Demographic effects of road mortality on mammalian populations: a systematic review

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Demographic effects of road mortality on mammalian populations: a systematic review

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ABSTRACT

In light of rapidly expanding road networks worldwide, there is increasing global awareness of the growing amount of mammalian roadkill. However, the ways in which road mortality affects the population dynamics of different species remains largely unclear. We aimed to categorise the demographic parameters in mammalian populations around the world that are directly or indirectly affected by road mortality, as well as identify the most effective study designs for quantifying population-level consequences of road mortality. We conducted a comprehensive systematic review to synthesise literature published between 2000 and 2021 and out of 11,238 unique studies returned, 83 studies were retained comprising 69 mammalian species and 150 populations. A bias towards research-intensive countries and larger mammals was apparent. Although searches were conducted in five languages, all studies meeting the inclusion criteria were in English. Relatively few studies (13.3%) provided relevant demographic context to roadkill figures, hampering understanding of the impacts on population persistence. We categorised five direct demographic parameters affected by road mortality: sex- and age-biased mortality, the percentage of a population killed on roads per year (values up to 50% were reported), the contribution of roadkill to total mortality rates (up to 80%), and roadkill during inter-patch or long-distance movements. Female-biased mortality may be more prevalent than previously recognised and is likely to be critical to population dynamics. Roadkill was the greatest source of mortality for 28% of studied populations and both additive and compensatory mechanisms to roadkill were found to occur, bringing varied challenges to conservation around roads. In addition, intra-specific population differences in demographic effects of road mortality were common. This highlights that the relative importance of road mortality is likely to be context specific as the road configuration and habitat quality surrounding a population can vary. Road ecology studies that collect data on key life parameters, such as age/stage/sex-specific survival and dispersal success, and that use a combination of methods are critical in understanding long-term impacts. Quantifying the demographic impacts of road mortality is an important yet complex consideration for proactive road management.

Key words: dispersal, genetic diversity, migration, population growth, population persistence, roadkill, study design, survival.

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I. INTRODUCTION

Recent estimates suggest that there are 21.6 million kilometres of roads globally, with an expected increase of 14–23% in road length by 2050 (Meijer *et al.*, 2018). Consequently, many conservation biologists argue that the effects of roads on wild animal populations are one of the most pressing contemporary conservation issues (Ibisch *et al.*, 2016; Barrientos *et al.*, 2021). Whilst roads cause substantial habitat loss, fragmentation, pollution (light, noise, chemical) and changes in animal movement (Carvalho *et al.*, 2018), the mortality caused by wildlife–vehicle collisions (WVCs) is perhaps the most obvious impact and has therefore received particular attention. Road mortality is considered one of the largest contributors to wild vertebrate mortality globally and, unlike other forms of direct anthropogenic mortality, it affects individuals irrespective of their body size, physical condition, and conservation status (Hill, DeVault & Belant, 2019).

Raw counts of the numbers of animals killed per unit length of road (hereafter 'roadkill') have been published for a broad range of vertebrate taxa. However, these raw counts alone provide little information about the impacts of WVCs on populations (Grilo *et al.*, 2021). Instead, roadkill counts need to be considered in relation to population demography. With this context, it is then possible to avoid simplistic or erroneous conclusions that a high roadkill rate is inevitably debilitating for a population or that low levels of road mortality are not negatively impacting populations (Ramp & Ben-Ami, 2006; Grilo *et al.*, 2021). In addition, impacts of road mortality are likely to be confounded by other forms of change around roads, such as habitat modification (Chambers & Bencini, 2010) and road effect zones (Ibisch *et al.*, 2016). To disentangle road mortality from other road impacts, demographic parameters must be quantified to reveal the relative importance of road mortality and if/how road mortality might be responsible for the observed population dynamics. For example, Jaeger & Fahrig (2001) and Ceia-Hasse *et al.* (2018) used individual-based models of 'virtual' species and demonstrated that road mortality is likely to have a greater impact on population persistence than barrier effects because of the cumulative depletion of individuals and lower connectivity when roadkill rates were high. Finally, by using population dynamics, studies can identify populations most at risk from roads and the specific threats against those populations, such that conservation strategies and actions can be defined and prioritised.

Approximately 27% of mammalian species are considered to be threatened with extinction (IUCN, 2020). However, most theoretical and empirical studies on the demographic impacts of road mortality to date have focused on reptiles and birds. For example, Borda-de-Água, Grilo & Pereira (2014) developed a stochastic, age-structured model and found that an annual road mortality rate of 5% can reduce barn owl (*Tyto alba*) populations to half their original size in 50 years. Population declines and/or biased population sex ratios resulting from even relatively low rates of female road mortality have been described for black ratsnakes (*Elaphe obsoleta*) (Row, Blouin-Demers & Weatherhead, 2007) and

freshwater turtles (Aresco, 2005). Like birds and herpetofauna, several mammalian groups, particularly small mammals and generalist carnivores, actively use roads as corridors for dispersal, routine movements or scavenging opportunities (Kautz *et al.*, 2021; Galantinho *et al.*, 2022). In doing so, individuals face an increase in the likelihood of vehicle collisions (Serieys *et al.*, 2021). Unlike other taxa however, vehicle collisions with mammals have shown a pronounced increase over time in response to a growing human footprint (Hill *et al.*, 2019). Moreover, hotspots of mammal roadkill are globally widespread (e.g. Coalition for Sonoran Desert Protection, 2022; Fahrig & Rytwinski, 2009) and Grilo *et al.* (2021) identified several regions where mammalian biodiversity may be lost due to the influence of existing transport infrastructure. Mammalian road mortality therefore remains a crucial area of study for conservationists.

Scientifically rigorous research into the demographic impacts of road mortality is key to influencing road planning decisions (Roedenbeck *et al.*, 2007). Sound research is also essential to justify recent and future mitigation projects, especially for large-scale, expensive measures that are often targeted at medium and large mammalian species (Huijser *et al.*, 2009). Using study designs capable of producing field data with evidential weight, however, can be challenging. The demography of a population can be poorly understood, obtaining roadkill data can be time-consuming and expensive, and accuracy can decline because of low carcass persistence for several taxa (Santos *et al.*, 2016). This particularly applies to taxa with small body sizes, such as small mammals (e.g. mice, voles and bats), which not only have lower detectability on roadkill surveys but have shorter persistence times compared to many taxa due to the ease of being scavenged (Ruiz-Capillas, Mata & Malo, 2015). Small sample sizes further preclude insight into long-term impacts on the structure and sustainability of populations. In general, there is a trade-off between spending resources to understand one population thoroughly, or several populations inadequately. As a result, guidance on how to design and maximise outputs from road mortality studies remains an important yet unfulfilled goal.

Although it is generally accepted that road mortality affects populations to some extent (Rytwinski & Fahrig, 2015), the literature is lacking a clear consensus on how road mortality affects the persistence of populations. This systematic review aimed to synthesise and categorise the direct and indirect demographic parameters in mammalian populations around the world that are affected by road mortality, as well as identify the study designs with the greatest inferential strength for assessing road mortality impacts at the population scale. By using a standardised systematic review protocol, existing knowledge can be gathered in an unbiased and comprehensive overview. The extent to which a road affects population persistence may depend on the particular circumstances, such as road density, species behaviour, species-specific habitat quality, and other threats (Roedenbeck *et al.*, 2007). Therefore, the scope of the present systematic review was kept global and broad to synthesise the results from studies conducted under a variety of circumstances. A focus on mammals is not only critical for their conservation, given the increasing threat of extinction of many mammalian populations, the wide range of mammalian life-history strategies provides valuable insight into different, simultaneous mechanisms affecting population resilience or vulnerability to road mortality (Grilo *et al.*, 2021). Recognising the demographic parameters affected by road mortality, or alternatively how populations cope under additional mortality, allows wildlife managers and conservationists to make transparent, quantitative, and informed decisions. Moreover, an understanding of robust study designs is imperative to build a strong evidence base for the targeted and effective actions around roads that are sorely needed.

