Perspectives in Ecology and Conservation 19 (2021) 411–416

Perspectives in ecology and conservation

Supported by Instituto Tecnológico Vale

www.perspectecolconserv.com

Essays and Perspectives

The lost road: Do transportation networks imperil wildlife population persistence?

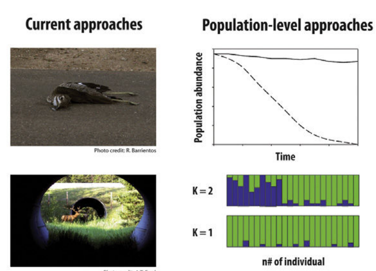
Rafael Barrientos[a,*], Fernando Ascensão[b], Marcello D'Amico[c], Clara Grilo[d], Henrique M. Pereira[c,e,f]

[a] Road Ecology Lab, Department of Biodiversity, Ecology and Evolution, Faculty of Biology, Complutense University of Madrid, José Antonio Novais, 12, E-28040, Madrid, Spain
[b] cE3c - Centre for Ecology, Evolution and Environmental Change, Faculdade de Ciências, Universidade de Lisboa, 1749-016, Lisboa, Portugal
[c] THEOECO, CIBIO-InBIO, University of Porto and University of Lisbon, Tapada da Ajuda Campus, 1349-017, Lisbon, Portugal
[d] Department of Biology, Faculty of Sciences of the University of Lisbon & Centre for Environmental and Marine Studies (CESAM), University of Aveiro, Portugal
[e] German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig Deutscher Platz 5e, 04103 Leipzig, Germany
[f] Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany

HIGHLIGHTS

- The global road network is rapidly growing.
- Population-level studies represent a minority on road ecology.
- Most of them focused large mammals from high-income countries.
- More research on threatened species from developing countries is need.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 7 May 2021
Accepted 21 July 2021
Available online 17 September 2021

Keywords:
Barrier effect
Fragmentation
Habitat loss
Mitigation
Population viability analysis
Roadkill

ABSTRACT

The global road network is rapidly growing associated with human economic development. This growth also entails a high toll for biodiversity, with several well-documented negative impacts on different species. However, there is still a great lack of knowledge about the effects of roads on the persistence of wildlife populations. Here, we aimed to summarize our current knowledge on this topic, based on systematic reviews. We found that only a small proportion of studies (8%) focused on the effects of roads on population persistence. Most of these studies were about large mammals and were performed in high-income countries. Furthermore, these works studied only 2% of those species identified by the IUCN Red List as threatened by roads. Overall, our results show that we are far from understanding how roads affect the long-term viability of wildlife populations inhabiting road-effect zones. Addressing this challenge will require modifying our conceptual perspective, from short-term to long-term studies, from single road sections to focusing the landscape scale, and strive to obtain empirical data to support sound analyses to assess how road impacts affect the survival of wildlife populations, namely with information required to perform approaches such as population viability analyses. We highlight some key studies from our reviews that have addressed this global conservation concern with population-oriented approaches.

Introduction

The global road network is spreading across the entire surface of the world, from deserts to tropical forests. Road development aims

* Corresponding author.
E-mail address: rbarrientos@ucm.es (R. Barrientos).

https://doi.org/10.1016/j.pecon.2021.07.004

to accelerate economic growth and social integration, facilitating the transportation of people and goods, and decreasing production costs (Laurance et al., 2014; Alamgir et al., 2017). However, roads and related human activity entail many negative impacts on wildlife, including both direct ones such as roadkill, barrier to movement, habitat loss and fragmentation or pollution, and indirect impacts such as overexploitation of resources or habitat degradation derived from the increased accessibility to natural areas (Laurance et al., 2014; van der Ree et al., 2015; Ascensão et al., 2018).

Overall, we know that most animal species can be impacted by roads to some extent, but our knowledge in this field is still far from understanding how these impacts threaten the persistence of their populations. Achieving this knowledge is essential to properly delineate future road development and to mitigate existing ones. To confirm the research needs, we conducted a literature search with the aim of assessing publication trends related to the effects of roadkills, habitat loss and fragmentation, and mitigation actions on population persistence. We aim that, by identifying current knowledge gaps in this discipline, we will help foster evidence-based conservation programs that result in more effective actions to ensure the survival of wildlife population impacted by roads.

Research trends on population persistence along roads

We carried out three systematic bibliographic searches to understand whether the impacts of roads on population persistence are receiving proper attention by scientists, focusing on roadkill, habitat loss and fragmentation, and mitigation effectiveness, respectively. While our goal was not to carry out an exhaustive review, our search represents a quantitative starting point to develop our suggestions.

