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META-ANALYSIS

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Cause-specific mortality of the world's terrestrial vertebrates

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Abstract

Aim: Vertebrates are declining worldwide, yet a comprehensive examination of the sources of mortality is lacking. We conducted a global synthesis of terrestrial vertebrate cause-specific mortality to compare the sources of mortality across taxa and determine predictors of susceptibility to these sources of mortality.

Location: Worldwide.

Time period: 1970–2018.

Major taxa studied: Mammals, birds, reptiles and amphibians.

Methods: We searched for studies that used telemetry to determine the cause of death of terrestrial vertebrates. We determined whether each mortality was caused by anthropogenic or natural sources and further classified mortalities within these two categories (e.g. harvest, vehicle collision and predation). For each study, we determined the diet and average adult body mass of the species and whether the study site permitted hunting. Mortalities were separated into juvenile or adult age classes. We used linear mixed effects models to predict the percentage of mortality from each source and the overall magnitude of mortality based on these variables.

Results: We documented 42,755 mortalities of known cause from 120,657 individuals representing 305 vertebrate species in 1,114 studies. Overall, 28% of mortalities were directly caused by humans and 72% from natural sources. Predation (55%) and legal harvest (17%) were the leading sources of mortality.

Main conclusions: Humans were directly responsible for more than one-quarter of global terrestrial vertebrate mortality. Larger birds and mammals were harvested more often and suffered increased anthropogenic mortality. Anthropogenic mortality of mammals and birds outside areas that prohibited hunting was higher than within areas where hunting was prohibited. Mammals experienced shifts from predominately natural to anthropogenic mortality as they matured. Humans are a major contributor to terrestrial vertebrate mortality, potentially impacting evolutionary processes and ecosystem functioning.

KEYWORDS
amphibian, biodiversity, bird, conservation, mammal, reptile, telemetry

[Correction added on 8 February 2019, after first online publication: The word 'permitted' in the sentence "Anthropogenic mortality of mammals and birds..." under the Main conclusions of the Abstract section has been changed to 'prohibited'.]

1 | INTRODUCTION

Human activities impact an estimated 75% of the land surface of the Earth (Venter et al., 2016). There is a growing consensus that human impacts are so pervasive they have shifted the planet into a new geological epoch termed the "Anthropocene" (Waters et al., 2016). In addition to changes in atmospheric composition and the spread of invasive species, widespread faunal extinctions are a defining trait of this epoch (Waters et al., 2016). From 1980 to 2004, 662 amphibian, 223 bird and 156 mammal species moved one category closer to extinction on the International Union for Conservation of Nature Red List (Hoffmann et al., 2010). Extinction rates of vertebrates during the last century are up to 100 times greater than background levels (Ceballos et al., 2015), and overall, an estimated 41% of amphibian, 25% of mammalian and 13% of bird species are threatened with extinction (Hoffmann et al., 2010).

Illegal killing is one of the largest threats to mammals (Cardillo et al., 2005), and billions of vertebrates die each year collectively from collisions with buildings, power lines and vehicles (Forman & Alexander, 1998; Loss, Will, & Marra, 2015). Mammals are frequently killed when they are deemed a threat to people or their property (Treves & Karanth, 2003). Other animals are killed by indirect human causes, such as the introduction of invasive species and habitat loss (Loss, Will, & Marra, 2013). Although it is often assumed that humans are directly responsible for a substantial proportion of wildlife mortality, there has been limited systematic examination of mortality sources for animals worldwide to compare the magnitude of anthropogenic and natural mortality.

The use of telemetry to monitor the fate of animals can offer valuable insights into the relative magnitude of anthropogenic mortality because it provides less biased estimates of the causes of mortality than other techniques, such as opportunistic captures of marked animals (Kays, Crofoot, Jetz, & Wikelski, 2015; Naef-Daenzer, Korner-Nievergelt, Fiedler, & Grüebler, 2017). In a meta-analysis of adult medium- and large-sized North American mammals using telemetry studies that monitored the mortality of 1,874 individuals, Collins and Kays (2011) found that legal harvest and vehicle collisions collectively accounted for nearly half of all mortality. However, an understanding of the sources of mortality for other animal classes and for locations beyond North America is currently lacking. We addressed this gap in knowledge by conducting a comprehensive global synthesis of cause-specific mortality of terrestrial vertebrates. Our analysis expands on the work of Collins and Kays (2011) by: (a) increasing the geographical scope to the entire world, (b) increasing the taxonomic scope to all terrestrial vertebrates, and (c) increasing the demographic scope to juveniles in addition to adults.