II. MATERIALS AND METHODS

(1) Literature search

Following the identification of a relevant topic, research aims were developed in consultation with external subject experts in the scoping phase of the review. Experts included researchers, ecological consultants, and non-governmental organisations working in mammal conservation, road ecology, and/or road safety, including Mott MacDonald (consultancy: international; https://www.mottmac.com/), Rimba (non-governmental organisation: Asia; https://rimba.ngo/) and National Highways (government-owned company: England; https://nationalhighways.co.uk/). Following the guidelines proposed by the Collaboration for Environmental Evidence (CEE) (Pullin & Stewart, 2006), we performed a systematic literature search for studies around the world that documented mammal–vehicle collisions and that also provided information relevant to population demography. The CEE guidelines were chosen to enable standardised subject-specific identification of evidence to support conservation practise and road management. The literature search was conducted in April 2021, using two electronic databases: *Scopus* and *Web of Science* Core Collection®. Importantly, *Web of Science* incorporates several regional databases that allow searches for non-English-language literature. The search was created by a thorough scoping of the literature and a benchmarking process. The following Boolean search string was used in each database: (road-kill OR road-kill OR 'road kill') OR (mortalit* OR fatalit* OR strike OR collision AND anthropogenic OR vehicle OR road OR highway OR traffic OR motorway OR freeway OR expressway) AND (survival OR population OR viability OR threat OR decline OR extinction OR extirpation OR depletion OR dispers* OR movement OR migrat* OR genet*) AND NOT (vessel OR boat). The search was performed in English, French, Spanish, Portuguese, and Brazilian Portuguese (see online Supporting Information, Table S1), and no country limitations were applied. To ensure objective and comprehensive coverage, we included studies published in any print outlet as well as multi-taxa studies that may have relevant mammalian demographic data amongst that of other taxa. The search was restricted to publications reporting data

from 2000 to 2021, inclusive, to account for the drastic historical increase in global traffic volume (Schafer & Victor, 2000). However, traffic volume has continued to increase annually and no comparisons were made between studies based on the relationship between traffic volume and road mortality impacts.

In addition, the first 400 results of an advanced title search using the same search string on the meta-search engine *Google Scholar* were also checked for relevance to increase grey literature returns, particularly in the non-English language literature (Haddaway *et al.*, 2015). We also searched for papers, conference proceedings and technical reports published on additional online platforms, including conferences such as the International Conference on Ecology and Transportation (ICOET) and from road ecology centres such as the Western Transportation Institute. Thesis repositories of *Ethos* (UK) and *ProQuest* (worldwide) were used to search for relevant theses.

(2) Screening and inclusion criteria

All selected studies were subject to a stepwise selection process. Before screening for relevance, all studies were screened for duplicate data sets between sources with the most complete sources selected. Studies were then selected for inclusion using the *a priori* criteria based on consultation with experts shown in Table 1.

We assessed scientific studies for inclusion at three successive levels: first on titles (N = 11,238), then abstracts (N = 1,025), and finally full texts (N = 624). If a study investigated more than one taxon, species, or demographic parameter, all mammalian species and parameters were considered and data on each were obtained separately. Table 2 lists the inclusion and exclusion criteria applied at the full-text stage. Kappa analysis was used to verify the level of reviewer agreement on article inclusion at the third screening stage between two reviewers (L.J.M. and R.W.Y.). A random subsample of 10% of the studies was used (Kappa = 0.63, indicating 'substantial agreement' *sensu* Landis & Koch, 1977). There was 82% agreement between the two reviewers on the random subsample of studies. As appropriate inter-rater agreement for systematic reviews is regarded to be >80%, sufficient comparability between reviewers was achieved for this literature search (McHugh, 2012).

Table 1. *A priori* criteria used to select studies for inclusion during the systematic review.

	A priori criteria
Population	Wild mammal population in any country.
Intervention	Road collisions leading to the mortality of a mammalian animal. Any road type was considered.
Comparator	No comparator, gradient, or Before–After–Control–Impact (BACI) methods were necessary for inclusion.
Outcome	Any effect on population biology, including (but not limited to) *per capita* mortality, age/stage/sex-specific mortality, reproductive rates, movement, growth rates, genetic structure.
Types of study	Any empirical study or simulation using real-world data.

Table 2. List of inclusion/exclusion criteria at the full-text stage during the systematic search.

	Criteria
Included in the final set of papers	**Original research** – studies that presented empirical data on road mortality with any demographic data. This included simulation studies if using real data, either collected by the authors or from existing literature post-2000.
	Systematic data collection – road mortality figures collected in a systematic manner or from monitoring wild populations (e.g. *via* radio-collars) to ensure accuracy of collated data. Papers were excluded if they were not explicit about data-collection methods.
	Road mortality only – studies that assessed the impacts caused by roads, excluding other transportation infrastructure such as railways. Data were only included if reports of road mortality were presented separately from other transport collisions.
Excluded from the final set of papers	**Public involvement** – studies using records that were reliant on public involvement, such as from rescue centres, wildlife hospitals or citizen science, because of potential recorder inaccuracies, spatial auto-correlation and/or non-exhaustive samples due to an unknown, variable, and unbalanced sampling effort.
	Lack of population context – reports of sex- and age-specific roadkill or spatiotemporal roadkill patterns with no population context, such as population size, sex- or age-ratio.
	Outside of desired time period – studies that reported data spanning pre- and post-2000 and that could not be separated for quantitative analyses.
	Opportunistic data – studies that reported on roadkill data collected systematically and opportunistically but did not separate the data.
	Literature reviews – including meta-analyses.

(3) Data extraction, qualitative synthesis, and quantitative analyses

Meta-data, such as species, conservation status, and country, were tabulated for each relevant research study found.

Relevant information relating to the road mortality and demographic parameters of studied populations was identified and subsequently categorised into direct or indirect parameters based on established demographic theory and further sub-categorised (Krebs, 2009). Categories were formulated once the relevant studies meeting the inclusion criteria for this review had been identified. Study designs were similarly categorised after identifying the relevant studies. A narrative synthesis was undertaken using tables and figures that describe the evidence base itself and the findings of individual studies. To standardise data extraction from the variety of study designs, the proportion of a population killed on roads was calculated per year for each population for which relevant data were provided. Chi-squared tests were used to quantify the presence or absence of sex- or age-biases in the roadkill records relative to the source population.

III. RESULTS

(1) Overall results from the scientific literature

The search identified 15,298 studies, totalling 11,238 when duplicates were removed. Of these, 624 were assessed at the full-text stage and 83 studies (13.3% of the 624 studies) met the inclusion criteria and were retained for analyses. The main reason for exclusion of studies was that they lacked demographic data to accompany the road mortality figs (259 studies). Details on the search, screening and quality assessment results are summarised in Fig. 1.

Although the literature search was conducted in five languages, all studies meeting the inclusion criteria were in English. During abstract screening, 5.1% ($N = 52$) of studies or, as a minimum their abstracts, were in non-English languages, including French ($N = 16$), Brazilian Portuguese ($N = 14$), Spanish ($N = 12$), German ($N = 7$), Croatian ($N = 1$), Dutch ($N = 1$), and Russian ($N = 1$). In addition, 2.6% ($N = 16$) of full texts screened had the whole text or abstract in Spanish ($N = 7$), Brazilian Portuguese ($N = 5$) or French ($N = 4$). The reasons for the exclusion of these non-English language studies followed the same pattern as the studies in English (Fig. 1). The most common type of document was journal article ($N = 75$), followed by PhD thesis ($N = 3$), technical or government report ($N = 3$), book chapter ($N = 1$), and conference proceeding ($N = 1$). The studies were collated from 22 countries with the majority (57.8%) from North America (Fig. 2).

The studies retained for analysis reported data on 69 mammalian species from 10 taxonomic orders (Fig. 3). Out of the 69 species identified, 54 are categorised as Least Concern, five are Near Threatened, four are Vulnerable and six are Endangered (IUCN, 2021). The review revealed a variable but overall increasing number of publications reporting mammalian road mortality and demography between 2000 and 2021, ranging between one and nine papers published each year.

