Mammal Review

Saving Britain's Wildlife

REVIEW OPEN ACCESS

Patterns and Determinants of Mortality in Grey Wolves (*Canis lupus*)

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Received: 8 April 2025 | **Revised:** 8 August 2025 | **Accepted:** 14 August 2025

Funding: This work was supported by Spanish Ministry of Science and Innovation and Universities (CGL2017-83045-R, PRE2018-086102, RYC2021-033192-I, JDC2023-050355-I) and Junta de Andalucía, Consejería de Universidad, Investigación e Innovación (QUAL21 020 EBD).

Keywords: human-dominated landscapes | human-wildlife conflict | hunting | large carnivores | poaching

ABSTRACT

Background: Understanding mortality is crucial to predict the dynamics of animal populations, especially for long-lived species subjected to widespread human pressure. This is the case for the grey wolf (*Canis lupus*), yet local studies provide an incomplete view of the patterns and determinants of this process.

Aims and Methods: We conducted a systematic review of the existing literature on grey wolf mortality across the species' distribution range (i.e., most of the Northern Hemisphere) to identify global patterns and potential differences across continents. Studies were analysed based on the type of information provided, including mortality rates, proportion of dead individuals by cause, and natural and human-related determinants of mortality.

Results and Discussion: We found high global minimum annual mortality rates in wolves (0.31 ± 0.18), compared to those reported under low human persecution (<0.2). Most deaths were linked to human activities, primarily deliberate (legal and illegal) killing ($60\% \pm 25\%$). Europe reported a higher percentage of human-related deaths ($86\% \pm 14\%$) than North America ($66\% \pm 24\%$). This is likely due to higher anthropogenic pressures in Europe and differences in carcass detection methods between continents (opportunistic recovery in Europe vs. tracking of collared wolves in North America). However, the lack of data from areas with low human influence (e.g., the Arctic and deserts) limits our understanding of the natural dynamics of mortality in the species. We found that many individual, social and environmental variables determine mortality values, and our global perspective allowed us to disentangle long-standing debates in large carnivore ecology, including support for the hypothesis that human-caused and natural mortality are additive.

Conclusion: Our review provides the baseline framework and a standardised global dataset to guide future research and policy-making on large carnivore conservation, emphasising the increased risk of mortality for wolves living alongside humans, an issue that may be particularly overlooked as populations expand.

1 | Introduction

Mortality shapes the dynamics of all wildlife populations (Crone 2001; Moore et al. 2023; Nisi et al. 2023). When deaths exceed natural expectations, they can drive negative population trends towards extinction (Benson et al. 2020; Ash et al. 2022), reduce genetic diversity (Jackson and Fahrig 2011), and disrupt key demographic processes such as reproduction

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(Wielgus and Bunnell 2000; Dahl et al. 2012; Paniw et al. 2019) and dispersal (Morales-González et al. 2022). This in turn may hamper the ecological functioning of species, particularly those with naturally low mortality rates (Kuijper et al. 2016; Ordiz et al. 2013). Understanding the magnitude and sources of mortality is a pressing global challenge, essencial for accurately predicting population dynamics and devising evidence-based management decisions (Loss et al. 2012; Darimont et al. 2015; Hill et al. 2019).

In a world experiencing increasing human-related pressures, species face both direct and indirect risks of mortality derived from human activities (Di Marco et al. 2015). For instance, habitat modification linked to the exploitation of resources (Crooks et al. 2017), the introduction of invasive species (Pyšek et al. 2020) and direct persecution of species subject to human-wildlife conflicts (Woodroffe 2000; Yusefi et al. 2022; Bond et al. 2023) are considered to be main threats for wildlife globally.

In addition to human-related causes, natural drivers of mortality vary among species (Snyder-Mackler et al. 2020). In group-dwelling species, the survival of individuals generally depends on factors related to the group performance at finding food, raising young and defending the territory (Alexander 1974). The intricate social interactions and distribution of roles between group members entail a high complexity of mortality patterns (Snyder-Mackler et al. 2020). For instance, the death of one of the breeders or a significant reduction in group size during the breeding season can compromise offspring survival (Borg et al. 2015). Group size also influences space use strategies (e.g., average distance travelled) and glucocorticoid levels, thus affecting health status and mortality risk (Markham et al. 2015). On the other hand, social proximity can result in fast pathogen transmission and mortality by disease outbreaks (Kappeler et al. 2015), and particularities of the social status and age categories can result in different mortality rates (Snyder-Mackler et al. 2020).

The grey wolf *Canis lupus* is a social canid species structured in family groups known as packs, that commonly consist of a breeding pair (the basic social unit) and their annual offspring, although they can include multi-year offspring and rarely >1 breeding pair (Tallian et al. 2023). The offspring often disperse at sexual maturity to form new packs or join existing packs (Morales-González et al. 2022). The wolf is also a large carnivore that occasionally predate upon livestock and is often viewed as a competitor with humans for game species (Graham et al. 2005). This has fuelled a deep-rooted hostility towards the species in human history and culture (at least in western culture in recent historic times) so that there has commonly been an intention to increase their mortality levels, unlike other species where human-related mortality is unintentional (Wolf and Ripple 2017). During the 19th century, wolves were eradicated from many parts of their former range that extended across the northern hemisphere, only persisting in areas with low human accessibility (Paquet and Carbyn 2003). Although they have remarkably recolonised areas with widespread human presence during the last decades, and most populations are currently increasing (Chapron et al. 2014; Kaczensky et al. 2024), many populations remain subject to lethal management (i.e., culling, harvest and hunting) and high levels of illegal killing (Creel and Rotella 2010; Tallian et al. 2023), which can have detrimental effects on population persistence (Nowak and Mysłajek 2017).

Despite the wide availability of information in the scientific literature on wolf mortality (Person and Russell 2008; Ausband, Mitchell, Stansbury, et al. 2017; Barber-Meyer et al. 2021), such information is scattered and unlinked across the literature, making it difficult to fully understand how human-related and natural factors shape mortality patterns. The information comes from very different study areas in terms of landscape configuration, human pressures and wolf densities among other factors. In addition, the use of different monitoring technologies and statistical analyses influence the results. For example, they can introduce variability in demographic estimates, which can hinder comparisons across studies (Morales-González et al. 2022). Identifying general patterns and determinants of wolf mortality requires us to synthesise and provide a critical appraisal of all available information as a whole. Interestingly, continental-scale differences may also arise, as documented for reproduction in brown bears (*Ursus arctos*), where a longer history of persecution in Europe may explain their larger litters (Zedrosser et al. 2011). Providing a worldwide framework on wolf mortality processes is much needed to quantify the costs of living alongside humans for a large carnivore, contextualise the current trend of expansion of wolf populations (Kaczensky et al. 2024) and to improve population projection models, thus allowing us to prioritise management and conservation actions (Urban et al. 2016).

Here, we provide a synthesis of the existing literature on grey wolf mortality with the following objectives, to identify the: (i) potential spatial biases on wolf mortality research; (ii) existing variability on annual mortality rates globally, potential differences between North America and Europe, and existing differences between individual status and between age categories; (iii) existing variability on the proportion of dead individuals by cause globally, and potential differences between North America and Europe; (iv) whole set of natural and human-related determinants (i.e., influential factors) of mortality, and the effect that each one of them has on mortality; and (v) knowledge gaps and future research needs.

2 | Methods

We conducted a systematic review of the literature on grey wolf mortality across its distribution range. We followed similar procedures to a previous review on grey wolf dispersal (Morales-González et al. 2022). We located studies using Elsevier's *Scopus* database and multiple terms that represent different parameters of grey wolf demography, including mortality: ("grey wolf" OR "*Canis lupus*") AND ("demography" OR "demographic" OR "population" OR "density" OR "abundance" OR "survival" OR "survive" OR "mortality" OR "die" OR "reproduction" OR "reproductive" OR "reproduce" OR "movement" OR "move" OR "dispersal" OR "emigration" OR "immigration" OR "solitary" OR "lone" OR "mating" OR "pregnancy" OR "birth" OR "denning" OR "breeding" OR "rendezvous" OR "maturity" OR "recruitment" OR "home range" OR "core area" OR "litter size" OR "pack size" OR "collar" OR "telemetry"). We only reviewed studies in which the authors referred to the study species as *Canis lupus*, thereby avoiding taxonomic debate surrounding other wolf-like canids (see Von Holdt et al. 2016). A first search was done for the title, keywords and abstract of articles in English published before 2020. We sorted the search results by relevance (i.e., articles that most closely matched the searched words) and reviewed the first most relevant 250 studies. The same search was performed for the period January 2020 to October 2024 and, in this case, all the resulting articles were reviewed. We also searched for the bibliography provided in the reference section of all retrieved articles (Morales-González et al. 2022). This included grey literature previously cited, which we did not exclude as it may contain valuable information not found in peer-reviewed articles. The publications with mortality information were retained, categorised and examined according to the type of information included: (1) rates of mortality; (2) proportion of dead individuals by cause; and (3) natural and human-related determinants of mortality (i.e., any natural or human-related factor that influences mortality). Publications that addressed several topics were included in more than one category. All retained publications are listed in Table S1, with those corresponding to grey literature ($n=4$) highlighted. We present a critical appraisal of all collected information.