2 | METHODS

We searched the following databases for studies of cause-specific mortality: JSTOR, BioOne, EBSCO Host, Google Scholar, Web of Science, ProQuest Dissertations and Theses, and SCOPUS. We searched documents for the terms "cause-specific mortality" or "telemetry" and "survival" or "telemetry" and "mortality". From the search results, we selected publications that met the following criteria: (a) used telemetry to track individuals, (b) attempted to locate carcasses of every dead individual to assign a cause of death, and (c) classified mortalities as being the result of natural or anthropogenic sources. We excluded studies of captive-reared, rehabilitated or translocated individuals, because these might not be representative of mortality of natural populations (Frair, Merrill, Allen, & Boyce, 2007). To ensure that the same individuals were not represented multiple times in the dataset, we excluded duplicates in which the same animals were used in multiple studies (i.e. the same species monitored in the same location over the same time period). The date range of studies in the analysis started at 1970, roughly the date when radio telemetry became common, and continued until February 2018 (Supporting Information Appendix S1, Figure S1.1).

For each study, we documented the species and age class (adult or juvenile) of study animals and classified mortalities as anthropogenic or natural, with categories within these divisions. Categories of anthropogenic mortality were legal harvest, illegal harvest, vehicle collision or other. Illegal harvest included cases where an animal was harvested on a site where harvest of the species was not permitted or was harvested outside the hunting season. Categories of natural mortalities were predation, disease, starvation, accident or other. For birds, we included an additional category of collisions with human-made structures (e.g. buildings, power lines and wind turbines) within anthropogenic mortality sources, and for mammals we included a category for management removal within anthropogenic mortality sources. For reptiles and amphibians, we used only the categories of total anthropogenic and total natural mortality because mortality from individual sources was infrequent.

We defined harvest policies for each study site as protected from harvest or unprotected from harvest. We defined sites protected from harvest as those that ban the harvest of all species year round, whereas sites unprotected from harvest permit the taking of at least one species (including species that were not tracked in the study) for some period during the year. We chose this classification because permitting hunting at a site might increase the risk of mortality from human sources owing to increased human access even if the species being studied cannot be harvested legally. We determined whether a site was protected from harvest using information available in the study or online reference material (e.g. harvest regulations listed on the webpages for publicly owned lands). We also documented the study year to examine how susceptibility to sources of mortality changed over time. We defined the study year as the midpoint of the time period over which the study took place. For each study species, we determined the average adult body mass and diet (carnivore, omnivore or herbivore) using the databases PanTHERIA (Jones et al., 2009) for mammals and EltonTraits 1.0 (Wilman et al., 2014) for birds. We used handbooks and field guides to derive these traits for reptiles and amphibians. We chose these variables because they can influence mortality. For example, larger animals are more likely to be harvested and to be considered a threat to humans (Jerozolimski & Peres, 2003; Linnell, Odden, Smith, Aanes, & Swenson, 1999;

Michalski, Boulhosa, Faria, & Peres, 2006). Diet has also been shown to influence susceptibility to predation and vehicle collisions (Collins & Kays, 2011; Cook & Blumstein, 2013).

We used linear mixed effects models to determine the best set of predictor variables for the proportion of mortality from each of the aforementioned mortality sources (i.e. number of individuals dying from the specific mortality source divided by number dying from all known causes). Our initial set of models for each taxonomic class included diet, age (juvenile or adult), study year and harvest regulations (protected from harvest or not protected from harvest) as fixed effects. We included taxonomy as a nested random effect (i.e. Order:Family:Genus:Species; Tucker et al., 2018) to control for phylogenetic relatedness and accounted for spatial autocorrelation by incorporating a Gaussian spatial autocorrelation structure using the coordinates of each study site (Dormann et al., 2007). Given that adults and juveniles often vary in their susceptibility to different sources of mortality, we did not include studies in our analysis that did not separate mortalities by age class. We ran another analysis using the same predictors and changed the response variable to the magnitude of mortality (i.e. number of individuals dying from any cause divided by number of individuals monitored). For this analysis, we excluded studies that did not document the number of monitored individuals.

We performed the same analyses using adults only, including $\log_{10}$-transformed body mass as a predictor and removing age, but keeping all other variables the same. We did not include the mass of juveniles as a variable because individuals classified as juveniles within the same species often spanned a range of developmental stages (e.g. fawn, yearling and subadult for deer), thus a single mass value would not adequately reflect the mass of the animals for which mortalities were documented. Given that our final dataset was biased towards studies in North America, we also ran a subset of the models using only studies that took place outside North America. We did not run a set of models incorporating age class for reptiles or amphibians because there were very few juvenile mortalities documented for reptiles and none for amphibians. Given that we represent the mortality data as proportions, we performed a logit transformation of the data before analyses (Warton & Hui, 2011).