We categorised nine research methods amongst the identified studies (see Table S2 for identified advantages and disadvantages of these methods). The most common methods were radio-tracking only ($N = 52$) and year-round population monitoring only ($N = 10$). Thirteen studies combined systematic

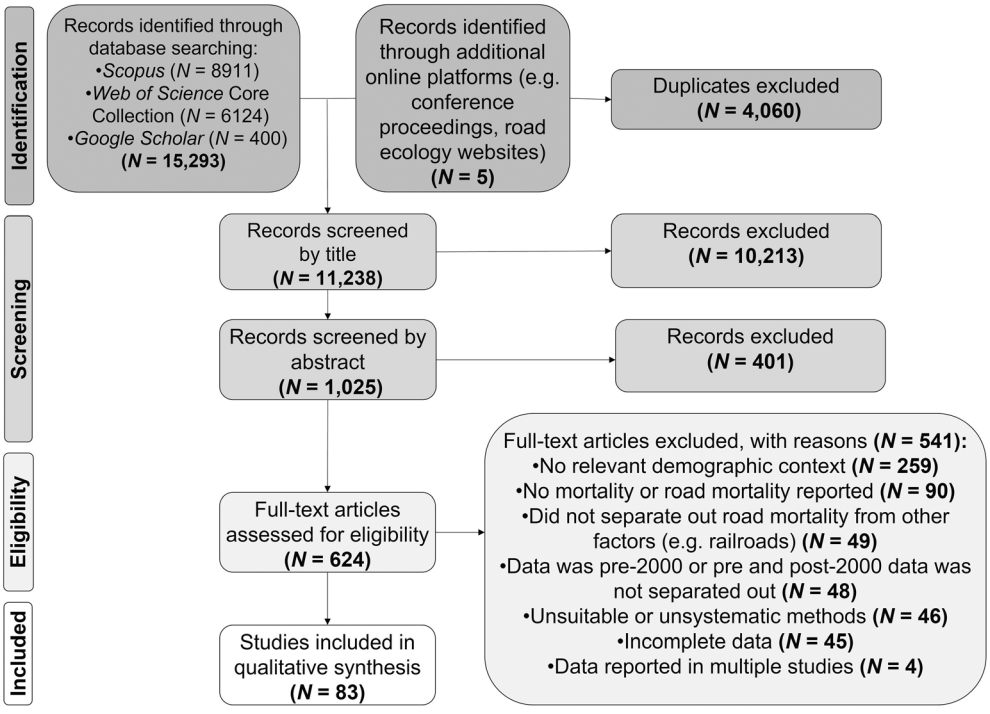

Fig. 1. Literature search and screening flow diagram of studies included and excluded from the systematic review.

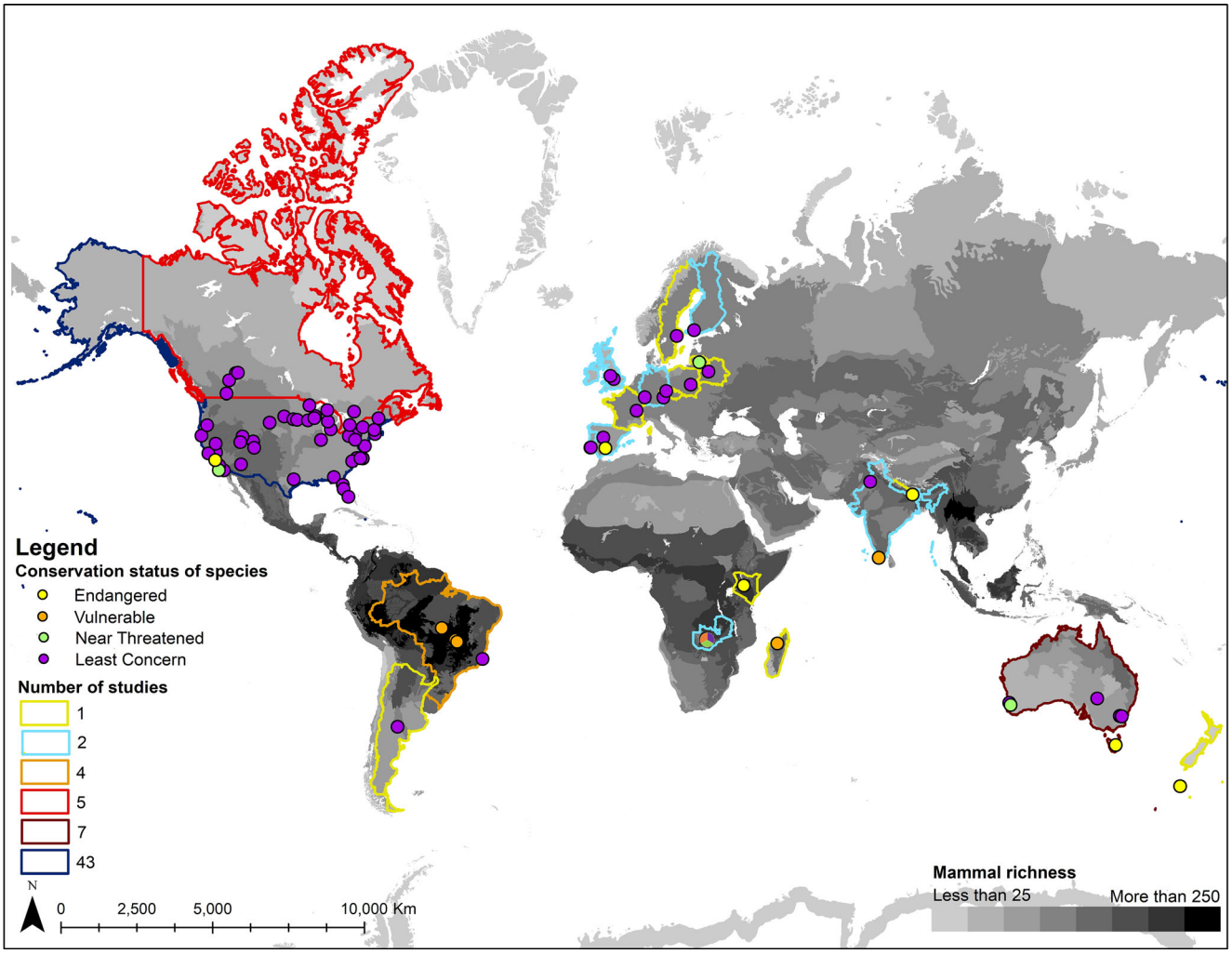

Fig. 2. Locations of the 83 studies included in the qualitative synthesis. Coloured points represent the centroid location of each study.

roadkill surveys with another survey method, including (*i*) a one-time population estimate (N = 6), (*ii*) radio-tracking (N = 1), (*iii*) population monitoring (N = 1), (*iv*) secondary population data (i.e. published population size estimates) (N = 3), (*v*) both radio-tracking and population estimate (N = 1). Two population estimates were conducted using genetic fingerprinting from hairs. Studies also combined population monitoring and radio-tracking (N = 3), and utilised simulations (N = 6) such as Population Viability Analyses. The average sample size for a radio-tracked population was 93 individuals (range: 2–492). Seven studies used Before–After (N = 2) and Control–Impact (N = 5) experimental designs but none used a Before–After–Control–Impact (BACI) design. Excluding simulation studies, study duration increased over time and ranged between less than 1 year to 17 years; four studies (5.2%) were less than 1 year in length, 52 studies (67.5%) were 1–5 years in length, 17 studies (22.1%) were 6–10 years in length, and four studies (5.2%) were 11–17 years in length.

Five direct and three indirect demographic parameters were identified in relation to road mortality (Table 3). Overall, 87.2% of the studies identified reported direct demographic effects of road mortality on the focal populations, whilst 12.8% reported indirect demographic effects of road mortality.

(2) Description of direct demographic parameters

(*a*) *Percentage of a population killed on roads per year*

Mortality on roads accounted for 0.02 to 50.0% of the local populations per year based on 61 studies, 40 species, and 85 populations. Twenty-six studies reported an annual loss of up to 1% on roads, 38 studies reported a loss of 1.1–5.0%, 14 studies reported a loss of 5.1–10.0%, four studies reported a loss of 10.1–20.0%, and the remaining three studies reported a loss of 30.0–50.0% from the population. Split by taxon, the percentage of the population killed on roads was greatest for Dasyuromorphia (quolls *Dasyurus* spp., Tasmanian devils *Sarcophilus harrisii*) and lowest for Cetartiodactyla (even-toed ungulates) (Fig. 4A). Intra-specific populations differed in the proportion of the population lost on roads annually. For example, white-tailed deer (*Odocoileus*