Bibliographic searches and filtering criteria

To understand whether population-level approaches in road ecology are receiving attention by scientists, we searched articles appearing in ecology-related journals focused in three topics: (i) mortality due to vehicle roadkill; (ii) fragmentation and habitat loss caused by roads; and, (iii) studies evaluating the actions addressed to mitigate these two impacts.

We used the ISI Web of Science (https://apps.webofknowledge.com) to search for publications focusing these topics. We limited the search to ecology-related journals, specifically in the categories *Biodiversity Conservation*, *Ecology*, *Environmental Sciences* and *Zoology*. We further considered only the Science Citation Index Expanded (SCI-EXPANDED) for the timespan 1900-present. Searches were performed on November 2nd, 2020. We performed three separate searches, according to the different topics related to road ecology research (see below, in bold), all with the common terms "*(wildlife OR animal*) AND (road* OR highway* OR motorway*)*".

We added specific terms in each of the three searches. Namely, for **Roadkill** we added "*AND (mortality OR roadkill* OR road-kill* OR "road kill*" OR collision* OR wildlife vehicle collision* OR accident*)*"; for **Habitat loss and fragmentation** we added "*AND (fragmentation OR avoidance OR "barrier effect" OR connectivity)*"; and for **Road mitigation** we added "*AND (mitigation OR "safe passage*" OR "canopy bridge*" OR ecoduct* OR bridge* OR "green bridge*" OR "wildlife bridge*" OR fencing OR fence OR "crossing structure*" OR culvert* underpass* OR overpass* OR "animal detection system*" OR "wildlife reflector*")*". In a second round of searches, we selected the **population-oriented** articles by including the following additional terms in each of the first three searches: "*AND ("population persistence*" OR "population viability" OR "population recovery" OR "population decline*" OR "population growth*" OR "population dynamic*" OR "population size*" OR "population structure*" OR "population density" OR "population genetics" OR "population health" OR "population viability analysis" OR extinction* OR extirpation* OR depletion*)*". One of us (RB) reviewed all the papers identified in these latter searches to confirm that they were really focused on population-level. We further retained information on where each study was carried out (country, classified as *high-income* or *others* following the World Bank criteria) and the target species. We also recorded the global category of threat of the target species following the Red List from the International Union for Conservation of Nature (IUCN).

Population-level studies from our searches cover topics such as how road mortality hampers population viability, genetic structuring caused by reduced connectivity or how road proximity conditions territory use or alters population density compared to locations away from roads. We note that our searches identified some studies in which road impact was not the main focus, as well as some papers appearing in more than one category (Table S1). We excluded the only study exclusively focused on railways.

We compared the categories of the taxa studied in the papers with the information provided by the IUCN on species threatened by roads. To identify the species included in the Red List as threatened by roads, we filtered the IUCN Red List with the following criteria: "Taxonomy" (we only included "Animalia") + "Red List Category" ("Critical Endangered", "Endangered" and "Vulnerable") + "Country Legends" ("Extant & Reintroduced" and "Extant (resident)") + "Threats" ("Roads & railroads") + "Systems" ("Terrestrial" and "Freshwater (=Inland waters)") as appear at https://www.iucnredlist.org/search.

Population persistence in the literature

Our first searches identified 898 studies on mortality, 775 on habitat loss and fragmentation and 589 on mitigation (totalling 1517 different studies). Although there may be other examples in the literature, our searches represent a quantitative starting point to develop our suggestions. Only 7% of studies on mortality, 12% of studies on habitat loss and fragmentation and 3% of studies on mitigation (totalling 117 studies, see Table S1 for the full list), corresponded to articles that used population-oriented approaches. Most of these population-level studies focused the effects of habitat loss and fragmentation (80%), followed by roadkill (55%), and mitigation actions (16%), as some papers appeared in more than one category (Table S1).

Taxa and country biases

We detected a publication bias on taxa studied (Fig. 1), as most studies focused on carnivores (36%), followed by ungulates (15%), marsupials (14%) and turtles (13%). Studies on invertebrates were anecdotal (Fig. 1). The vast majority (ca. 90%) of the population-oriented studies were carried out in high-income countries (Fig. 2). Some regions like Southeast Asia, South America or Central Africa have very few studies despite hosting mega-diverse regions, including hundreds of road-threatened species (Fig. 2).