We calculated the sample size-corrected Akaike's information criterion (AIC_c) for all possible model combinations. For each model combination set, we considered the best-approximating model as the model with the lowest AIC_c, and the difference in AIC_c values between this model and all additive model combinations (represented by Δ_i) was calculated (Burnham & Anderson, 2002). Only models with $\Delta_i \leq 2$ were selected for further consideration (Burnham & Anderson, 2002). We calculated Akaike weights (w_i) for candidate models to examine the relative weight of evidence for each model. If the best-approximating model, per model set, had a small w_i ($w_{ibest} <$ 0.9), we used multi-model inference to calculate a weighted average of parameter estimates with 85% confidence intervals (CIs) across competing models (Arnold, 2010; Burnham & Anderson, 2002).

3 | RESULTS

We compiled a dataset consisting of 1,114 studies that collectively monitored the fates of 120,657 animals representing 305 vertebrate species (Figure 1; Supporting Information Appendix S1–S2, Table S1.1; a list of data sources is provided in Appendix 1). From this, we determined 48,791 total mortalities, 42,755 of which had a

FIGURE 1 Locations of studies of cause-specific mortality of terrestrial vertebrates used for analysis

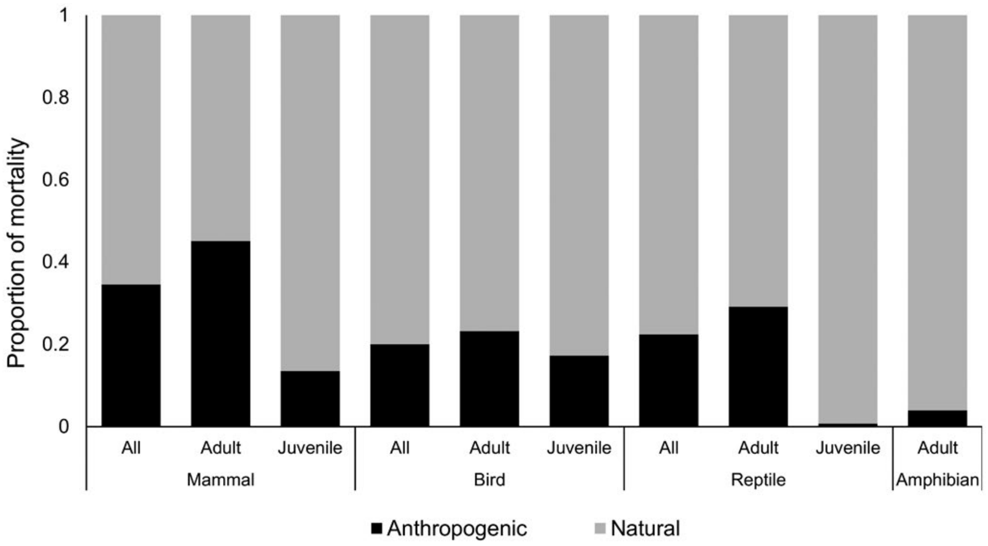

FIGURE 2 Natural versus anthropogenic sources of mortality for terrestrial vertebrates

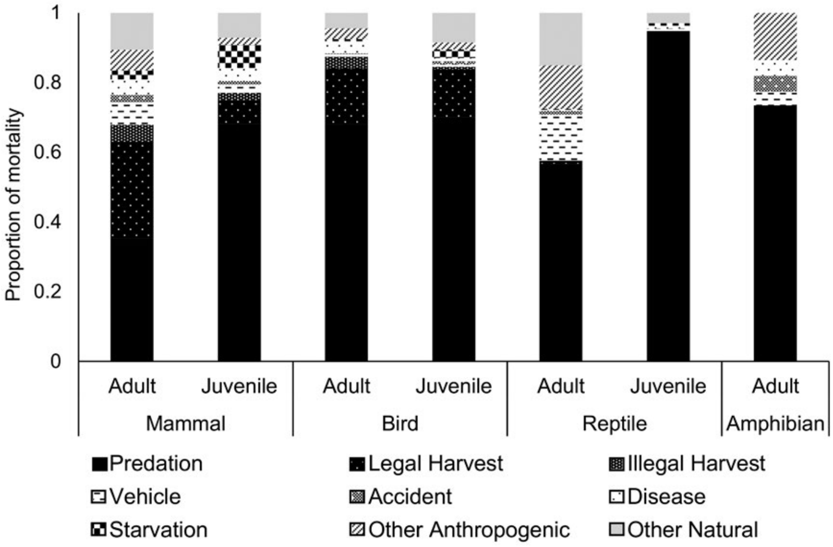

FIGURE 3 Proportion of causes of mortality for taxonomic classes of terrestrial vertebrates