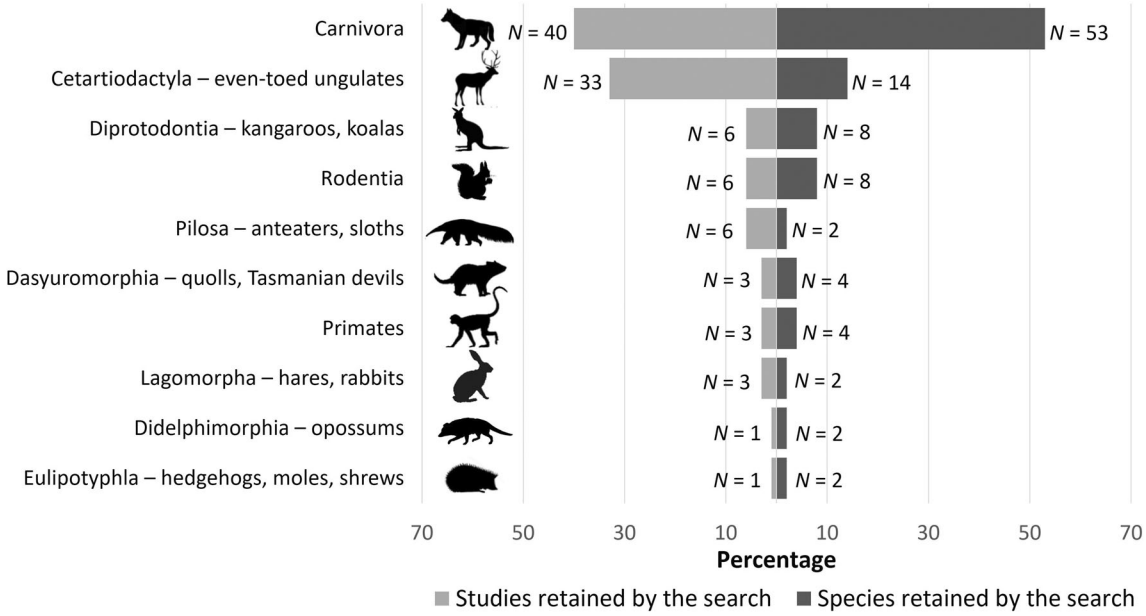

Fig. 3. Percentage and numbers of studies and species included in the systematic review, by taxon. Note that some studies reported data on several species. Various Artists/Shutterstock.com.

Table 3. Descriptions of the eight parameters categorised from the 83 papers retrieved during the systematic review.

	Demographic parameters	Description	Number of studies (percentage of studies)*
Direct	Percentage of a population killed on roads per year	The number of individuals killed on roads as a percentage of the total population per year.	61 (36.1%)
	Contribution to total mortality	The contribution of road mortality deaths relative to the total mortality rate in a set time period, such as a year.	58 (34.3%)
	Sex-biased road mortality	The ratio of males: females found killed on roads relative to the sex ratio in the population (i.e. whether one sex is killed on roads more than expected given their prevalence in the population). A significant chi-squared result was considered to represent a bias.	16 (9.5%)
	Age-biased road mortality	The ratio of adults: sub-adults: juveniles found killed on roads relative to the age ratio in the population. A significant chi-squared result was considered to represent a bias.	13 (7.7%)
	Roadkill during inter-patch or long-distance movements	Road mortality interfering with the success of movement-related behaviour that is not part of day-to-day activities (e.g. foraging), such as mortality during known dispersal events or migration.	7 (4.1%)
Indirect	Population growth rates	Temporal changes to population growth rate because of animals removed by road mortality.	7 (4.1%)
	Population persistence	The extent to which road mortality impacts the persistence of populations.	5 (3.0%)
	Genetic diversity	Changes to the heterozygosity within/between populations as a result of road mortality.	2 (1.2%)

*Note that several papers reported on more than one demographic parameter.

virginianus) had an 11.5-fold difference in proportional loss across four studies, whilst the annual proportional loss of beech martens (*Martes foina*) ranged from 1.11 to 33.0% between two studies (Table S3). In one study of six populations of American black bear (*Ursus americanus*) in Florida, USA, annual proportional loss ranged between 0.76 and 11.49% (Simek *et al.*, 2005).

(*b*) *Contribution to total mortality*

Between 1.1% and 80.0% of a population's total known mortality was due to roadkill out of 58 studies, 35 species, and 69 populations. Thirty-two studies reported a 1.0–15.0% contribution from road mortality to total mortality, 16 studies reported a 15.1–30.0% contribution, nine studies reported a 30.1–45.0% contribution, six studies reported a 45.1–60.0%

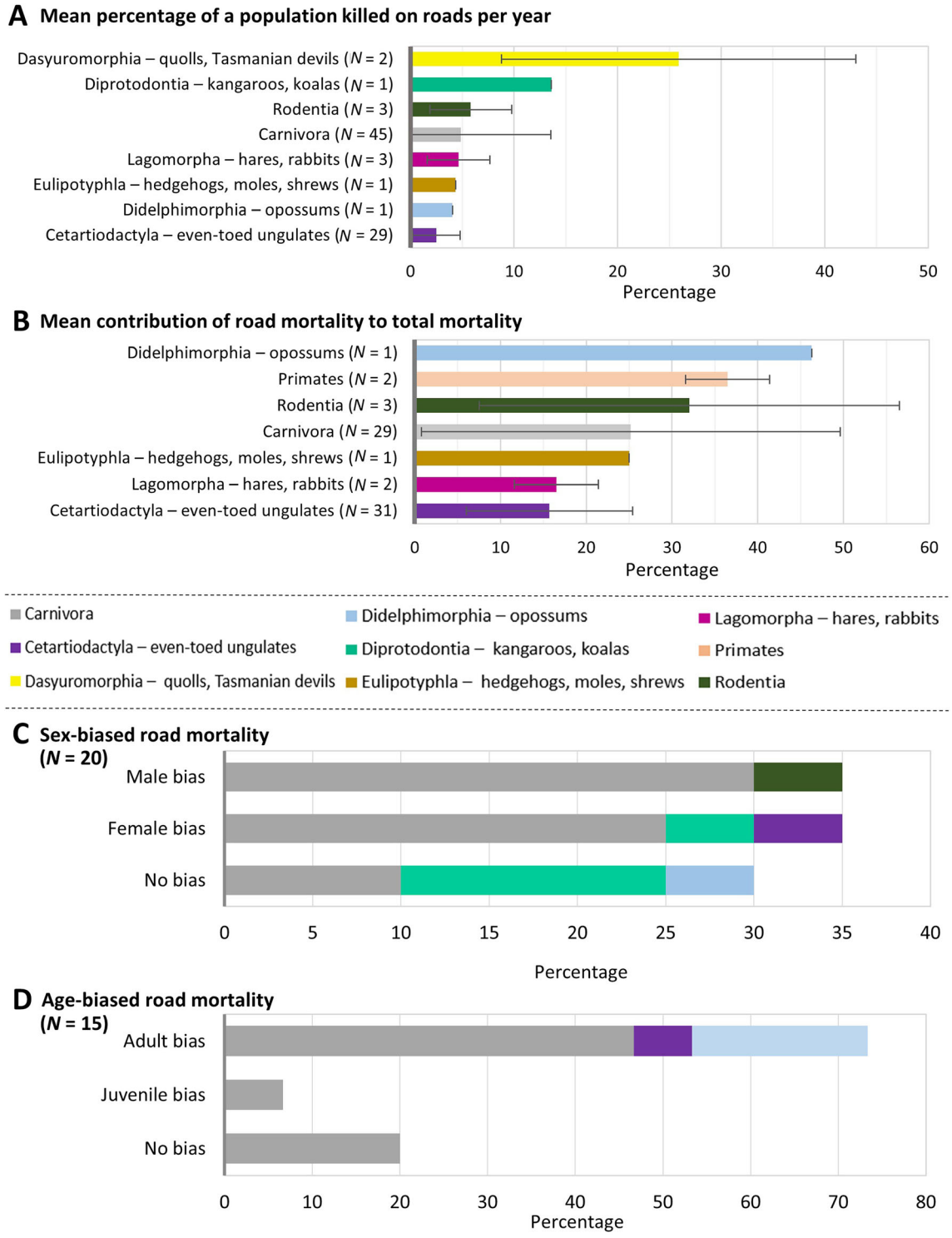

Fig. 4. Results from four direct demographic parameters identified by the systematic search. The number of studied populations is provided in brackets. (A) Mean percentage of studied populations killed on roads. (B) Mean contribution of road mortality to total mortality for the studied populations. (C) Percentage of populations with male-biased, female-biased and no sex bias to the road mortality records. (D) Percentage of populations with adult-biased, juvenile-biased and no age bias to the road mortality records. Error bars in A and B represent ±1SD.

contribution, and three studies reported a 60.0–80.0% contribution from WVCs to total known mortality. Split by taxon, the mean contribution of road mortality to total mortality was greatest for Didelphimorphia (opossums) and lowest for Cetartiodactyla (even-toed ungulates) (Fig. 4B). Data on cause-specific mortality was provided for 57 populations. Of these, 28.1% experienced road mortality as the largest contributor to total mortality, with a further 29.8% and 31.5% of populations experiencing road mortality as their second and third largest mortality factor, respectively. Other prevalent causes of mortality were hunting, predation and disease. Intra-specific population differences were evident for several Cetartiodactyla species such as elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*) and white-tailed deer, and Carnivora such as American black bear and puma (*Puma concolor*). For example, out of four studies, elk populations had a 20-fold difference in the contribution of road mortality to total mortality, whilst the contribution differed between six puma populations by 7.9-fold (Table S3).