Population-level studies on red-listed species

The IUCN red list has 193 *Critically Endangered*, 372 *Endangered*, 413 *Vulnerable*, 351 *Near Threatened*, 543 *Least Concern* and 90 *Data Deficient* species threatened by roads (Fig. 3). Of the 135 species included in any of the articles identified as population-level studies, 3 are classified as *Critically Endangered*, 6 as *Endangered*, 14 as *Vulnerable*, 14 as *Near Threatened*, 97 as *Least Concern* and 1 species is not listed (Table S1; Fig. 3). Thus, current scientific literature

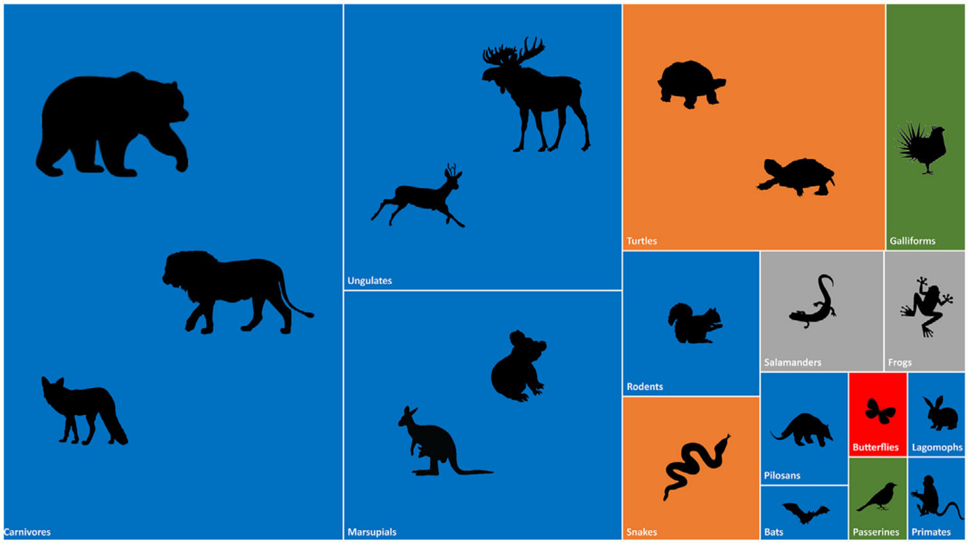


Fig. 1. Percentage per taxa of studies on the impacts of roads on wildlife population persistence identified in our systematic searches (Table S1). Color codes are blue for mammals, brown for reptiles, grey for amphibians, green for birds and red for invertebrates.

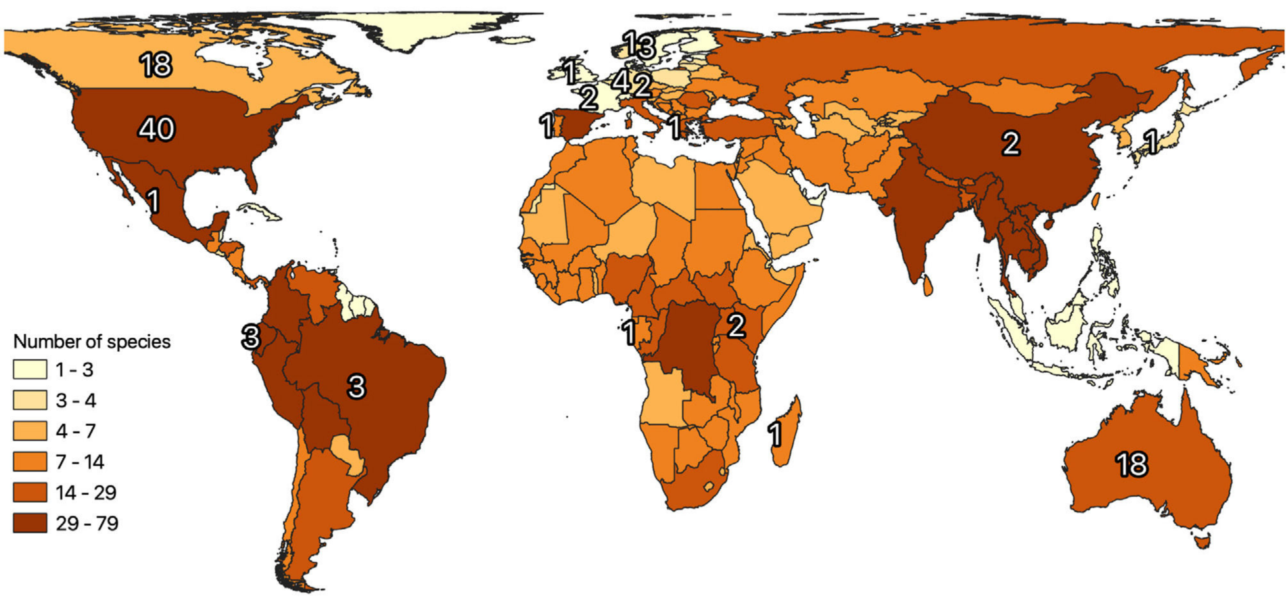


Fig. 2. Number of population-level studies per country (figures) in our systematic searches compared with the number of species threatened by roads (CR, EN and VU) based on IUCN red list present in every country (color scale).