known cause. Overall, 28% of total mortality was directly caused by humans, whereas 72% of mortality was the result of natural causes (Figure 2). The single largest source of mortality was predation (55%), followed by legal harvest (17%; Figure 3; Supporting Information Appendix S1, Table S1.2). All other sources of mortality, including vehicle collisions, illegal harvest, starvation, accidents and disease, each accounted for < 10% of total mortality (Supporting Information Appendix S1, Table S1.2).

Among mammals, juveniles were less likely than adults to die from anthropogenic causes ($\beta = -0.719$; 85% CI = −0.8394, −0.6845; marginal $R^2 = 0.064$). Juveniles were more likely to die from predation ($\beta = 0.5242$; 85% CI = 0.4528, 0.5956; marginal $R^2 = 0.080$), but less likely to die from harvest ($\beta = -0.5764$; 85% CI = −0.6420, −0.5108; marginal $R^2 = 0.042$). Juvenile birds were not more likely to die from anthropogenic causes overall than adults ($\beta = -0.0054$; 85% CI = −0.0441, 0.033; marginal $R^2 = 0.004$), but were less likely to

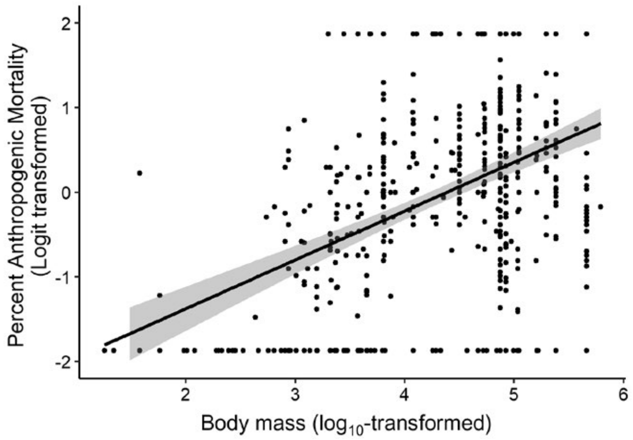

FIGURE 4 Percentage of anthropogenic mortality as a function of body mass for adult mammals

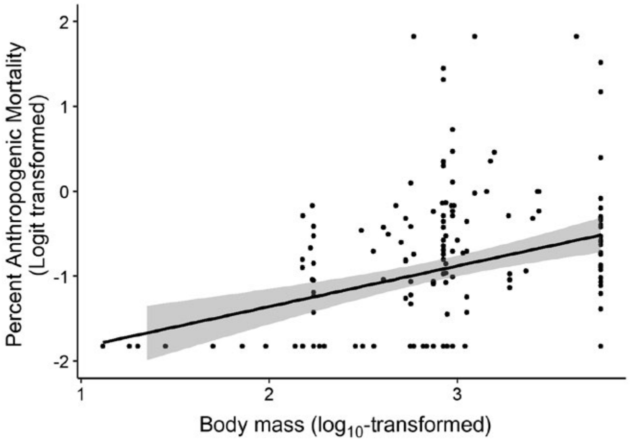

FIGURE 5 Percentage of anthropogenic mortality as a function of body mass for adult birds

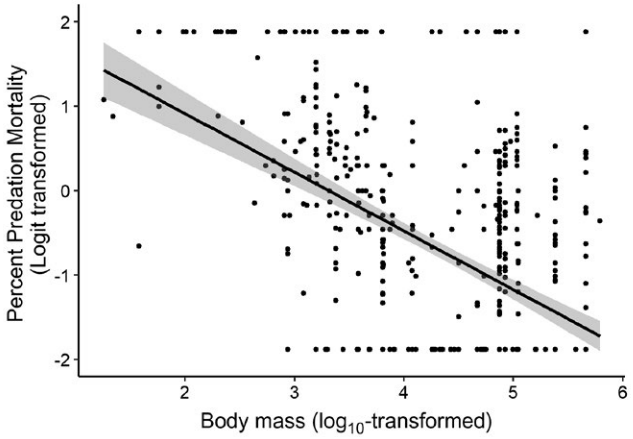

FIGURE 7 Percentage of predation mortality as a function of body mass for adult mammals