(c) *Sex-biased road mortality*

Many studies that reported the sex ratio of roadkill (16 papers, 15 species, 20 populations) did so on small sample sizes of roadkill and therefore inference power of the results is low (Fraser *et al.*, 2013). Seven populations (35% of studied populations) experienced significantly more female road mortality than would be expected by chance (Fig. 4C; see Table S3 for chi-squared test results). For example, whilst female bobcats (*Lynx rufus*) made up 38% of the radio-collared population, 75% ($N = 4$ WVC) of the roadkill were females (Serieys *et al.*, 2021). Likewise, common wallaroo (*Osphranter robustus*) females were killed more than expected (observed: 9, expected: 2.4) relative to males (observed: 25, expected: 31.6) (Klöcker, Croft & Ramp, 2006). Conversely, seven populations (35% of studied populations) showed significantly male-biased road mortality, although again with small sample sizes (Fig. 4C; Table S3). For example, whilst 42% of American fishers (*Pekania pennanti*) in a population in California, USA, were male, 100% of the roadkill was male ($N = 2$ WVC) (Sweitzer *et al.*, 2016). Additionally, six populations (30%) identified in this review did not show any sex bias of the roadkill. Intra-specific population comparisons were possible for three species. Whilst two populations of red kangaroo (*Osphranter rufus*) showed the same lack of bias, two populations of both coyote (*Canis latrans*) and common wallaroo showed differing sex biases in their roadkill records (Table S3).

(d) *Age-biased road mortality*

Many studies that reported the age ratio of roadkill (13 papers, 9 species, 15 populations) did so on small sample sizes of roadkill and therefore inference power of the results is low (Fraser *et al.*, 2013). Eleven populations (73% of studied populations) experienced significantly more adult road mortality than would be expected by chance (Fig. 4D; see Table S3 for chi-squared test results). For example, whilst 54% of an American black bear population was comprised of adults, 100% ($N = 11$ WVC) of the roadkill was adults (Tri *et al.*, 2017). In comparison, coyote was the only species reported where sub-adults in the population were killed more frequently than would be expected by chance (25% of the population comprised of subadults, 100% of the roadkill was subadults, $N = 2$ WVC) (Stevenson *et al.*, 2016). In three populations (20% of studied populations), adults and juveniles were killed on roads in similar proportions to their populations (Table S3). Intra-specific population comparisons were possible for four species. Whilst two populations of white-tailed deer showed the same adult bias in road mortality, two populations of both coyote and puma showed differing age biases in their roadkill records. Out of five American black bear populations across two studies, four populations showed an adult bias whilst one population showed no bias in the roadkill records.

(e) *Roadkill during inter-patch or long-distance movements*

Seven studies on six species and 14 populations revealed movement parameters that are directly affected by roadkill. Two studies compared the routine movements of resident animals to the exploratory and migratory movements of translocated animals (Frair *et al.*, 2007; Wright *et al.*, 2020). For both elk and mule deer, authors reported that non-resident animals were more commonly killed on roads compared to residents (Frair *et al.*, 2007; Wright *et al.*, 2020). Moreover, three studies reported road mortality of dispersing animals (Kanda, 2005; Fey, Hämäläinen & Selonen, 2016; Carvalho *et al.*, 2018). Dispersal movements were shown to correspond to a heightened road mortality rate for young common genets (*Genetta genetta*) ($N = 38$ WVC) (Carvalho *et al.*, 2018). Two of the three dispersing rural female Virginia opossums (*Didelphis virginiana*) were killed on roads during dispersal movements (Kanda, 2005). Again, caution is recommended in interpreting these results because of the low inference power derived from small sample sizes. High road mortality of dispersing animals was not universally reported. One (3.2%) of the 32 tracked juvenile red squirrels (*Sciurus vulgaris*) died during dispersal movements in Finland, although three other dispersing individuals disappeared and traffic mortality remains a possible cause (Fey *et al.*, 2016). Migration was discussed in one paper: four (1.1%) out of 359 mule deer were killed in WVCs during migration in south-central Oregon, USA (Coe *et al.*, 2015).

(3) Description of indirect demographic parameters

(a) *Population growth rates*

Population growth rates were examined and reported in seven studies on 20 species and 22 populations. Chambers & Bencini (2010) examined population growth rates for three tammar wallaby (*Notamacropus eugenii*) populations. Road mortality reduced the population growth rate between

2005 and 2007 by 1–6% for a population in the relatively undisturbed southern bushland and 8–16% for populations in a highly developed neighbouring site. Desbiez, Bertassoni & Traylor-Holzer (2020) used empirical roadkill data for a Population Viability Analysis in Brazil and showed that the road mortality of giant anteaters (*Myrmecophaga tridactyla*) decreased the stochastic growth rate of that population by half. While population growth rates remained over 2% per year, the population's ability to withstand and recover from other anthropogenic threats such as fire and disease outbreaks was considered to be lower. Three studies collected empirical data on both road mortality rates and population growth for 16 populations, including Northern bushbuck (*Tragelaphus scriptus*), oribi (*Ourebia ourebi*), common hippopotamus (*Hippopotamus amphibius*) and common warthog (*Phacochoerus africanus*) (Belant, 2007; Ruiz-Capillas *et al.*, 2015; Nyirenda, Namukonde & Fushike, 2017). The road mortality rates of each of the 16 populations appeared sustainable and the population sizes continued to grow over several years. For example, an American marten (*Martes americana*) population experienced 12.5% of its mortality from vehicle collisions, yet the population size continued to increase at a rate of 16% per year over 3 years (Belant, 2007).

(*b*) *Population persistence*

Population persistence was reported in five studies on three species and 22 populations. Desbiez *et al.* (2020) reported that a loss of 18% of the adult giant anteater population due to road mortality in the Brazilian Cerrado resulted in a 47% probability of extinction in 100 years, compared to no extinction risk over 100 years of a baseline population under no significant threats. Desbiez *et al.* (2020) also reported a difference in effects based on sex-biased road mortality, whereby female-only roadkill produced a 46% probability of extinction in 100 years, compared to a 0.1% chance from male-only roadkill. Diniz & Brito (2013) calculated that if 15% of a giant anteater population in Parque Nacional Brasília, Brazil, were killed on roads, the population would reduce in size by 78% (180 to 40 individuals) in 5–6 years, followed by local extinction in <8 years. Finally, Roger, Laffan & Ramp (2011) conducted a sensitivity analysis for common wombats (*Vombatus ursinus*) in New South Wales, Australia. Populations with 40% annual road fatality (26.7 individuals ± 13.8 SD) presented high probability (50%) of decline, even for the largest initial abundance and carrying capacity values.

(*c*) *Genetic diversity*

Genetic diversity was examined in two studies, each examining a different giant anteater population in Brazil and showing similar results. Diniz & Brito (2013) examined the heterozygosity of giant anteaters in Parque Nacional Brasília in several roadkill scenarios. The simulations showed that with 25 individuals killed per year (15% of the population), most of the original genetic diversity within the population was maintained. For a giant anteater population in the Brazilian Cerrado, Desbiez *et al.* (2020) showed that the population at year 100 had 95% genetic diversity remaining under the present road mortality scenario. However, genetic diversity was more severely reduced in simulated populations experiencing road mortality of both sexes (heterozygosity = 0.798), followed by female-only mortality (heterozygosity = 0.835), compared to male-only mortality (heterozygosity = 0.948) (Desbiez *et al.*, 2020).