2.1 | Identifying Spatial Biases on Mortality Research

To identify potential spatial biases on wolf mortality research, we recorded for each study the name of the study area/s given by the authors (hereafter referred to as location; e.g., "Superior National Forest, Minnesota"). For continents with information from more than five studies (i.e., North America and Europe), we plotted in a continental map how many studies were located within the following areas: western Canada, eastern Canada, Alaska, Rocky Mountains States and Great Lakes States in North America; and each of the nine populations described by Kaczensky et al. 2021 in Europe (i.e., north-western Iberia, Alpine, Italian Peninsula, Dinaric-Balkan, Carpathian, Baltic, Central European, Scandinavian, Karelian). In contrast to Europe, wolf distribution in North America is mostly continuous, i.e., there is no description of different populations. We specified the location/s assigned to each study in Table S1.

2.2 | Standardising Data on Mortality Rates

For each study we extracted the annual rates of mortality provided by the authors. If the study provided the annual rate of survival, we used the inverse value. For the few studies (<10 studies) that provided the rate for a time period other than annual, we raised it to the corresponding value to obtain the annual rate (e.g., we raised monthly survival rates to ^12 to obtain annual survival rates). We recorded if the rate corresponded to residents, dispersers or an unspecific status; and if the rate corresponded to pups (wolves <12 months), yearlings (12–24 months), adults (≥ 24 months) or an unspecific age class. For each rate we retained information on the location, time period and methodology used. If a study provided two or more rates that differed on the location, time period and/or methodology used, we retained all of them. For residents, pups and adults, we retained several rates if they were provided per specific status (e.g., breeders and non-breeders), per month interval (e.g., from June to December) and for senescent wolves within adults (i.e., wolves >7 years old). If the study provided rates per any other classification (e.g., per sex or group size), per year, or per age within adults, we used the mean value. If the study provided an overall rate and status (or/and age class) specific rates, we retained only the latter. We categorised the methodology that authors used to obtain each rate into: (i) Heisey-Fuller method (Heisey and Fuller 1985), i.e., a simple cumulative survival estimator where survival rate over a discrete time unit, e.g., a day, is determined from the number of death events per radio-days (we also included rates obtained by the analogous method proposed by Trent and Rongstad 1974, that uses a piecewise exponential model); (ii) Kaplan–Meier method (Kaplan and Meier 1958), which differs from Heisey-Fuller in considering the specific timing of death events in defining the survivor function (Murray 2006); (iii) Proportions, e.g., proportions based on the number of pup counts between specific dates (Nowak and Mysłajek 2016) and proportion of monitored wolves that died per year (Treves, Langenberg, et al. 2017); (iv) Modelling approaches, e.g., Cox Proportional Hazards (O'Neil et al. 2017); and (v) Other methods, e.g., Lunn-McNeil (Murray et al. 2010) and Heisey-Patterson approaches (Liberg et al. 2012). We did not convert to annual rates those provided as the proportion of wolves monitored that died during a given study period as the number of wolves monitored and dead each year was unknown. We provide the raw and standardised data per study in Table S2.

2.3 | Standardising Data on the Proportion of Dead Individuals by Cause

For each study we considered the total number of known dead wolves and reclassified the documented causes of mortality. We did a first reclassification into three broad mortality causes: human, natural and unknown. When information was available, we did a second reclassification of human and natural causes into the following subcategories: human causes into legal (i.e., any means of lethal persecution allowed by legislation such legal hunting and control of individuals by authorities), illegal (i.e., any means of lethal persecution not allowed by legislation such illegal shooting and poisoning), vehicle (e.g., deaths by collision with cars and trains) and human other (e.g., accidental deaths derived from scientific captures and electric lines); and natural causes into disease and starvation (e.g., rabies, mange, parvovirus and malnutrition), intraspecific aggression (i.e., wolves killed by other wolves) and natural other (e.g., avalanche, interspecific killing and drowning). For each study we then calculated the proportion of dead wolves in each category and subcategory. We only assigned a 0 value to a category/subcategory when the study allowed us to do so confidently (e.g., all documented causes were reclassified into a subcategory and we assigned 0 value to those that remained empty). If no information was available for a category/subcategory and could not be inferred as stated previously, we left the box blank (e.g., if authors only provided the proportion of dead wolves by intraspecific aggression, we left the box blank for all the categories and the rest of the subcategories). For each study we retained information on the location, time period and type of monitoring of dead wolves. We did more than one entry per study if the study specified the information for different locations, time periods and/or types of monitoring. If the study provided the information in any other classification (e.g., per sex), we merged the data (if the raw number of individuals was not available, we used the mean proportion). We categorised the type of monitoring of dead wolves into radio- and/or GPS-tracking (i.e., detection of mortality relied on radio- and/or GPS-tracking of collared wolves), opportunistic (i.e., detection of mortality relied on random encounters and/or reported legally killed individuals) or both methods combined. We provide the raw and standardised data per study in Table S3.

2.4 | Standardising Data on the Natural and Human-Related Determinants of Mortality

We retained studies that statistically analysed the effect of individual (e.g., age and sex), social (e.g., intraspecific density and breeder loss) and/or environmental (natural and human; e.g., interspecific density and poaching, respectively) factors on mortality. For each study, we recorded the effect of each potential determinant on each mortality response variable; and the location and time period of the study. For categorical variables, we recorded the levels included and their effects as provided by the authors, e.g., the effect of each level compared to the others and the level that showed the highest mortality. If the study indicated that the effect applied to a specific subset (e.g., certain age class, season and methodology used), we retained such information. We reclassified the mortality response variable into mortality overall, human overall, legal, illegal, vehicle, natural overall, intraspecific aggression and disease (see definitions above). If different determinants were proxies of a common property (e.g., meadows and muskeg habitats are proxies of open habitats, and human density and distance to populated area are proxies of human presence), we reclassified the determinant as the common property. We excluded analyses where the mortality response variable included two causes of mortality or other causes than those mentioned above, and analyses where the determinant was too specific (e.g., road sinuosity). For each potential determinant, we obtained the percentage of effects registered as positive, negative and null, and retained the percentage for the predominant effect/s. We provide the raw and standardised data per study in Table S4 (indicating those analyses that were excluded).

2.5 | Statistical Analysis

We performed pairwise comparisons to test for significant differences in: (i) the annual rate of mortality between North America and Europe; (ii) the annual rate of mortality between status (resident non-pups vs. dispersers); (iii) the annual rate of mortality between age classes (pups vs. yearlings and adults); (iv) the proportion of dead individuals by the set of causes between North America and Europe (i.e., multigroup comparisons); (v) the proportion of dead individuals by each cause between North America and Europe; and (vi) the proportion of dead individuals between causes for North America and Europe. All are single-group comparisons but (iv) corresponds to multigroup comparisons. For single-group comparisons, we performed the Kruskal–Wallis test followed by post hoc procedures (stats and pgirmess packages in R software; Giraudoux 2024; R Core Team 2021). For multigroup comparisons, we performed permutational multivariate analysis of variance using Bray–Curtis dissimilarity (PERMANOVA, vegan package in R software; Oksaken et al. 2020). We set statistical significance levels at <0.05.