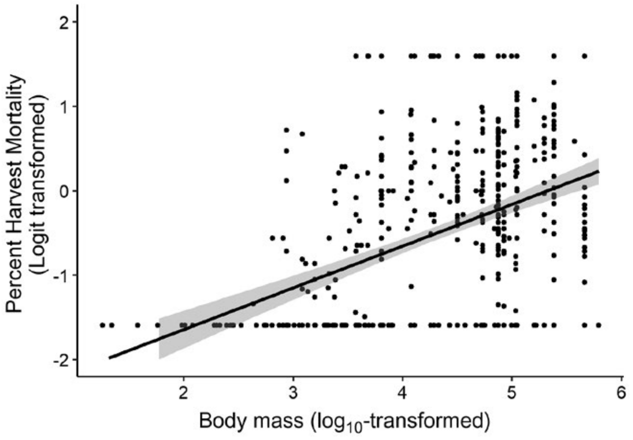

FIGURE 6 Percentage of harvest mortality (legal and illegal) as a function of body mass for adult mammals

die from harvest ($\beta = -0.0979$; 85% CI = −0.1583, −0.0374; marginal $R^2 = 0.004$).

Anthropogenic mortality increased with increasing body mass for mammals ($\beta = 0.5529$; 85% CI = 0.4493, 0.6564; marginal R^2 = 0.073; Figure 4) and birds ($\beta = 0.5806$; 85% CI = 0.3973, 0.7639; marginal R^2 = 0.049; Figure 5). Harvest mortality also increased with increasing body mass for birds ($\beta = 0.3360$; 85% CI = 0.1583, 0.5136; marginal R^2 = 0.029) and mammals ($\beta = 0.4620$; 85% CI = 0.3710, 0.5530; marginal R^2 = 0.061; Figure 6). Larger mammals were more likely to be killed than smaller mammals through management removal ($\beta = 0.0312$; 85% CI = 0.0115, 0.0509; marginal R^2 = 0.023) and were less likely to die from predation ($\beta = -0.7541$; 85% CI = −0.8691, −0.6391; marginal R^2 = 0.130; Figure 7). Larger birds were more likely to die from vehicle mortality ($\beta = 0.2284$; 85% CI = 0.2274, 0.2294; marginal R^2 = 0.014) and collisions with human-made structures ($\beta = 0.3603$; 85% CI = 0.1866, 0.5340; marginal $R^2 > 0.001$) than smaller birds. Carnivorous birds were more likely than omnivores to die from vehicle mortality ($\beta = 0.2612$; 85% CI = 0.0954, 0.4269; marginal R^2 = 0.010).

The percentage of anthropogenic mortality of mammals ($\beta = -0.4422$; 85% CI = −0.6254, −0.2591; marginal R^2 = 0.064) and birds ($\beta = -0.5144$; 85% CI = −0.8689, −0.1599; marginal R^2 = 0.004) was lower in areas where harvest was prohibited than in areas where it was allowed. However, protection from harvest was not a parameter in top models of illegal harvest for mammals and did not significantly influence illegal harvest of birds ($\beta = -0.0027$; 85% CI= −0.0192, 0.0138). Protection from harvest did not influence the magnitude of mortality for mammals ($\beta = -0.0427$; 85% CI = −0.1257, 0.0404) or birds ($\beta = -0.0253$; 85% CI = −0.1449, 0.0943). Among mammals, vehicle mortality increased over time ($\beta = 0.0026$; 85% CI = 0.0011, 0.0041; marginal R^2 = 0.003), whereas predation mortality of adults decreased ($\beta = -0.0078$; 85% CI= −0.0132, −0.0022; marginal R^2 = 0.130). Year was not a significant predictor of the magnitude of mortality for any taxa.

When examining only studies outside North America, we found that juvenile mammals were less likely to die from anthropogenic sources of mortality than adults ($\beta = -0.4308$; 85% CI = −0.6256, −0.2360), as were juvenile birds ($\beta = -0.4325$; 85% CI = −0.6683, −0.1967). Juvenile mammals were more likely to die from predation ($\beta = 0.2062$; 85% CI 0.1153, 0.2970) but less likely to die from harvest compared with adult mammals ($\beta = -0.3544$; 85% CI = −0.5260, −0.1827). Among adult mammals outside North America, mortality from harvest ($\beta = 0.5300$; 85% CI = 0.3787, 0.6813) and anthropogenic causes ($\beta = 0.5279$; 85% CI = 0.0023, 0.5302) increased with increasing body mass, whereas predation mortality decreased ($\beta = -0.7219$; 85% CI = −0.9312, −0.5126). Results of all models and R^2 values are reported in Supporting Information Appendix S1, Tables S1.4–S1.32. The significance of parameter estimates is detailed in Tables 1 and 2.

