta-aminolevulinic acid dehydratase has been reported at blood lead concentrations <5 μg/dL (Pattee and Pain, 2003). Secondly, the shape of the log-normal distribution of liver lead concentrations usually found in raptors (e.g. Taggart et al., 2020) means that many more individuals have values close to, but below the threshold than have values close to, but above the clinical threshold. This is likely to result in numbers of 'false positives' from our method, if they occur (i.e. above-threshold birds that did not die from lead poisoning), being more than cancelled out by false negatives (Green et al., 2016b).

Our second key assumption was that the samples of dead wild raptors whose liver lead levels were determined are representative. Biases are likely to occur in the proportion of birds found dead with lead poisoning due to the nature of surveillance schemes. Many dead raptors are found and reported by members of the public. Hence, birds that die in areas of high human population density may predominate and these may have been disproportionately killed by vehicles or flying into overhead cables or other built structures. By contrast, much hunting and exposure of raptors to ammunition-derived lead takes place in areas with relatively low human population density. In addition, lead poisoning generally causes a chronic weakening in birds and sick and weakened birds have a tendency to hide to avoid potential predators (Friend and Franson, 1999). This may also result in poisoned birds being underreported. Hence, we conclude that bias due to failures of our two main assumptions are more likely to result in underestimation than overestimation of the prevalence of lead poisoning.

Our assessment of the likely effects of lead poisoning on population sizes of European raptors depend upon several simplifying assumptions about demographic rates and density dependence. Of these, the most likely to be influential are the assumptions made about the form and strength of density dependence and the stage or stages of life history upon which it operates. For simplicity, we assumed that only the per capita recruitment to the adult population of young adults was density-dependent and that it was affected only by the density of adults. This simplification seems to us to be reasonably well-supported by results from population studies of raptors (Newton, 1979), but the true situation will probably be different and more complicated for some species. Another important assumption is about the shape of the relationship between recruitment and adult density. As far as we know, this shape has never been determined rigorously using empirical data from field studies of raptor populations. We assumed an exponential relationship, which is a special case of a Weibull relationship with shape parameter $\alpha = 1$. Altering the assumed value of α upwards or downwards from one would increase or decrease the degree to which lead poisoning is expected to reduce adult population size (see Supplementary Fig. B4).

5. Conclusions

This is the first study to attempt an assessment of the impact of lead poisoning on population sizes of raptors throughout Europe. Our results indicate that that there are likely to be effects of lead poisoning on adult population size of up to 14% for individual species and estimated 55,000 fewer adults because of lead poisoning in European raptor species as a whole. Intraspecific and geographical variation in the prevalence and annual rate of mortality attributed to lead poisoning were related to variation in exposure to spent lead ammunition from hunting.

CRediT authorship contribution statement

Rhys Green: Conceptualization, Methodology, Software, Formal analysis, Writing, Reviewing and editing. **Deborah Pain:** Conceptualization, Methodology, Data curation, Original draft preparation, Writing, Reviewing and editing. **Oliver Krone:** Data curation, Reviewing and editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix. Supplementary data

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