3 | Results and Discussion

3.1 | Spatial Biases on Mortality Research

We extracted data on mortality from 140 studies (Figure 1; Table S1). Most of them were ($N=89$) from North America, a smaller but considerable number ($N=47$) from Europe and only three from Asia. An additional study (Brainerd et al. 2008) includes study areas in both North America and Europe. In North America, the information mainly stemmed from two areas that have been studied over the long term, i.e., the Rocky Mountains of the United States ($N=38$ studies; mainly Yellowstone National Park and surroundings after wolf reintroduction in 1994) and the Great Lakes of the United States ($N=36$ studies; mainly the Superior National Forest and Isle Royal). These areas, together with Alaska ($N=13$ studies), comprise the distribution range of wolves in the United States. However, considering that wolves are broadly distributed across Canada, there is very little information here ($N=11$ and $N=9$ studies in western and eastern Canada, respectively, mostly done in the southern parts of British Columbia, Alberta, Ontario and Quebec, where most people live). In Europe, information is scattered among the often highly fragmented wolf subpopulations, with relatively less research (compared to the distribution range of the species) in Eastern Europe ($N=6$, 3 and 2 studies in the Baltic, Carpathian and Dinaric-Balkan wolf populations, respectively). Data on wolf mortality is altogether missing in remote and low populated areas of the Arctic (i.e., northern Canada and Russia) and Siberia; and in developing countries or in regions undergoing armed conflict, where wildlife research is not prioritised—for example, countries in the Middle East, Kazakhstan and Mongolia. Limited accessibility, lack of funding and high risk of getting involved in political conflict scenarios may explain the scarcity of studies found in such situations (Watson et al. 2017; Christie et al. 2021). In large countries with active scientific publishing, such as Russia and China, it may be possible that more information exists but it is not available in English (and thus not detected by our search).

Gathering geographically more even data would allow us to test if the economy of a country determines variations in mortality processes (Kojola et al. 2018). Likewise, obtaining wolf demographic data in remote areas is particularly relevant because it would serve as a reference for the natural dynamics of mortality processes in the least human-modified landscapes. For instance, to compare them with areas heavily used by humans such as Denmark, which has recently been colonised by wolves (Sunde et al. 2021). Information in the remote (northern) areas of Canada would also be especially useful because wolf dynamics in southern Canada and the United States depend on wolf dynamics (e.g., immigration and emigration processes) in the adjacent areas of northern Canada (Creel et al. 2015; Morales-González et al. 2022). Moreover, we note that the implementation and maintenance of long-term research projects is crucial to

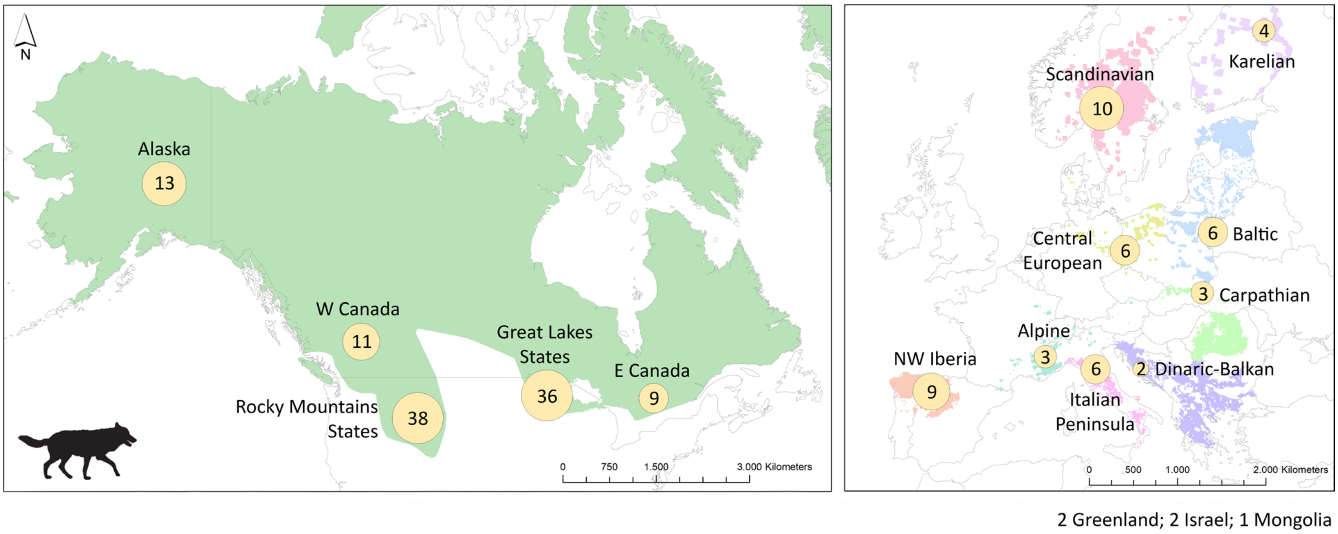

FIGURE 1 | Location of studies that provided data on wolf mortality (up to October 2024; $N=140$ studies). Yellow circles depict the number of studies (circle size is proportional to the number of studies) in different areas (detailed in the map) of North America (A) and Europe (B) within the distribution range of the species (coloured background). For North America, we used the distribution range by the IUCN Red List of Threatened Species (Boitani et al. 2018). For Europe, we used an updated version by Kaczensky et al. 2021, and depicted with different colours the nine populations recognised by the authors. Although not represented in the figure, two studies provided data on wolf mortality in Greenland, and three studies provided data on wolf mortality in Asia (two and one in Israel and Mongolia, respectively). We located each study in the area/s for which it provided information. Details on the location of each study are in Table S1. Studies: Adams et al. 2008; Almberg et al. 2009, 2015; Álvares et al. 2000; Apollonio et al. 2004; Ausband and Mitchell 2021; Ausband et al. 2015; Ausband 2016, 2019, 2022; Ausband, Mitchell, and Waits 2017; Ausband, Mitchell, Stansbury, et al. 2017; Ballard et al. 1987, 1997; Bangs et al. 1998; Barber-Meyer et al. 2021; Barroso et al. 2016; Blanco and Cortés 2007, 2009; Borg et al. 2015, 2016; Boyd and Pletscher 1999; Boyd et al. 1995; Brainerd et al. 2008; Brandell et al. 2021; Caniglia et al. 2012; Cassidy et al. 2023, 2024; Chakrabarti et al. 2022; Chapron et al. 2016; Chavez and Gese 2006; Colino-Rabanal et al. 2011; Coulson et al. 2011; Creel and Rotella 2010; Creel et al. 2015; Crouse et al. 2022; Cubaynes et al. 2010, 2014; Fernández-Gil et al. 2016; Forbes 1995; Forbes and Theberge 1996; Forshner et al. 2004; Fritts and Mech 1981; Fritts et al. 1985; Fuller et al. 2003; Fuller 1989; Gehring et al. 2003; Gude et al. 2012; Harrington et al. 1983; Hayes and Harestad 2000; Hebblewhite and Whittington 2020; Hedrick et al. 2019; Hefner and Geffen 1999; Hill et al. 2022; Horne et al. 2019; Huber et al. 2002; Jędrzejewska et al. 1996; Jędrzejewski et al. 2005, 2007; Jimenez et al. 2017; Kaczensky et al. 2008; Kojola et al. 2006, 2009; Kuzyk et al. 2006; Liberg et al. 2005, 2008, 2012, 2020; Light and Fritts 1994; Llaneza and Ordiz 2003; Llaneza et al. 2004; Lovari et al. 2007; MacNulty et al. 2009; Mancinelli et al. 2018; Marquard Petersen 2008, 2012; Marucco et al. 2009, 2012; Mech and Barber-Meyer 2017; Mech and Goyal 1993, 1995, 2011; Mech 1977, 1989; Messier 1985; Milleret et al. 2022; Mitchell et al. 2008; Mörner et al. 2005; Murray et al. 2010; Musto et al. 2021; Nakamura et al. 2021; Nowak and Mysłajek 2016, 2017; Nowak et al. 2021; O'Neil et al. 2017; Oliynyk 2023; Parker and Luttich 1986; Person and Russell 2008; Peterson and Page 1988; Peterson et al. 1984; Peterson et al. 1998; Petracca et al. 2024; Planillo et al. 2024; Plaschke et al. 2021; Pletscher et al. 1997; Potvin 1988; Recio et al. 2018; Reichmann and Saltz 2005; Santiago-Ávila and Treves 2022; Santiago-Ávila et al. 2020; Scandura et al. 2011; Schmidt et al. 2015; Schmidt et al. 2017; Seal et al. 1975; Sells et al. 2021; Serrouya et al. 2017; Sidorovich et al. 2017; Smietana and Wajda 1997; Smith and Almberg 2007; Smith et al. 2010; Smith et al. 2015; Stahler et al. 2013; Stenglein et al. 2018; Šuba et al. 2021; Sunde et al. 2021; SunderRaj et al. 2022; Suutarinen and Kojola 2017, 2018; Theuerkauf et al. 2007; Thiel 1985; Treves and Louchouarn 2022; Treves et al. 2021; Treves, Artelle, et al. 2017; Treves, Langenberg, et al. 2017; Turner et al. 2023; Van Ballenberghe et al. 1975; Vucetich et al. 1997; Wabakken et al. 2001; Webb et al. 2011; Wydeven et al. 2009.

acquire the necessary data to obtain robust estimates and inferences about mortality processes (Franklin 1989).