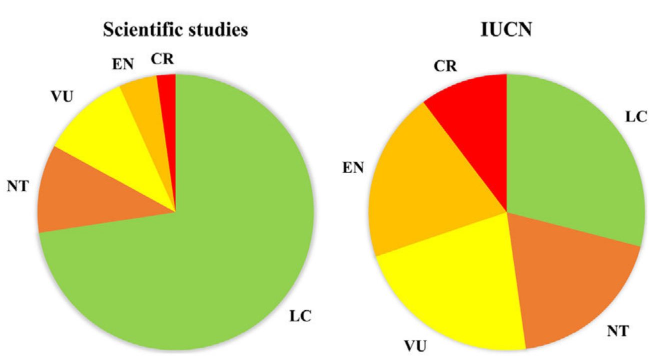


Fig. 3. Comparation between the percentage of scientific studies focused on the different threat categories in our systematic searches and these same percentages in the IUCN red list (only considering those threatened by roads). CR = critically endangered, EN = endangered, VU = vulnerable, NT = near threatened, LC = least concern.

contributing with empirical data on the effects of roads on population persistence covers a small proportion (2%) of those species identified by IUCN as threatened by roads.

Does roadkill deplete populations?

Roadkill is the most visible road impact, with billions of animals dying annually, from small insects to large mammals (Table S2). Recent work found that between 1–13% of monitored terrestrial vertebrates died due to roadkills, and that this rate increased over time for mammals (Hill et al., 2019). Several studies showed that wildlife abundance generally decreases close to roads (e.g., Benítez-López et al., 2010; Rytwinski and Fahrig, 2012). Although wildlife abundance can be reduced due to roadside avoidance, roadkills can deplete otherwise abundant populations. There is evidence that the impact of roadkills on population persistence is larger on species with greater mobility, larger home ranges, lower reproductive rates, or late maturity age (Rytwinski and Fahrig, 2012; Grilo et al., 2020).

Some theoretical studies predict higher impact of road mortality than connectivity reduction on population persistence and on genetic diversity (e.g., Ceia-Hasse et al., 2018). However, our search evidenced that, although most of studies covered roadkills, only 7% of these assessed how road mortality can compromise population survival in the long term. For instance, a study on *endangered* spotted turtle (*Clemmys guttata*) in Canada used a population viability analyses to find that probability of quasi-extinction within 150 years increased from 20–24% to 93–94% when road mortality was included in the model (Howell and Seigel, 2019). A study on *vulnerable* diamondback terrapin (*Malaclemys terrapin*) in USA obtained similar findings, as models predicted population decline in 50 years if roadkills are not mitigated (Crawford et al., 2018). Overall, studies agree in that adult (and very specially, female) survival is the key parameter to ensure population viability (Crawford et al., 2018; Howell and Seigel, 2019).

Do habitat loss and fragmentation threat populations persistence?

Habitat loss

Several telemetry-based studies proved how the behavioral avoidance of road surroundings can force animals to use less suitable habitats, implying an indirect habitat loss. This was the case of Dwinnell et al. (2019) when tested the Behaviorally Mediated Forage-Loss Hypothesis with mule deer (*Odocoileus hemionus*) in USA. Due to the perceived risk that this species showed close to roads, deer avoided high-quality feeding habitat that would otherwise be available. As such, the amount of indirect habitat loss (high-quality feeding habitat not used by deer) was 4.6 times the direct habitat loss due to road surface occupation (Dwinnell et al., 2019). A group especially sensitive to the habitat loss caused by roads are the large carnivores. In their study on grizzly bears (*Ursus arctos*) in USA, authors estimated that road network decreased habitat carrying capacity by over 30% (Lyons et al., 2018). Similar findings were obtained with a landscape genetics approach for this same species, as bear density concentrated on areas of high habitat quality away from main roads (Lamb et al., 2018). How this habitat loss translates into population persistence rates remains to be investigated.