IV. DISCUSSION

Gathering mammalian demography data is notoriously difficult (Stenglein *et al.*, 2015). During the stepwise selection process, 305 studies were removed because of a lack of demographic data accompanying roadkill counts or the use of unsystematic study design, leading to an incomplete or unreliable data set for population-level assessments. Therefore, despite intensive global research over the past 20 years, many critical questions about long-term impacts of road mortality remain unanswered. We explicitly searched for and retained studies reporting road mortality impacts on demographic parameters for this review because we intended to synthesise data on how road mortality affects populations and not the extent of road mortality worldwide. As such, this review draws no conclusions about the number of populations free from the risk of WVCs, although previous studies have indicated that most terrestrial populations are vulnerable to vehicle collisions (Barrientos *et al.*, 2021; Hill *et al.*, 2019). It must be emphasised that several studies identified in this review are based on small roadkill sample sizes. This may be a function of the relatively short duration of many studies and the difficulty in identifying sex from decomposed or damaged carcasses. Therefore, it is unclear how well these results represent the wider population.

Despite our systematic literature search being conducted in five languages and studies included from 22 countries, studies that met the inclusion criteria were only in English. This could be a result of a publication bias towards research-intensive and developed countries that have a greater prevalence of English speakers (Nuñez & Amano, 2021), and/or that non-English studies often have less-robust study designs than the English literature (Amano *et al.*, 2021). Consequently, the latter may result in English-language studies being published in higher-impact journals that stipulate articles to be written in English, which also have more thorough indexing procedures for well-known literature search systems compared to non-English journals (Amano *et al.*, 2021).

(1) Direct demographic parameters

(*a*) *Depletion effects*

Many studies identified in this review revealed that road mortality can remove a large number of animals from the population compared to population size or other mortality factors (e.g. Grueber *et al.*, 2017; Seiler, 2003; Lehrer, Schooley & Whittington, 2012; McCleery *et al.*, 2008).

In particular, road mortality was the greatest source of mortality for approximately one-third of populations for which data were provided ($N = 16$ out of 57 populations). Twelve of these populations were surrounded by urbanisation or anthropogenic development, as opposed to natural forests, savannahs, and National Park for example. This highlights the well-cited link between urbanisation and additional anthropogenic mortality (McCleery *et al.*, 2008; Tri *et al.*, 2017; Wright *et al.*, 2020). Large individual losses on roads can directly reduce the effective population size and/or increase mortality rates above recruitment rates, therefore making populations vulnerable to environmental and demographic stochasticity, as shown for many species (Carvalho & Mira, 2011; Roger *et al.*, 2011).

The way in which high roadkill rates shape population persistence is likely to be nuanced, possibly explaining the variation in road mortality impacts on intra-species populations identified in this review. The impacts likely depend on the suitability of the surrounding environment and associated background demographic parameters such as population growth and the potential for compensating mechanisms (Seiler, 2003) (see Sections III.3 and III.4). Crucially, the relative importance of road mortality is likely to be context specific as the road configuration and habitat quality surrounding a population can vary, for example between core and edge habitats or along the urban–rural gradient (Lehrer *et al.*, 2012). These in turn affect population dynamics, including population densities which are a key factor in determining the level of road mortality that a population can sustain (Wright *et al.*, 2020).

For some populations, roadkill can have a small effect on the persistence of the population (Cypher, Bjurlin & Nelson, 2009; Sidorovich, Novitsky & Solovej, 2020). It is thought that species with fast life histories experiencing high fecundity, large population densities and rapid population growth are more able to replace lost individuals quickly (Rytwinski & Fahrig, 2015). Fifteen populations identified in this review continued to show stable or increased growth rates over three or more years despite relatively high road mortality. Many of the identified species meet some or all elements of fast life histories, such as American martens and 13 ungulate species (Belant, 2007; Ruiz-Capillas *et al.*, 2015; Nyirenda *et al.*, 2017). A knowledge gap remains for small mammals, such as mice, voles and bats, however. This is because low carcass detectability and persistence preclude accurate roadkill rate estimates and therefore conclusions about the extent that roadkill depletes these populations. Of note, 14 of the 15 populations shown to have stable or increased growth rates despite road mortality inhabited National Parks. This suggests that high-quality, protected environments can contribute to the resilience of populations to anthropogenic threats such as roads (Nyirenda *et al.*, 2017; Pereira *et al.*, 2010).

(*b*) *Sex- and age-biased road mortality*

It is noteworthy that road mortality appeared to be adult-biased in 10 out of 15 studies that provided relevant data, which is likely a consequence of the greater roaming behaviour of adults to find mates and food. Mammalian age-specific survival is typically characterised by low rates in young animals and high rates in adults (Arso Civil *et al.*, 2019). Changes in adult survival can have the greatest effect on population trajectories, particularly for species where adult lifespans are long relative to the time taken to reach maturity (Chambers, 2009). Therefore, adult-biased road mortality is a pertinent concern as it reduces effective population sizes and reproduction rates. However, whether adults and juveniles have different detection probability (e.g. because of the smaller size of juveniles), which may bias estimates of population structure and therefore any inference from the data, remains unknown.

As sex structure and mortality are central to population stability, a sex bias in road mortality can be used in projections of longer-term impacts (Klöcker *et al.*, 2006). A relatively even spread of male, female and no bias to roadkill was found amongst the retained studies, although the number of studies identified was small. A lack of sex bias in road mortality is unlikely to affect a population's persistence beyond the general depletion of individuals as the population structure is likely to remain unchanged. There is a strong narrative in the literature that males are more vulnerable to roadkill than females (Green-Barber & Old, 2019; Miotto *et al.*, 2012). However, whilst males are often killed on roads more frequently than females, this review shows that males are not necessarily killed more than would be expected based on their numbers in the population. Variations in sex-specific survival rates moderate population dynamics and the severity of these impacts is likely to depend on the species' social structure and mating systems. Female survival typically exerts a greater effect on population trends than male survival. Low, but consistent, female road mortality may cause a male-skewed population, as similarly shown for reptiles (Mitro, 2011); males become mate limited and female fecundity is reduced, generating Allee effects and increasing population extinction risk (Simmons *et al.*, 2010).

For species that live in family groups, female road mortality has been shown to exert indirect, sublethal effects on the recruitment of populations. The death of a mother by vehicle collisions can lead to the death of dependent juveniles, either by starvation (Snow *et al.*, 2012) or infanticide (Logan & Runge, 2021). Vehicle collisions of male or females were responsible for 2.1% of bond dissolution within a grey wolf (*Canis lupus*) population in Scandinavia, which can destabilise social structure and reduce population growth (Milleret *et al.*, 2017). For solitary and territorial species, the impact of male- or female-biased road mortality may be dependent on territory ownership and whether other reproductively viable individuals are able to fill the vacant breeding territories (Riley *et al.*, 2006; Mumme *et al.*, 2000). Overall, studies identified in this review agreed that adult-biased, and specifically female-biased, road mortality are likely to be critical to population dynamics.

(*c*) *Roadkill during inter-patch or long-distance movements*

Three out of the four studies reporting information on the road mortality of dispersing animals reported relatively high

roadkill rates (Kanda, 2005; Carvalho *et al.*, 2018; Pereira *et al.*, 2010). Risk of road mortality during dispersal or extra-territorial excursions has also been shown for some birds (Mumme *et al.*, 2000; Bujoczek, Ciach & Yosef, 2011) and reptiles (Bonnet, Naulleau & Shine, 1999). A suite of geographical positioning system (GPS)/radio-tracking data indicate that the risk could be a function of a greater road crossing frequency during dispersal than during exploratory or routine movements (Grilo *et al.*, 2012; Fey *et al.*, 2016). When road mortality of dispersing animals is high, patch connectivity is limited and gene flow is restricted (Jackson & Fahrig, 2011; Balkenhol & Waits, 2009). In extreme cases, high road mortality for populations in patchy habitat networks may lead to source–sink dynamics, as speculated by Grilo *et al.* (2012) for a roadside population of beech martens in Portugal. Collevatti *et al.* (2007) also suggest that the high inbreeding within a giant anteater population in Emas National Park in Brazil may be, at least in part, a result of extensive roadkill between the park and nearby Cerrado fragments, hence decreasing migration and gene flow. Therefore, it remains possible that road mortality may be influencing the dynamics of subpopulations far from roads. However, a high mortality of dispersers does not necessarily lead to subdivision (Carvalho *et al.*, 2018), suggesting that in some cases, even a small number of successful dispersers can ensure sufficient gene flow and prevent the development of spatial genetic structuring.