3.2 | Variation in Annual Mortality Rates

We extracted data on the rates of mortality from 76 studies (53 in North America, 21 in Europe and two in Asia; Figure 2; Table S2). The global annual rate of mortality was 0.31 ($\pm$0.18; Median $\pm$ Median absolute deviation), and we found no differences between North America (0.3 ± 0.15) and Europe (0.32 ± 0.21; $X^2=1.86$, DF $=1$, $p=0.17$). These rates are higher than would be expected for the species under natural conditions. We do not have such a baseline value (see above), but we know that rates are often <0.2 in areas where direct persecution is low (e.g., non-hunted wilderness areas of the Great Lakes, Yellowstone National Park and areas of recent colonisation by the species in Washington, Germany and the western Alps in Italy and France; Table S2). Moreover, these rates should be considered as minimum values because the proportion of monitored wolves with unknown fate is expected to be high (0.35 ± 0.292 for dispersers; Morales-González et al. 2022), and many of these disappearances may correspond to poached wolves (as levels of unreported illegal killing are often high; Liberg et al. 2012; Treves, Langenberg, et al. 2017; Sunde et al. 2021). Interestingly, in adjacent areas to Algonquin Provincial Park (Ontario), where admixed grey wolves coexist with eastern wolves (*Canis lycaon*) and coyotes (*Canis latrans*), eastern wolves face higher mean annual mortality—0.61 vs. 0.34 for coyotes and 0.37 for admixed grey wolves (Benson et al. 2014, 2024). A similar mean annual

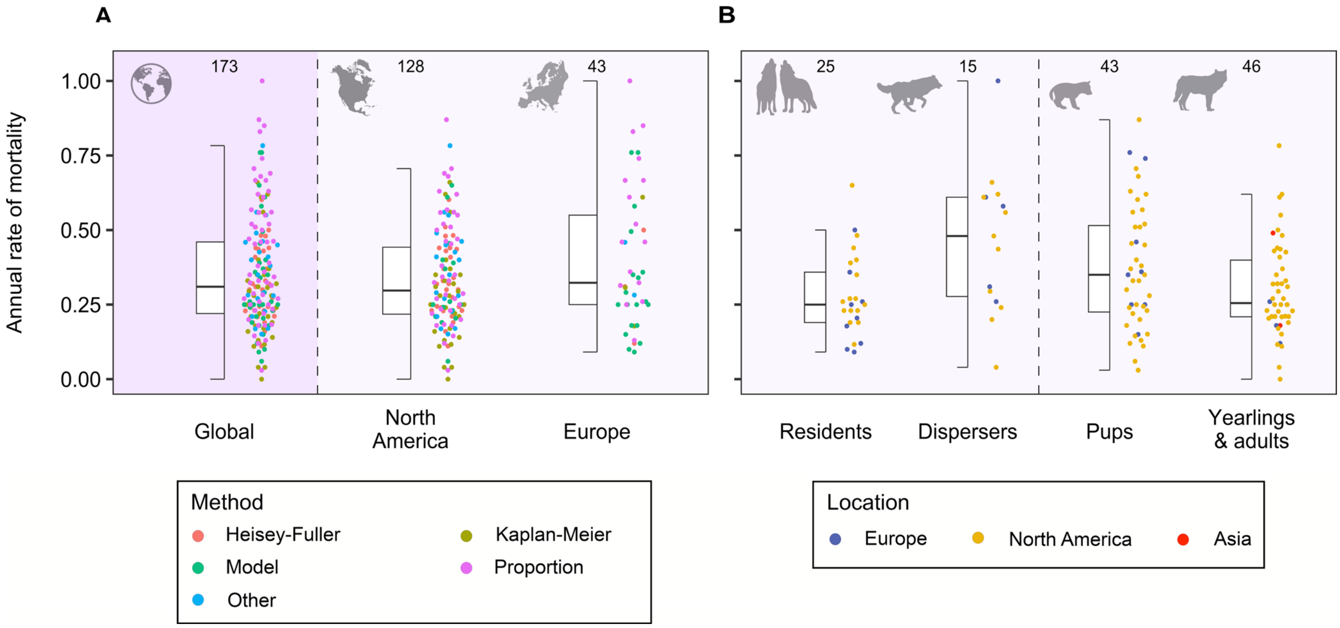

FIGURE 2 | Annual rates of mortality documented in the scientific literature (up to October 2024) for the grey wolf across its distribution range. (A) Rates for the global distribution range of the species (including North America, Europe and Asia; $N = 76$ studies; darker coloured background) and differentiating between North America ($N = 53$) and Europe ($N = 21$). (B) Rates per status (resident non-pups vs. dispersers) and per age class (pups vs. yearlings and adults). The colour of points refers to the methodology used to obtain the rate and the location where the rate was obtained for A and B, respectively (shown in legend). We indicate the sample size for each boxplot on top of it. A single study can provide several rates, and thus sample sizes of boxplots can be larger than the number of studies. The raw and standardised data per study are in Table S2.

mortality rate was found for red wolves (*Canis rufus*) – 0.64 for individuals between 2 and 4 years of age (Hinton et al. 2017).

We found high variability in the methodological steps followed by authors to obtain the rates, which may contribute to explaining the high variability observed in annual rates. In particular, we identified variability in the type of wolf monitoring (e.g., opportunistically found carcasses, systematically monitoring using tracking devices and monitoring of certain wolf individuals); the treatment given to wolves with unknown fate (i.e., in general excluding them from analysis but some assuming they died or were alive); and the statistical approach used (e.g., from simple proportions to complex models; see Table S2). Other studies also suggest that methodological differences add variability to mortality rates in comparative studies (Forbes 1995; Murray et al. 2010; Smith et al. 2010; Schmidt et al. 2015; Treves, Langenberg, et al. 2017) and to dispersal metrics in a global review (Morales-González et al. 2022). On the other hand, we should make comparisons between Europe and North America with caution because the sample size for Europe is small (i.e., may not be enough to obtain a robust estimate) and because data is missing from the large areas of North America where accessibility to humans is very low (see above).

We found differences in the annual rates of mortality between status, i.e., dispersers experienced higher mortality (0.48 ± 0.25) than non-pup residents (0.25 ± 0.11; $X^2 = 6.54$; DF = 1; $p = 0.01$; Figure 2). Note, however, that a larger sample size for dispersers is required to obtain a more robust estimate. Surprisingly, we found no differences between the age classes considered, i.e., pups (0.35 ± 0.24) and yearlings plus adults (0.26 ± 0.11; $X^2 = 2.67$; DF = 1; $p = 0.10$; Figure 2); and the variability within pups was particularly high. Merging rates from different study areas is important to provide useful baseline values but may overlook differences between age classes, as higher mortality for young wolves often arises when comparisons are done within the same study area (see '(4) Natural and human-related determinants of mortality'). Moreover, the challenges of field monitoring early-stage wolf pups, whose mortality is expected to be higher (Chapron et al. 2016), likely lead to underestimates of pup mortality. It is also important to highlight that little information is available in Europe on annual rates of mortality per wolf age and social status.