4 | DISCUSSION

We found that humans were directly responsible for more than one-quarter of terrestrial vertebrate mortality worldwide. However, the

TABLE 1 Parameter estimates for models of mortality sources and magnitude of mortality for birds and mammals (adults and juveniles combined)

		Age: Juvenile	Diet: Carnivore	Diet: Herbivore	Protected from harvest	Year
Mammals	Total human	−0.7619	0.7760	−0.3000	−0.4422	0.0003
	Total natural	0.7619	−0.7760	0.3000	0.4422	−0.0003
	Total harvest	−0.5764	0.5909	−0.0228	−0.3593	−0.0029
	Legal harvest	−0.4199	0.1599	0.0116	−0.3374	−0.0010
	Illegal harvest	−0.0816	0.2570	−0.0117		−0.0018
	Vehicle	−0.0649	0.0060	−0.0245	−0.0022	0.0026
	Management	−0.0150	−0.0353	−0.0634	0.0594	0.0000
	Predation	0.5242	−1.0221	0.2686	0.0949	
	Magnitude	0.2092	0.1524	0.1633	−0.0427	−0.0008
Birds	Total human	−0.0054			−0.5144	−0.0085
	Total natural	0.0054			0.5144	0.0085
	Total harvest	−0.0979	−0.2022	0.1580	−0.0601	−0.0151
	Legal harvest	0.0260	−0.1327	0.2195	−0.0540	−0.0127
	Illegal harvest	−0.0101			−0.0027	−0.0046
	Vehicle	−0.0365	0.2612	−0.0233	−0.0871	−0.0015
	Collision	0.0028			−0.0414	0.0005
	Predation	−0.1140	−0.7064	−0.0118	0.2127	0.0118
	Magnitude	0.1902	−0.0460	0.1743	−0.0253	−0.0020

Note. Values in blue have $p < 0.15$, values in yellow have $p < 0.05$, and values in red have $p < 0.001$. Boxes in grey did not include the variable in models with difference in sample size-corrected Akaike's information criterion less than or equal to 2 from the top model for the mortality source. [Colour table can be viewed at wileyonlinelibrary.com]

amount of total anthropogenic mortality is likely to be higher than we reported when indirect impacts, such as the introduction of invasive species, habitat loss and poisoning, are considered. A mortality we classified as natural could have been the result of human activities, and several studies in our analysis explicitly addressed this issue. For example, the largest source of mortality for the endangered Lower Keys marsh rabbit (*Sylvilagus palustris*) was predation by feral cats (Forys & Humphrey, 1999), which are estimated to kill billions of birds and mammals annually (Loss et al., 2013). Likewise, predation mortality of Lumhultz's tree kangaroos (*Dendrolagus lumholtzi*) increased after clearcutting removed tree cover and left them vulnerable to predators (Newell, 1999). Fishers (*Pekania pennati*) died from seemingly natural causes after exposure to toxicants caused by consuming prey that had ingested rodenticide (Thompson et al., 2014). In cases of poisoning, human impacts underlying the proximate mortality cause may go undiagnosed, particularly when investigations of mortality rely on field post-mortem examinations (Thompson et al., 2014). Thus, our classification of anthropogenic and natural mortalities does not fully convey the extent of anthropogenic mortality and is likely to underestimate the degree to which human activities result in the death of wildlife.

Legal harvest constituted the single greatest source of anthropogenic mortality of wildlife. Harvest can affect population dynamics and exacerbate the severity of stochastic environmental events even when regulated (Wright, Peterson, Smith, & Lemke, 2006). Larger bird and mammal species might have been more susceptible to harvest than smaller ones because larger animals provide hunters with more meat per unit effort, leading to increased hunting pressure on these species. Neotropical hunters, for example, show a marked increase in selectivity for prey species > 6.5 kg, and prey mass explained up to 83% of variation in hunter selectivity (Jerozolimski & Peres, 2003). Larger game species in Africa are also more valued by hunters because trophy size generally increases with body mass (Johnson, Kansky, Loveridge, & Macdonald, 2010). Larger mammal species were more likely to experience mortality from management removal (i.e. killed in accordance with a depredation permit or in defence of life or property). Among birds and mammals, species with greater body mass experienced increased anthropogenic mortality, suggesting that they are disproportionately killed as a direct result of human activities.