(2) Indirect demographic parameters

Several authors highlighted the vulnerability of population growth rates of some, but not all, populations to road mortality in the short term. Changes to growth rates, and hence population persistence, as a result of roadkill may be mediated by lower effective population sizes and/or altered mortality:recruitment ratio. Population persistence may be particularly threatened by roadkill if the (sub)population exhibits site fidelity and/or lives in patchy habitat that may decrease immigration due to increasing patch isolation (Snow *et al.*, 2012). It is possible that under certain conditions, such as areas extensively and/or rapidly modified by humans, individuals select roadside habitats for favourable resource availability. In turn, these populations are subject to ecological trap dynamics following lower survival in roadside habitats (Battin, 2004). These dynamics can shape population structure and sustainability and have previously been reported for Eurasian lynx (*Lynx lynx*) (Basille *et al.*, 2013) and several bird species including mourning wheatears (*Oenanthe lugens*) (Ben-Aharon, Kapota & Saltz, 2020) and Florida scrub jays (*Aphelocoma coerulescens*) (Mumme *et al.*, 2000).

Road mortality may not directly cause local extinctions for all impacted populations, especially if the species-specific habitat quality is high and so populations are relatively resilient to environmental stressors. However, collisions can make populations more vulnerable to environmental and demographic stochasticity, as shown for common wombats (Roger *et al.*, 2011) and giant anteaters (Desbiez *et al.*, 2020). Most animal populations are subject to multiple stressors that operate at various spatial and temporal scales and interact to some degree, either additively or synergistically (Doherty *et al.*, 2015). For example, Roger *et al.* (2011) showed that intermediate levels of roadkill of common wombat individuals in the Kosciuszko National Park in New South Wales, Australia, caused the population to be more sensitive to variation in juvenile survival and even low roadkill levels increased their vulnerability to fires. For species with slow breeding rates, as is the case for common wombats, populations are less able to offset high mortality rates attributed to roads or other threats. In turn, immigration from the surrounding area will be important for the persistence of these roadside populations (Rytwinski & Fahrig, 2015).

It is possible that road mortality can indirectly impact populations that are otherwise resilient to WVCs by causing the loss of ecologically functional species, such as apex predators. Trophic cascades and changes to interspecific associations are a well-known result from the decline of key species (Fischer *et al.*, 2012). Road mortality that causes the local extinction of key predator species may incite a mesocarnivore influx, changing ecosystem structure and the vital rates of populations in the wider ecological community (as reported for other mortality causes; Hollings *et al.*, 2014).

(3) Compensatory and additive mechanisms of road mortality

The demographic impacts of road mortality were shown to be highly variable amongst the study species and intraspecific populations identified in this review. This may be a function of the small roadkill sample sizes of several studies retained by the search, which makes the results inherently inconsistent. The variable results also demonstrate that the interplay of roadkill with other context-specific factors, and how that affects the mortality:recruitment ratio, will influence the capacity for populations to persist despite road mortality (Roger *et al.*, 2011). Extrinsic and intrinsic factors can affect whether road mortality is additive to natural mortality, resulting in a net reduction in total survival rates, or is compensated for by a reduction in natural mortality and/or increased reproductive rates (Sparkman, Waits & Murray, 2011). Studies identified in this review report both additive and compensatory mechanisms of road mortality. For example, Burroughs *et al.* (2006), Tri *et al.* (2017) and Logan & Runge (2021) found that white-tailed deer, pumas and American black bears had a greater level of road mortality in conditions with lower mortality from other anthropogenic causes (e.g. harvesting, humane lethal control). However, Chambers & Bencini (2010) found both compensatory and additive mechanisms for the road mortality of tammar wallaby populations in Australia, suggesting that road mortality impacts depend on other factors that also affect vital rates. Additive road mortality has also been reported in red wolves (*Canis rufus*) (Sparkman *et al.*, 2011) and, in addition to mammals, in several bird species

(Bujoczek *et al.*, 2011), spotted salamander (*Ambystoma maculatum*) (Gibbs & Shriver, 2005) and turtles (Congdon, Dunham & van Loben Sels, 1994). It is likely that, in many cases, road mortality is neither completely additive nor compensatory. This is because road mortality is, to some extent, influenced by density-dependent mechanisms and its consequences on population dynamics can also depend on which individuals are killed on roads and when (Desbiez *et al.*, 2020). This is corroborated by Lehnert, Bissonette & Haefner (1998) who demonstrated that for a mule deer population in the USA, 50% of all animals killed on the highway would have died from non-road causes before the next breeding season. Nevertheless, mechanisms underlying either compensatory or additive effects of road mortality remain poorly understood and warrant further investigation to improve the accuracy of road mortality assessments.

Of great concern is that rare and threatened species often have (sometimes naturally) small population sizes and/or a population growth rate that is close to zero or negative (Desbiez *et al.*, 2020). As such, even a low but uncompensated road mortality rate can remove a significant percentage of the population, thereby constraining annual survival and inducing or exacerbating population decline (Sparkman *et al.*, 2011). This has important implications for conservation because when road mortality is additive, mitigation efforts around roads are a more pressing requirement than if compensatory mortality is assumed.

(4) Considerations for road ecology study design

It can be argued that population growth is a fundamental parameter of interest in studies of anthropogenic mortality and quantifying it should be prioritised. Although population size and raw roadkill counts are useful, they are a stationary snapshot and unlike population growth, they do not consider the impact of demographic variability and its role in any compensatory processes (Seiler, 2003).

The methods used and sample sizes collected can drastically alter the conclusions of road mortality impacts. There are typically three methods to obtain roadkill data: (1) systematic road surveys; (2) radio-tracking (and associated telemetry technologies such as GPS and satellite tracking) or constant population monitoring; and (3) opportunistic records (often via unstructured citizen science) (see Table S2). Radio-tracking tailored to the focal species provide a less-biased sample because most road mortalities are usually detected. Roadkill surveys, whether systematic or not, are more targeted and can detect a large proportion, but rarely all, of the roadkill present. However, efficiency of the surveys and carcass detectability can be low depending on survey frequency and carcass size. Non-systematic surveys such as from citizen science participants have additional issues of bias across the survey area depending on the geographic spread of surveyor effort. Moreover, opportunistic records such as *ad hoc* observations from park wardens or tourists could bias the significance of mortality factors because death events are detected differently (Pereira *et al.*, 2010). However, data from radio-tracking can often only be based on a small sample of individuals. Such studies might not be free of bias nor be representative of the wider population depending on the method used for capture (Stenglein *et al.*, 2015), meaning mortality data should also be interpreted cautiously. For example, Pereira *et al.* (2010) reported that 18% (seven individuals) of a Geoffroy's cat (*Leopardus geoffroyi*) population in central Argentina was killed on roads when using opportunistic sampling and ranger interviews to record carcasses, yet only 5% (one individual) of a radio-tracked subset of the same population was killed on roads.

(a) *Improving study design*

Replicated, manipulative study designs such as BACI are considered the highest standard of study design in road ecology (Rytwinski & Fahrig, 2015). These studies can be used to detect demographic changes, particularly at the genetic level, and to separate confounding factors (Fig. 5). Of the 83 studies included in this review, seven studies used experimental designs – two studies used Before–After and five studies used Control–Impact, often comparing urban or high-density road networks to rural or low-density areas. Collecting sufficiently long-term data both pre- and post-road construction, as per BACI protocol, is usually difficult to achieve because many roads have already been built or their construction is imminent at the research conception stage. The majority (72.7%) of studies identified in this review were less than 5 years in duration. The length of a study on road mortality should be species-appropriate and cover more than one generation. Longer-term studies can overcome the challenges of small roadkill sample sizes and of quantifying population demographics and their variability, particularly for long-lived species and when combined with individual-based methods such as marking individuals (Desbiez *et al.*, 2020). The large costs associated with long-term, manipulative studies can be shared with collaborative research action (see below) (Fraser *et al.*, 2013).