3.3 | Variation in the Proportion of Dead Individuals by Cause

We extracted data on the proportion of dead wolves per cause from 83 studies (50 in North America, 29 in Europe, three in Asia and one covering Europe and North America; Figure 3; Table S3). Our results (considering the observed annual rates of mortality) confirm that living alongside humans entails a very high risk of mortality by human-related causes (Woodroffe 2000; Stier et al. 2016; Morales-González et al. 2020). Most wolves died of human-related causes in all cases, i.e., globally (0.74 ± 0.23; $X^2 = 318.45$, DF = 9, $p < 0.0001$), in North America (0.66 ± 0.25; $X^2 = 206.27$, DF = 9, $p < 0.0002$) and in Europe (0.86 ± 0.14; $X^2 = 145.52$, DF = 9, $p < 0.0001$; Figure 3). In particular, the main human cause of mortality was intentional killing, i.e., legal and illegal sources of mortality, globally (0.29 ± 0.35 legal; 0.26 ± 0.31 illegal; 0.60 ± 0.26 legal and illegal), in Europe (0.12 ± 0.18; 0.39 ± 0.24; 0.7 ± 0.3) and in North America (0.3 ± 0.28; 0.21 ± 0.31, 0.56 ± 0.28; Figure 3). We did not find differences

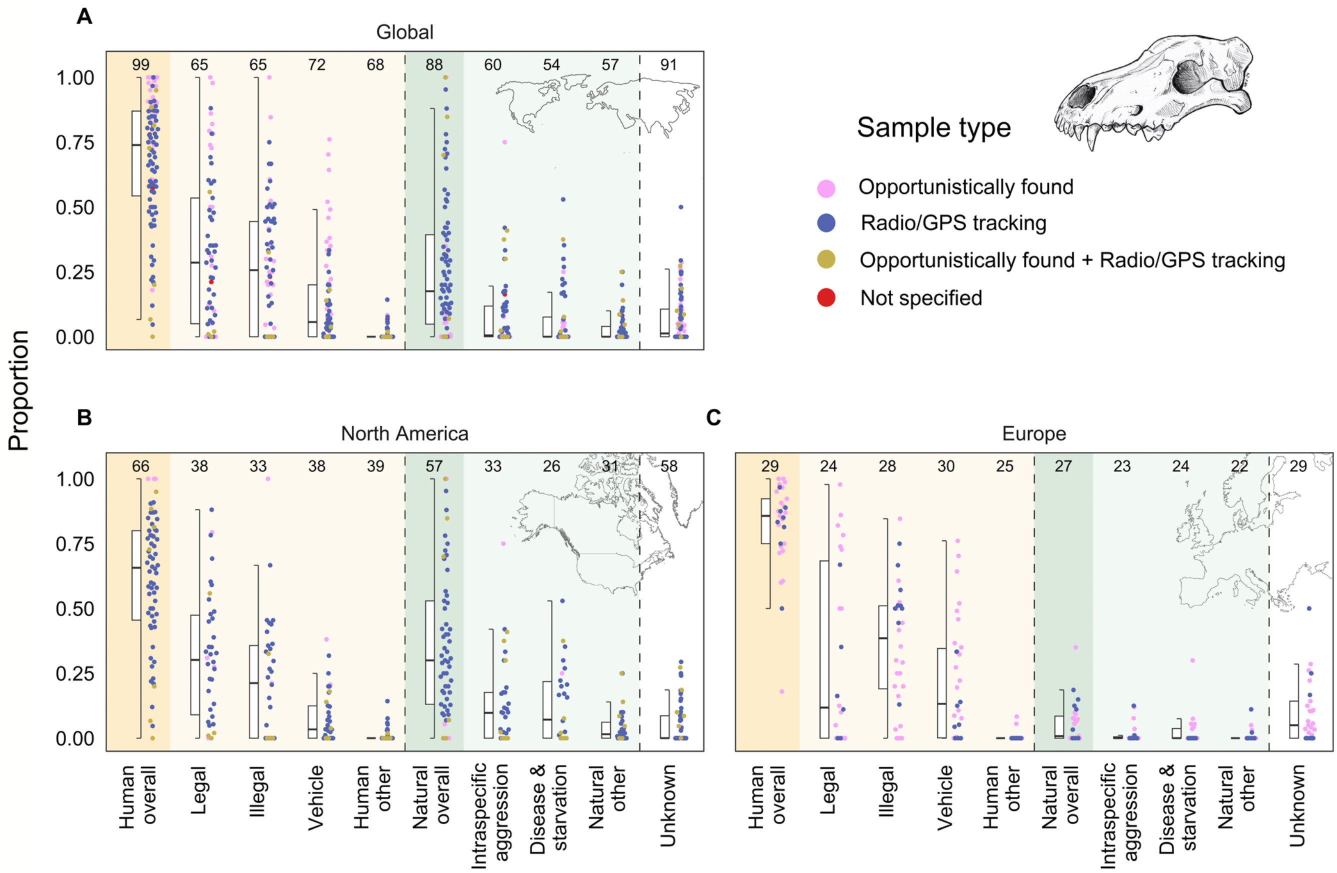

FIGURE 3 | Proportion of dead individuals by cause documented in the scientific literature (up to October 2024) for the grey wolf across its distribution range. (A) Proportions for the global distribution range of the species (including North America, Europe and Asia; $N=83$ studies). (B) Proportions for North America ($N=50$) vs. (C) Europe ($N=29$). The x axis depicts the cause of mortality. Yellow, green and white coloured backgrounds highlight human, natural and unknown causes, respectively (darker colours highlight overall human and natural causes, respectively). The colour of points refers to the type of sample (shown in legend). We indicate the sample size for each boxplot on top of it. When a given study provided proportions for different time periods or locations, we treated such data separately (note that sample sizes of boxplots can be larger than the number of studies). The raw and standardised data per study is in Table S3.

between the two types of intentional killing within each of these regions (North America $X^2=206.27$, DF$=9$, $p=0.69$; Europe $X^2=145.52$, DF$=9$, $p=1$; Figure 3); however, as most illegal kills are never reported, the proportion of mortality by illegal sources is expected to be much higher (Treves, Artelle, et al. 2017). Comparing the three sympatric wolf species in adjacent areas to Algonquin Provincial Park, eastern wolves showed higher vulnerability to hunting, trapping and road mortality than admixed grey wolves and coyotes (Benson et al. 2014, 2024). Red wolves may also be particularly vulnerable to human-caused mortality, which accounted for 73% of all deaths—of which 51% were attributed to illegal killing (Hinton et al. 2017).

The presence of large carnivores across multi-use landscapes leads to a number of real and perceived conflicts with human interests, e.g., damage to livestock and competition with hunters for game species (Kaczensky 1997; Madhusudan 2003), which most likely explain the magnitude of intentional killing (Kissui 2008). The pattern found for grey wolves is similar to that found for other large mammals subject to lethal management, such as ungulates in Europe (Apollonio et al. 2010; Collins and Kays 2011). However, increased mortality from intentional killing has particularly detrimental effects on the behaviour, demography and conservation status of apex predators, including wolves (Ripple et al. 2014; Milleret et al. 2017; Quevedo et al. 2019; Recio et al. 2020; Ausband et al. 2025). For instance, they are not evolutionarily adapted to high predation rates and naturally occur at low population densities (Stier et al. 2016). Indeed, although wolf numbers and distribution range are generally increasing, the species is far from being at a favourable conservation status across Europe. Six out of the nine populations are vulnerable or near-threatened according to the IUCN Red List assessment (Boitani 2025), and the wolf is still in an unfavourable-inadequate conservation status in six out of the seven biogeographical regions (European Environment Agency 2020). Our findings reveal what mortality values are responsible for the observed population trends.

A higher proportion of wolves died by human causes compared with natural causes in Europe than in North America ($X^2=16.92$, DF$=1$, $p<0.0001$; Figure 3). This can at least be partially explained by methodological differences. In Europe, most data were obtained from opportunistically found wolf carcasses (Figure 3), which inarguably biases the causes of mortality towards those that leave an easily detectable wolf body (e.g., road and legal kills) while underestimating those causes of mortality for which wolf bodies are difficult to find opportunistically (e.g., illegal and natural mortalities; Ciucci et al. 2007; Stenglein et al. 2015). In contrast, most data on wolf mortality from North America come from systematically monitored individuals (by radio and GPS collar devices), which makes it more likely to find the wolves that died by natural causes, thus providing a more realistic representation of the causes (Stenglein et al. 2015). Note that deaths by illegal sources are also difficult to find through collaring as poachers may often destroy the collars (Liberg et al. 2012). Apart from the above methodological differences, wolves in Europe occupy more human-dominated landscapes than they do in much of North America (Nowak and Mysłajek 2016; Kuijper et al. 2019; Ausband and Mech 2023). Increased contact between humans and wolves in the European context may result in higher mortality by human causes for large carnivores (Hill et al. 2022). Regarding intentional killing, we found a higher proportion of deaths by illegal means in Europe than in North America ($X^2=5.97$, DF = 1; $p<0.02$) and a similar proportion of dead wolves by legal means ($X^2=0.55$, DF = 1; $p=0.46$; Figure 3). However, we do not know to what extent underestimating the proportion of natural mortalities in Europe influences the observed differences.