Areas that prohibited hunting reduced the proportion of anthropogenic mortality for birds and mammals, but did not influence the amount of mortality of either taxa. This could have resulted from animals leaving the boundaries of areas protected from harvest and coming into conflict with humans (Woodroffe & Ginsberg, 1998). Additionally, in some areas, human populations increase disproportionately along the borders of areas where harvest is prohibited, mitigating their effectiveness at preserving biodiversity (Wittemyer, Elsen, Bean, Burton, & Brashares, 2008). Protecting areas from harvest was also not successful in preventing illegal

TABLE 2 Parameter estimates for models of the sources of mortality and the magnitude of mortality for mammals, birds, reptiles and amphibians (adults only)

		Mass	Diet: Carnivore	Diet: Herbivore	Protected from harvest	Year
Mammals	Total human	0.5529	0.4178	−0.4793	−0.4961	0.0004
	Total natural	−0.5529	−0.4178	0.4793	0.4961	−0.0004
	Total harvest	0.4620	0.3600	−0.1451	−0.4103	−0.0023
	Legal harvest	0.2989	0.0307	−0.0160	−0.3690	0.0007
	Illegal harvest	0.1140	0.1848	−0.0403	0.0028	−0.0018
	Vehicle	0.0037				0.0047
	Management	0.0312	0.0191	−0.0738	0.0149	
	Predation	−0.7541	−0.5548	0.5411	0.1313	−0.0078
	Magnitude	−0.0975	0.1793	0.1718	−0.0412	−0.0016
Birds	Total human	0.5806				−0.0032
	Total natural	−0.5806				0.0032
	Total harvest	0.336	−0.0348	0.0068		−0.0074
	Legal harvest	0.0914	−0.0099	0.1443		−0.0025
	Illegal harvest	0.2629	−0.0454	−0.0553	0.0854	−0.011
	Vehicle	0.2284	0.1891	−0.1535		
	Collision	0.3603			0.1142	
	Predation	−0.6162	0.0529	0.251		0.0071
	Magnitude	0.0603	−0.0856	0.1067		−0.0005
Reptiles	Total human	0.1462				−0.1038
	Total natural	−0.1462				0.1038
Amphibians	Total human					
	Total natural					

Note. Values in yellow have $p < 0.05$, and values in red have $p < 0.001$. Boxes in grey did not include the variable in models with difference in sample size-corrected Akaike's information criterion less than or equal to 2 from the top model for the mortality source. [Colour table can be viewed at wileyonlinelibrary.com]

harvest of birds or mammals, because harvest status was not a significant predictor of poaching mortality for either taxa. This might result from a higher density of animals in protected areas, which could inadvertently incentivize poaching in such places (Jachmann, 2008). Our results indicate that preventing harvest might have the potential to reduce anthropogenic mortality, but its effectiveness is likely to vary based on factors such as location and target species.

Larger birds were more likely to die from collisions with vehicles or with human-made structures. The latter included mortality from electrocution, which often impacts larger birds because larger wingspans increase the likelihood of touching multiple parts of a power line simultaneously (Janss, 2000). The largest species in our dataset were wild turkeys (*Meleagris gallopovo*), and large terrestrial birds might be particularly susceptible to collisions with structures owing to lack of maneuverability in flight (Bevanger, 1998; Shaw, Jenkins, Ryan, & Smallie, 2010). Large predatory birds also have increased vulnerability to many types of collisions because they have reduced vigilance as a result of being a top predator and might be less aware of structures owing to fixation on prey while hunting (Shaw & McKee, 2008).

Most sources of mortality did not change significantly over the time period encompassed by our dataset, because study year was infrequently a significant predictor of mortality for any source. The percentage of mammals dying from vehicle collisions increased over time, which might be a result of the increase in road networks or human population over this time period (Cohen, 2003; National Research Council, 2005). Predation mortality of adult mammals decreased significantly over time, potentially as a result of extirpation of top predators, which decreased prevalence of mortality from predation (Crooks & Soulé, 1999; Estes et al., 2011). The overall magnitude of mortality from 1970 to 2018 did not change significantly for any taxa, indicating that anthropogenic mortality of wildlife could be largely compensatory. Alternatively, advancements in technology could have increased survivorship of tracked animals through use of smaller devices and more efficient deployment over time. If this is the case, increasing survivorship of tracked animals might have masked true increases in wildlife mortality that occurred concurrently.

The high proportions of natural mortality we documented differ from the results of Collins and Kays (2011), probably as a consequence of additional taxa, juveniles and increased geographical scope, which resulted in a > 22-fold increase in mortality events examined. Considering only adult mammals from North America, the extent of the former study, we also found anthropogenic and natural mortality to be roughly equal (55 and 45%, respectively), but we found that juvenile mammals had greater natural mortality. Adult mammals were more likely to die from harvest and vehicle collisions, whereas juveniles were more likely to die from predation. As they mature, mammals experience a shift from predominately natural to predominately anthropogenic sources of mortality, probably driven by hunter selectivity of adults over juveniles (Mysterud, Tryjanowski, & Panek, 2006).