Genetic studies are a critical component of examining the long-term viability of roadside populations. However, neither of the two retained studies that reported the effects of road mortality on genetic diversity used empirical genetic data (Diniz & Brito, 2013; Desbiez *et al.*, 2020). The development of genotypic approaches (analyses based on the genotypes of individuals) and high-resolution molecular markers (e.g. single nucleotide polymorphisms) offers powerful methods to examine fitness-related genetic effects, such as population genetic structure, fragmentation, and diversity (Balkenhol & Waits, 2009; Simmons *et al.*, 2010; Jackson & Fahrig, 2011). For example, genotypic approaches such as genetic pedigree, spatial-autocorrelation, and parentage analysis can identify important within-population processes, including demographic history and sex-biased dispersal (e.g. across roads) (Balkenhol & Waits, 2009). Such approaches can be informative at fine spatial and temporal scales, can be readily scaled up, are complementary to the other field-based approaches, and are becoming less

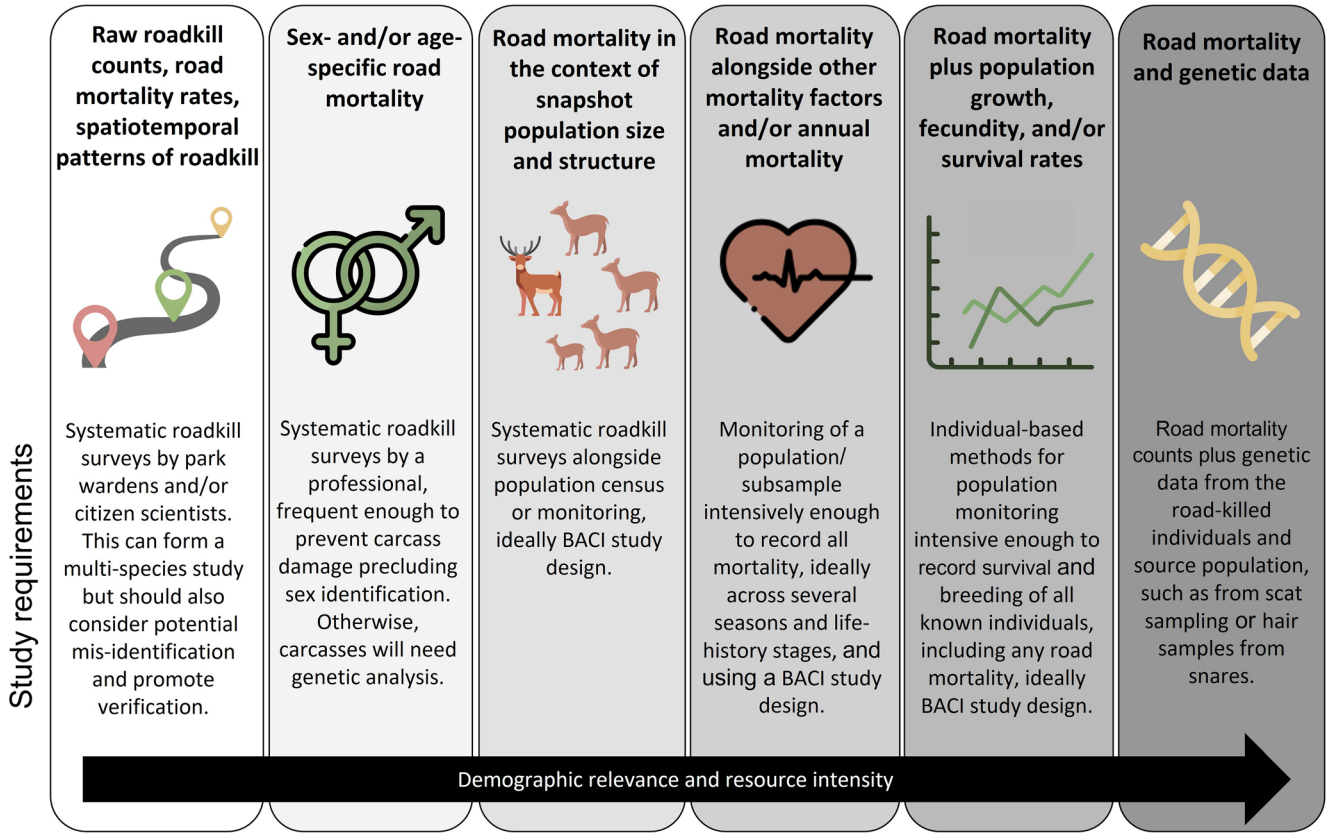

Fig. 5. Suggested hierarchy and requirements of study designs relevant to examining the impacts of road mortality on population persistence. BACI, Before–After–Control–Impact. Various Artists/Flaticon.com.

expensive over time (Corlett, 2017). Moreover, advances in laboratory protocols, such as polymerase chain reaction (PCR) from tissues of road-killed animals, can improve sex identification of badly decomposed or damaged roadkills, or roadkills of monomorphic species (Barragán-Ruiz *et al.*, 2021).

Population viability can depend on the extent and nature of dispersal and immigration between road and non-road habitats (Mumme *et al.*, 2000). Therefore, studies that combine radio-tracking data, or radio-frequency identification (RFID) tags and related transponders (Testud *et al.*, 2019), with roadkill data can incorporate explicit assumptions about successful and unsuccessful road crossings (Fahrig & Rytwinski, 2009; Riley *et al.*, 2006). Ultimately, a blend of genetic and field-based approaches with appropriate statistical modelling, as shown by Carvalho *et al.* (2018), is needed to assemble the suite of relevant data for accurate road mortality assessments (Fig. 5). Importantly, cost analyses should be integrated into study planning to enable efficient resource allocation for research, and likewise for any subsequent mitigation, in turn improving returns for investment (White *et al.*, 2022). Sharing the monetary costs associated with robust study design will likely require collaborative experimental research at an international scale. Collaborations can pool resources more easily, including expertise, money, and equipment, across several road networks, simultaneously improving the quality of study design and sample sizes (Fraser *et al.*, 2013; Rytwinski & Fahrig, 2015).

(5) Future research directions

Despite the increasing interest and research focus over recent decades, more detailed road mortality studies are needed to ensure a robust understanding of demographic impacts on mammalian populations and that efforts to reduce such impacts are focussed on the most at-risk populations. The interaction between road mortality and movement behaviours, such as dispersal and migration, remains relatively under-studied. Future research should investigate the replacement rate following the death of a breeder in areas intersected by roads and the success rate of dispersing individuals across roads. Appropriate context will be essential in interpreting these results, considering that road crossings by dispersing subadults do not necessarily translate into gene flow (Riley *et al.*, 2006). How often road mortality contributes to the reduction in genetic integrity and the shape of that decline over time (e.g. linear, exponential) should also receive research attention. To understand a population's capabilities to sustain ongoing road mortality, investigations into whether road mortality is compensated for, even partially, by

increased survival, reproduction or migration should be prioritised.

V. CONCLUSIONS

(1) The conservation of wildlife populations impacted by roads has gained recognition as an issue of worldwide concern. We found that studies collecting data on the demographic effects of road mortality are relatively rare, but some generalities emerge from the existing literature. The 83 retained studies from the systematic search demonstrate that road mortality can place substantial pressure on population size and/or background mortality rates. Female-biased road mortality appears more frequent than previously recognised in the literature and is likely to be a critical element in negative population trajectories. Due to a common occurrence of adult-biased road mortality, wildlife–vehicle collisions (WVCs) place a heavy toll on species that naturally experience high adult survival.

(2) It is evident that the demographic effects of road mortality are not limited to the immediate location or time period of the WVCs. Long-term (meta-)population dynamics and populations far from roads may be affected by lower survival and unsuccessful dispersal near roads inciting source–sink dynamics. However, some populations can tolerate additional mortality and maintain population growth over several years, most likely a result of high reproductive rates.

(3) Understanding how road mortality shapes the structure and sustainability of wildlife populations is challenged by the complexity of underlying processes. Road mortality interacts with demographic and environmental variability in populations, causing context-specific responses to road mortality.

(4) This review stresses that conservation strategies that seek to address the impact of roads must collect data on relevant demographic parameters, such as population growth and survival rates, as well as an assessment of concurrent threats to the target population(s). Studies that use rigorous study design, ideally with a combination of methods and/or using an experimental design, will hold the greatest inferential strength for assessing population-level impacts of WVCs. Examining the link between road mortality and movement behaviours, as well as additive or compensating mechanisms to road mortality, should be research priorities for more accurate insight into long-term consequences.

(5) The knowledge gathered from this review is a step towards sustainable road development and maintenance amidst growing road networks, particularly in megadiverse and developing countries that hold some of the world's most threatened species and last remaining wilderness areas. Moving forward, quantifying the demographic impacts of road mortality should become an established process within comprehensive road mortality assessments and the planning of impact mitigation to enable proactive conservation action of populations at risk.

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VIII. SUPPORTING INFORMATION

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

Table S1. Search strings of the five languages used in the systematic literature search.
Table S2. Suggested advantages and disadvantages of various study designs identified in the systematic review in relation to their ability to collect data relevant for interpreting population-level impacts of road mortality.
Table S3. Key data collated from the final set of articles identified in the systematic search.

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