Mortality by vehicle collision is the second highest human-related mortality globally (0.06 ± 0.08), in Europe (0.12 ± 0.19) and in North America (0.03 ± 0.05); with this proportion being also higher in Europe than in North America ($X^2=6.44$, DF = 1, $p=0.01$; Figure 3). These differences may also be the product of the methodological and landscape contexts mentioned above. Europe indeed reports the highest density of roads worldwide (Meijer et al. 2018).

The main causes of natural mortality are intraspecific aggression, disease and starvation, with a smaller proportion of mortality attributed to old age, interspecific aggression and accidents such as avalanche and drowning. We found no differences within regions between the main causes of natural mortality ($X^2=318.45$, DF = 9, $p=1$; Figure 3). Between regions, on the other hand, we detected a higher proportion of dead wolves by natural mortality in North America (0.3 ± 0.29) than in Europe (0.01 ± 0.01; $X^2=30.95$, DF = 1, $p<0.0001$; Figure 3); but these differences, at least partially, stem from the methodological differences outlined above as the proportion of deaths by natural mortality is highly underestimated for wolves in Europe. The proportion of dead wolves by each natural cause in North America was 0.1 (± 0.14) by intraspecific aggression, 0.07 (± 0.11) by disease and starvation and 0.02 (± 0.02; Figure 3) by natural other. Multiple landscape differences between Europe and North America may also cause differences in natural mortality risk. For instance, wolves tend to occur at lower densities in many European landscapes (1.3–2.7 and 2–18.2 wolves/100 km^2 in Europe and North America, respectively; Blanco et al. 1992; Mech and Tracy 2004; Nowak et al. 2008; Cassidy et al. 2015; Kojola et al. 2018; Merli et al. 2023), which may result in a lower risk of intraspecific aggression (see '(4) Natural and human-related determinants of mortality'). The expansion of the highly fragmented populations in Europe also suggests that wolves have remained below carrying capacity, further supporting a low risk of intraspecific aggression (Smith and Cassidy 2024).

Lastly, the proportion of dead wolves by an undetermined cause was slightly higher in Europe (0.05 ± 0.07) than in North America (approx. 0; $X^2=4.58$, DF = 1, $p=0.03$), which may simply indicate that it takes longer to recover dead bodies in Europe.

3.4 | Natural and Human-Related Determinants of Mortality

We extracted data on the determinants of mortality from 77 studies (58, 18 and one studies from North America, Europe and both regions, respectively; Table 1; Table S4). We found that multiple individual, social and environmental (human and natural) factors determine mortality, thus indicating that biological differences are key to explaining the observed variability in annual mortality rates. Hereafter, when we indicate that a certain factor (or level in the case of categorical variables) increased, decreased or had no effect on mortality, we refer to the effect that had more support in the literature, i.e., more analyses showed such an effect. However, we found high variability in the effect for most determinants, which indicates high context dependency (examples below).

3.4.1 | Individual Determinants

The life-stage of wolves determined mortality, with dispersers showing higher mortality than residents (Table 1). Such differences in mortality can relate to the protection benefits of cooperative behaviour for residents (e.g., hunting and territorial defence; Clutton-Brock 2021; Houslay et al. 2020) and the risks of travelling long distances across unfamiliar areas for dispersers (Bonte et al. 2012; Morales-González et al. 2022). Indeed, the mortality costs of dispersal have been widely documented, particularly in social species (Bonte et al. 2012; Maag et al. 2022; but see Behr et al. 2023). The effect of age on overall and human-caused mortality was unclear (Table 1), with a similar amount of evidence supporting either no effects or increased mortality for young wolves (approx. <2 years old). Higher mortality for young individuals is often observed in large carnivores and most mammals (Swanepoel et al. 2015; Gervasi et al. 2017). The lack of an age effect may stem from methodological issues, such as small sample sizes and/or the grouping of age classes with different mortality rates. Although rarely studied, senescent wolves (>6 years old) also exhibited higher mortality (Cubaynes et al. 2014; Cassidy et al. 2024). Moreover, wolves from 2 to 4 years old were particularly vulnerable to vehicle collisions (Table 1). As for other mammals (Paniw et al. 2022), increased body mass was often associated with reduced overall mortality (Table 1). Moreover, mortality increased with genetic inbreeding and certain genotypes (Table 1). As for other species (Keller and Waller 2002), inbreeding may be a particularly important determinant in populations with a low number of wolves (e.g., Isle Royale National Park; Åkesson et al. 2016) or coming from a small number of founders (e.g., Scandinavia; Liberg et al. 2005). Regarding genotypes, in the United States, black heterozygotes had the lowest risk of mortality followed by grey homozygotes, and black homozygotes had a much higher probability of mortality (Coulson et al. 2011). Differences in cellular immunity may explain these patterns (Candille et al. 2007). Movement characteristics (i.e., velocity and sinuosity of movements, distance travelled from familiar areas and time in extraterritorial forays) may influence mortality. However, analyses often reported null

TABLE 1 | Determinants of mortality documented in the scientific literature (up to October 2024; $N = 77$ studies) for the grey wolf across its distribution range.

A

Individual determinant		Mortality cause: Overall	Human	Legal	Illegal	Vehicle	Natural	Intraspecific aggression	Diseases
Age		53% 43|20	54% 13|2		100% 1|1	2–4 years old 2|1	93% 14|3	100% 1|1	
Breeding status		100% 5|1		100% 2|1					
Dispersal status		78% 9|5	+/ne 50% 4|1	100% 1|1	100% 1|1		80% 5|2		
Other status		Non-scent marking wolves 100% 2|2		Dispersers vs. breeders 100% 1|1				Social status in group 100% 1|1	
		Dispersers vs. breeders 100% 1|1							
		loners 100% 1|1							
Body mass		−/ne 50% 2|2				100% 1|1			
	P	100% 2|2							
Inbreeding		100% 1|1			100% 1|1				
	P	100% 1|1							
Genotype		Black heterozygotes 100% 3|3							
Movement distance		100% 3|2							
Movement velocity		100% 1|1	100% 1|1						100% 1|1
Movement sinuosity			100% 1|1						100% 1|1
Movement extraterritorial			100% 1|1						100% 1|1
Sex		73% 22|17	+female/+male 50% 2|2	57% 7|5	100% 2|2		100% 1|1	100% 2|1	
	P	100% 2|2							

(Continues)

TABLE 1 | (Continued)

B									
		Mortality cause							
Social determinant		**Overall**	**Human**	**Legal**	**Illegal**	**Vehicle**	**Natural**	**Intraspecific aggression**	**Diseases**
Wolf density		39% 18∣10	+/ne 50% 6∣3		+/ne 50% 2∣2		75% 4∣1	67% 3∣2	
	P	67% 3∣3							
Aggresive interactions								+/ne 50% 2∣2	
Infected mates									100% 1∣1
Group size		56% 9∣2							100% 1∣1
	P	45% 11∣7							
Territory size		100% 1∣1							
Group extraterritorial forays		100% 1∣1							
Genotype of parents	P	black heterozygote mother 100% 1∣1							
Inbreeding of parents	P	67% 3∣2							
Breeder loss	P	100% 1∣1							
Breeder turnover	P	80% 5∣2							
Pair bond duration	P	100% 2∣2							
Age of breeders	P	−/+/ne 33% 3∣3							
Litter size	P	67% 3∣3							
Den characteristics	P	+/ne 50% 4∣1							

(Continues)

TABLE 1 | (Continued)