Our results might have been influenced by both geographical and taxonomic biases in coverage of cause-specific mortality studies. Studies from North America made up 85% of our dataset, which could have influenced our estimates of mortality, especially for poaching. The illegal trade and consumption of wildlife is widespread across Africa, but < 2% of our studies were from this continent (Brashares, Golden, Weinbaum, Barrett, & Okello, 2011). Rosen and Smith (2010) traced the majority of seized illegal wildlife to Southeast Asia, another area poorly represented in our dataset. However, when we examined studies of mammals outside North America, many of the same trends were found as with the entire dataset, such as increased anthropogenic mortality of adults compared with juveniles and increasing anthropogenic mortality with increasing body mass. Thus, we believe that many of our conclusions are applicable to vertebrate species worldwide, despite geographical biases in the dataset.

In addition to geographical biases, there was a taxonomic bias towards animals that are harvested, particularly from the orders Carnivora and Artiodactyla, which collectively constituted 53% of our studies and 44% of individuals monitored overall (Supporting Information Appendix S1, Table S1.1). In contrast, some orders, such as Primates and Chiroptera, were entirely absent. In its early years, wildlife management was closely related to game management; therefore, research was focused on groups such as ungulates and predators that were harvested (Collins & Kays, 2011). This might have caused an overestimate of the amount of anthropogenic mortality because the dataset is biased towards game animals (Supporting Information Appendix S1, Table S1.3). Earlier studies might also have been biased owing to limitations of telemetry technology at the time. Radio collars attached to animals are generally < 5% of the individual's body mass, and as the size of tags has decreased over time, it has become possible to track increasingly smaller animals (Kays et al., 2015). Thus, our conclusions might have also been influenced by the disproportionate number of larger species present in our dataset.

Although we believe that telemetry studies provide the most accurate data on cause-specific mortality, we acknowledge that this methodology is not without biases. Attaching a radio tag to an animal requires trapping it, and there are often differences in capturability among individuals. For example, individuals prone to risk-taking might be more likely to be caught in traps (Biro & Dingemanse, 2009; Boon, Réale, & Boutin, 2008). Certain demographic groups might also be more prone to capture based on factors such as home range size (Buskirk & Lindstedt, 1989). If differences in capturability are correlated with susceptibility to particular sources of mortality, estimates of cause-specific mortality could be biased because the animals tracked are not a representative sample of the population.

We recognize that many of the R^2 values for our models are relatively low (< 0.10). However, this is not unexpected because our study was not a highly controlled experiment, but rather a large compilation of studies with a temporal span of > 45 years and a geographical range that encompassed the entire globe. Although we attempted to control for spatial and temporal autocorrelation, there are a number of site-specific factors for which we were undoubtedly unable to control. The presence of significant parameter estimates despite such a complex dataset indicates that these are probably accurate and ecologically relevant trends. Moreover, many of our major conclusions, such as the increase of anthropogenic mortality with body size for mammals and birds, are supported by highly significant p-values < 0.001. Thus, despite low R^2 values, we believe that our results can provide valuable insights into the susceptibility of terrestrial vertebrates to anthropogenic causes of mortality.

Humans directly cause more than one-quarter of terrestrial vertebrate mortality worldwide, potentially exerting selective pressures on wildlife populations. Hunter selection of bighorn rams with larger horn sizes, for example, led to increased prevalence of smaller rams with shorter horn lengths (Coltman et al., 2003). This selection may impact population viability, because body size may be correlated with traits that impact survival (Coltman, Pilkington, Kruuk, Wilson, & Pemberton, 2001). Hunting might also induce selection of behavioural traits, because hunters have been shown disproportionately to harvest animals that exhibit bolder behaviour and have increased movement rates (Ciuti et al., 2012). Hunters can also impact population dynamics by selecting individuals from different demographic groups more often than natural predators (Wright et al., 2006). Anthropogenic mortality might affect ecosystem structure and functioning via the extirpation of vertebrates that disperse seeds (Peres & Palacios, 2007), consume carcasses (Hill, DeVault, Beasley, Rhodes, & Belant, 2018) and provide other essential ecosystem services (Şekercioğlu, Wenny, & Whelan, 2016). The magnitude of anthropogenic mortality of wildlife across the globe is substantial and undoubtedly has ecological ramifications that extend beyond the individual animals that are killed.

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DATA ACCESSIBILITY

All data are contained in the Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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