C

Natural determinant		Mortality cause: Overall	Human	Legal	Illegal	Vehicle	Natural	Intraspecific aggression	Diseases
Diseases		67% 3|2						100% 1|1	
	P	67% 12|8							
Season		Winter 54% 13|11			Late autumn 100% 1|1	late Autumn & winter 100% 1|1		100% 1|1	
	P	Summer 67% 3|3		Late autumn & winter 100% 1|1					
Wild prey		Abundance of main prey/s 80% 5|3	100% 1|1	100% 4|1					
		Mule deer as main prey 67% 3|1							
	P	100% 1|1							
Weather severity		86% 7|4	100% 1|1	100% 1|1	100% 1|1	100% 1|1	100% 1|1		
	P	100% 1|1							
Refuge habitat		50% 4|2				100% 2|1			
Open habitat		70% 10|1	100% 1|1						100% 1|1
Natural habitat			100% 1|1	−/ne 50% 2|1					
Edge density		100% 1|1				100% 2|1			
Water courses		67% 3|2				100% 1|1			
Elevation		75% 4|2							
Slope		100% 1|1				100% 1|1			

(Continues)

TABLE 1 | (Continued)

D

Human determinant		Overall	Human	Legal	Illegal	Vehicle	Natural	Intraspecific aggression	Diseases
		Mortality cause							
Lethal management		87% 8|7	67% 3|3	100% 3|3	57% 7|4	100% 1|1	50% 4|4	100% 1|1	
	P	100% 3|3							
Game hunting		100% 1|1		100% 1|1	+/ne 50% 2|2	100% 1|1	100% 1|1		
Human presence		100% 1|1		100% 1|1	−/ne 50% 2|2	100% 1|1			
	P	100% 1|1							
Domestic prey		78% 9|2	75% 4|1				75% 4|1		
Damages					100% 2|1				
Conflicts			100% 1|1	75% 4|2	100% 1|1				
Agricultural land		100% 3|2		100% 1|1	100% 1|1	100% 2|1			
Road density		60% 5|4	100% 1|1	60% 5|3	+/ne 50% 4|3	100% 1|1			
Distance to roads			100% 3|2			100% 1|1			100% 1|1
Private land		75% 4|2	75% 4|1				75% 4|1		
Federal land		100% 2|1							
State land		100% 1|1							
Wilderness land		75% 4|1	100% 1|1						
Protected land		75% 4|3							

Note: We classified determinants into four categories: individual (A), social (B), environmental natural (C) and environmental human (D). We show the effect of each determinant on mortality overall and by specific causes. Specific causes are human overall, legal, illegal, vehicle, natural overall, intraspecific aggression and disease. Colors indicate the most frequently reported effect in the literature: pink = positive effect (increased mortality '+'), green = negative effect (decreased mortality '−'), orange = no effect ('ne'). In case of a tie, the tied effects are shown separated by slashes (e.g. +/ne). Blank cells indicate that the relationship has not been studied. For categorical determinants, the level/s at which the effect applies are indicated. The numbers to the left and right of the vertical bar represent the total number of analyses and studies, respectively. We show the percentage of analyses reporting the effect/s shown. Effects specific to pups (wolves < 1 year old) are indicated with 'P'.

effects (Table 1) likely because identifying such effects is difficult as they may interact with other determinants such as landscape characteristics and human disturbance during movement (O'Neil et al. 2017). Most analyses reported no sex differences in mortality (Table 1).

3.4.2 | Social Determinants

The effect of wolf local density on overall mortality was most frequently (39%; $N = 18$ analysis) positive; yet a similar percentage of analyses (33%) yielded no effects, and a few found negative (22%) and U-shaped relationships (6%; Table 1). The effects of density on cause-specific mortalities (human, illegal, natural and intraspecific aggression) also varied (Table 1). These variations can be explained by the use of different statistical analyses (e.g., the use of simple tests often yielded no effects; Murray et al. 2010), the inclusion of pups in density estimates (which also yielded no effects; Barber-Meyer et al. 2021; Cubaynes et al. 2014) and the interaction of wolf density with other factors such as the status of the population (i.e., relative density) and prey availability during the study period (Cubaynes et al. 2014; Stenglein et al. 2018). The most plausible pattern, supported by studies on wolves and other mammals (Gaillard and Yoccoz 2003; Cubaynes et al. 2014), is that wolf density increases adult and pup mortality in populations with high and low ungulate densities, respectively. The former occurs because wolves reach high densities, in turn leading to increased intraspecific aggression, whereas the latter is caused by limited food availability. Group size did not have an effect on mortality overall (Table 1). This is not surprising because optimal group size varies with natural environmental surroundings (Tallian et al. 2023), meaning that groups of different sizes may have similar survival if their size is optimal according to the natural environmental conditions. For pups, increased group size reduced overall mortality (Table 1), which can be explained by food provisioning by helpers (Brainerd et al. 2008). This effect is particularly evident when breeders are lost (Brainerd et al. 2008). Interestingly, but rarely evaluated, are how group and disease dynamics interact (Brandell et al. 2021; Paniw et al. 2022). Mortality of infected individuals decreased with group size, possibly because group members offset the individual costs of infection (Almberg et al. 2015), and increased with the proportion of infected group members (Table 1). As expected for a species that lives in family groups, our results show that social factors are key to predicting wolf pup survival. Besides wolf density and group size, the status of breeders (i.e., genotype, inbreeding, breeder loss, breeder turnover, pair bond duration and age of breeders), litter size and den characteristics also determined overall pup mortality (Table 1). Except for studies focused on pups, very few studies analysed how social factors influence mortality (Table 1).

3.4.3 | Natural Environmental Determinants

Researchers analysed the effect of different landscape characteristics (e.g., elevation, slope, edge density and water courses), including cover types (e.g., refuge vegetation and open habitats such as meadows) on mortality. However, the effects greatly varied among study areas and were often null (Table 1). In a generalist species like the wolf, it is likely that the actual or most influential determinant of mortality is landscape accessibility to humans rather than landscape characteristics per se. For instance, old clear-cuts where roads persist were associated with high risk of mortality for dispersers (residents avoided these areas) even though they had dense vegetation cover (Person and Russell 2008). Remarkably, open habitats (mostly urban and other highly modified habitats) increased mortality by diseases (Table 1), in line with previous studies reporting higher prevalence of diseases in these environments (Brearley et al. 2013). Moreover, diseases (e.g., canine parvovirus and mange) increased overall mortality but reduced intergroup aggression and thus mortality by intraspecific aggression (Brandell et al. 2021) (Table 1).

Mortalities often peak during late autumn to winter, particularly for legal, illegal, vehicle and overall mortality (Table 1). This pattern may be linked to the timing of the hunting season, which coincides with these months across most of the wolf distribution range (Hebblewhite and Whittington 2020; Schmidt et al. 2015). The higher incidence of vehicle collisions likely relates to the higher spatial mobility of the species, which also overlaps with hours of human activities during this season (Kusak et al. 2005). Mortality by illegal sources (also by natural but not by legal and vehicle sources) also increased with the presence of snow cover (Table 1), possibly because of increased wolf track detection by poachers (Santiago-Ávila and Treves 2022). Snow tracking is mainly restricted to Northern environments, which may explain why other studies found no effects of weather severity on overall mortality (Table 1).

Interestingly, the abundance of wild prey decreased mortality by legal sources (Table 1), possibly because in high-prey areas hunters do not perceive wolves as competition for game species (Treves et al. 2013). For pups, diseases, summer season, weather severity and low wild ungulate availability increased overall mortality; and no other factors were tested (Table 1).

3.4.4 | Human Determinants

A long-held debate in large carnivore population ecology is whether human-related mortality adds to natural mortality or is (totally or partially) compensated by reductions in natural mortality (Burnham and Anderson 1984; Murray et al. 2010; Benson et al. 2023). We showed that mortality by legal sources (i.e., lethal management of wolves) increased human-caused mortality as well as overall mortality (the latter also found for pups; Table 1), which does not support the hypothesis that anthropogenic mortality is compensatory in wolves. Moreover, four studies analysed the effect of hunting on natural mortality (Table 1). Two found a null effect (Adams et al. 2008; Cassidy et al. 2024); the third found a positive effect (Santiago-Ávila et al. 2020); and the fourth showed that even though natural mortality dropped in the first hunt year, it gradually increased during the following years (Oliynyk 2023). Thus, the degree to which partial compensation may occur in wolves appears minimal if not null (Cassidy et al. 2024) and may depend on life history traits (such as age class and dispersal status; Murray et al. 2010), population density and other factors affecting natural mortality (Creel et al. 2015; Stenglein et al. 2018).

Another controversial question is whether allowing killing decreases mortality by illegal sources (presumably because it improves tolerance regarding coexistence with wolves vs. it sends a negative message about the value of wolves). A reduction in reported illegal killing was supported by two studies (Table 1), carried out in Finland (Suutarinen and Kojola 2018) and Scandinavia (Liberg et al. 2020). In contrast, an increase was observed among wolves living primarily in Yellowstone National Park, when hunting was permitted outside the Park (Cassidy et al. 2024). Interestingly, a study in Wisconsin (Santiago-Ávila et al. 2020) revealed that although reported illegal killing decreased slightly, this was outweighed by a larger increase in the incidence of wolf disappearance, with cryptic poaching identified as the most likely explanation for these missing wolves (Chapron and Treves 2016). This suggests that allowing killing increases illegal deaths and emphasises that the cryptic nature of poaching events precludes obtaining reliable estimates of mortality from illegal sources (Liberg et al. 2012).

Studies support the hypothesis that game hunting of other species increases illegal killing of wolves (Table 1). Whereas the proportion of hunters in the population (Suutarinen and Kojola 2018) and buck kill index (O'Neil et al. 2017) may not have an effect on illegal and overall mortality, respectively; illegal killing increased during game hunting seasons with snow cover, possibly due to an increased number or activity of poachers (Santiago-Ávila and Treves 2022). On the other hand, the occurrence of game hunting (Santiago-Ávila and Treves 2022) did not have an effect on mortality by legal and vehicle means, but, surprisingly, had a positive effect on natural mortality rates, which remained unexplained (Table 1).

We found high variation in the effects of human presence on mortality by different sources (Table 1). The use of different proxies of human presence (e.g., human population density in an area (Suutarinen and Kojola 2018), distance to populated area (Person and Russell 2008) and percentage of impervious surface (O'Neil et al. 2017)) precluded identifying a general pattern. Domestic prey density did not show a clear effect (Table 1). It varied among study areas and was influenced by the sample of monitored wolves and the statistical approach used (Murray et al. 2010; Smith et al. 2010). This may be because higher densities of domestic prey do not necessarily lead to increased conflict. A recent review showed that wild prey biomass is the main predictor of livestock predation by wild carnivores (Alquinta et al. 2025). In the case of wolves, livestock numbers were unrelated to an increased number of complaints (Fernández-Gil et al. 2016). Instead, media news on wolf predation, management practices and the history of coexistence between humans and wolves may be more important in determining the severity of conflicts (Fernández-Gil et al. 2016; Durá-Alemañ et al. 2024). Legal culling increased under the occurrence of conflict scenarios regardless of the actual occurrence of damages—i.e., measured by comparing reestablished vs. established populations in North America (with expected higher and lower levels of conflicts, respectively; Hill et al. 2022), the number of paid compensations and the amount of news on wolf damage (Fernández-Gil et al. 2016) (Table 1). Real and perceived conflicts may exert pressure on politicians who may respond by increasing legal culling (Selva et al. 2023; Ordiz et al. 2024).

Agricultural cover did not affect mortality rates due to vehicle collisions but decreased mortality due to legal and illegal killing. However, this determinant increased overall mortality (Table 1). Agricultural areas cover half of the global land surface, and addressing their impacts on species survival is a major challenge in global change ecology (Mendenhall et al. 2014; Semenchuk et al. 2022). Future metanalyses including different study areas and covering the whole range of observed values of agricultural cover may aid a better understanding of the topic. Similarly, roads occupy a significant portion of the global surface (e.g., 19 million kilometres of roads cover 53 countries in Europe; Brons et al. 2022) and can have severe ecological effects on the dynamics of wildlife populations (Forman 2000). Likely because they act as points of access (Person and Russell 2008), we found that road density increased mortality by vehicle and by legal sources in wolves, it sometimes increased mortality by illegal sources and led to an increase in overall mortality (Table 1). Accordingly, distance to roads reduced human-caused mortality (Table 1). However, the use of roads by wolves is complex and the density of roads and human activity in some areas may not reach the threshold to facilitate human-caused mortality, which can explain some null or even negative effects on mortality (O'Neil et al. 2017; Hill et al. 2022). Some land status or ownership affected mortality. In particular, wilderness and protected areas were associated with reduced human-caused mortality rates (Table 1). However, although protected lands support wolf survival, it is well known that large carnivores have extensive spatial requirements that extend far beyond these areas, leaving their survival highly compromised if mortality risk is high outside (Benson et al. 2024; Cassidy et al. 2024).

4 | Conclusions

Our review reveals that wolves coexisting with humans face a high risk of mortality. Their minimum annual mortality rate in North America and Europe (0.31 ± 0.18) is much higher than rates reported in scenarios with low human persecution (< 0.2). Indeed, intentional killing is by far the leading cause of death ($60\% \pm 25\%$), with reported similar percentages of wolves killed legally ($29\% \pm 36\%$) and illegally ($26\% \pm 33\%$). This reflects the intense hostility and social conflict generated by the species' presence in a given territory. Although rates may be similar for other large mammals, the vulnerability of apex predators to increased mortality from intentional killing highlights the need for special attention to maintain populations in a favourable conservation status. Assessing the extent of cryptic poaching is crucial to improving the accuracy of mortality costs for wolves. At a minimum, studies should report uncertainty specific to this event. Europe reports a 20% higher percentage of human-related wolf deaths ($86\% \pm 14\%$) than North America ($66\% \pm 24\%$); and although we found that monitoring in Europe underestimates natural mortalities, differences in human pressures require further investigation.

The large variability observed in mortality rates can be partially attributed to differences in wolf monitoring and statistical methods between studies, but primarily arises from the pooling of status and age class-specific rates, which are influenced by numerous individual, social and environmental factors. Our critical discussion of the effects of this array of factors reshapes previous hypotheses, including those of particular relevance for the management of large carnivores (e.g., supporting additivity between human-induced and natural mortality). We recommend that the effects of some determinants (e.g., agricultural cover) require future meta-analyses to capture the variability of scenarios where such a generalist species occurs, ideally involving cross-border cooperation between researchers. We also showed that disentangling the effects of natural factors (e.g., landscape characteristics) is hindered by the strong influence of human-related determinants and by the lack of data from the least human-influenced landscapes where wolves are widely distributed (e.g., northern Canada, Russia and Siberia). This data gap also prevents us from establishing baseline annual mortality rates under natural conditions, which we estimated (<0.2) from areas where the species faces low direct persecution.

Author Contributions

A.M.-G., H.R.-V., E.R., M.P.: conceptualization; A.M.-G., H.R.-V.: methodology, investigation, visualization and writing – original draft; E.R: funding acquisition; A.M.-G., H.R.-V., E.R., M.P., M.Q., A.F.-G.: writing – review and editing.

Acknowledgements

We acknowledge the support provided by grant no. CGL2017-83045-R (from the Spanish Ministry of Science and Innovation and Universities, the Agencia Estatal de Investigación and the Fondo Europeo de Desarrollo Regional) to E.R. and A.M.-G.; by grant no. PRE2018-086102 (predoctoral grant from the Spanish Ministry of Science and Innovation and Universities) to A.M.-G.; by grant no. JDC2023-050355-I (from the Spanish Ministry of Science and Innovation and Universities, the Agencia Estatal de Investigación and the European Social Fund Plus) to H.R.-V.; by grant no. RYC2021-033192-I (from the Spanish Ministry of Science and Innovation and Universities, the Agencia Estatal de Investigacion and the European Union) to M.P.; and by grant no. QUAL21 020 EBD (from the Junta de Andalucía, Consejería de Universidad, Investigación e Innovación) to E.R. We also thank two referees and the journal editors for their positive feedback.

Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Scientific studies ($N = 140$) on grey wolf mortality (up to October 2024) across the distribution range of the species. These are studies that provided data on the rates of mortality, the proportion of dead wolves by cause and/or the natural and human-related determinants of mortality. For each study we provide the reference, study area, wolf population and whether they correspond to grey literature. **Table S2:** Raw and standardised data on the annual rates of mortality documented in the scientific literature (up to October 2024) for the grey wolf across its distribution range. **Table S3:** Raw and standardised data on the proportion of dead individuals per cause documented in the scientific literature (up to October 2024) for the grey wolf across its distribution range. **Table S4:** Raw and standardised data on the natural and human-related determinants of mortality documented in the scientific literature (up to October 2024) for the grey wolf across its distribution range.