Connectivity reduction

Roads can alter habitats in different ways, but most studies to date focused on how these infrastructures reduce connectivity (reviewed in van der Ree et al., 2015; Bennett, 2017; see also Table S1). One of the few examples from developing countries on how this reduced connectivity can constrain population survival is the study on *near threatened* jaguar (*Panthera onca*) meta-population in Southwestern Brazil (Cullen et al., 2016). These authors found that the subpopulations with the most fragmented habitat by roads were predicted to have lower persistence in the next 100 years when models included no dispersal, because fragmentation in these units resulted in lower habitat availability, and, consequently, lower density of jaguars (Cullen et al., 2016). Furthermore, road-mediated habitat fragmentation exacerbated roadkills, as highly fragmented subpopulations had higher density of roads per individual compared to the best-preserved units (Cullen et al., 2016).

Does mitigation improve population persistence?

There is great lack of evidence on the effectiveness of mitigation actions in reducing negative impacts on population persistence, as only 3% of the studies that focused this topic used empirical population-oriented approaches (see examples below). Dedicated studies are essential to confirm the effectiveness of road mitigation to ensure (or not) the viability of populations inhabiting road vicinity (Lesbarrères and Fahrig, 2012; Rytwinski et al., 2015).

Comparing the impacts before and after road construction with controls, both for no road and for road with no mitigation measure (i.e., Before-After-Control-Impact, BACI designs) provide less biased findings and allow stronger inferences than simpler observational designs (Lesbarrères and Fahrig, 2012; Christie et al., 2020). These designs will avoid erroneous findings like, for instance, attributing an improvement in population viability due to a reduction in mortality after implementing a mitigation action when this reduction is actually due to a population depression caused by previous road mortality (Ascensão et al., 2019).

One of the best tools to evaluate the effectiveness of mitigation actions in restoring functional connectivity are molecular techniques. It has been found that wildlife road-crossing structures facilitate some degree of gene flow and genetic admixture in both grizzly and black bears (*U. americanus*) in Canada (Sawaya et al., 2014). However, these patterns were species-specific, as wildlife crossing structures were more effective to connect black bear populations (Sawaya et al., 2014). A BACI approach was employed to study the effectiveness of crossing structures to maintain the genetic admixture in a squirrel glider (*Petaurus norfolcensis*) population bisected by a freeway in Australia (Soanes et al., 2018). Authors found that the use of these mitigation structures reduced the genetic differentiation (if any) and increased the number of mixed pairs between individuals from both sides of the road (Soanes et al., 2018). As costs for genetic analyses are become lower, this will allow more ambitious designs in future studies (e.g., road network scale).

Few studies have explored the effectiveness of mitigation actions at population levels with other than genetic approaches. For instance, Lamb et al. (2018) demonstrated that road closures increased grizzly density, at least in small areas, by 27%. An important finding of a study on diamondback terrapin was that installing a flashing warning signage was associated with a 30% increase in crossing success rate, which slightly improved the population persistence probability (Crawford et al., 2018). However, a theoretical study combining decision theory with a metapopulation modeling concluded that multispecies mitigation provides better results (i.e., highest number of persisting populations), than single species planning (Polak et al., 2019). An ever-present problem in mitigation programs is their high economic costs. In their case study with *vulnerable* koala *Phascolarctos cinereus*, Polak et al. (2014) explored different combinations of fencing and wildlife crossings to identify what mitigation action maximized the persistence of the population at the lower economic cost. Authors concluded that there was no 'win-win' solution for their koala population, as any reduction in the budget resulted in a substantial reduction in expected population size (Polak et al., 2014). Surprisingly, fencing all road segments while combing them with wildlife crossings did not maximize mean population abundance, despite being the most expensive alternative (Polak et al., 2014).

An alternative to reduce conservation costs is the use of volunteer-based programs. One of the most popular is the rescue of amphibians from roadsides by volunteer patrols. The authors of a study in USA on spotted salamander (*Ambystoma maculatum*) simulated different efforts of volunteers (i.e., mitigation actions) related to the population persistence (Sterrett et al., 2019). They found that conservation outcomes (i.e., minimum population size, population growth and years to extinction) benefited from almost every volunteer-based mitigation strategy compared to a no-action strategy, especially when focusing on rescuing larvae (Sterrett et al., 2019).

Rethinking the focus of road studies

Our three systematic searches show that most of population-level road ecology studies were carried out in high-income countries and were focused on large mammals like carnivores or ungulates. Furthermore, population-level road ecology studies are not paying attention to those species identified by IUCN as threatened by roads. Given the current rate of road expansion worldwide (Laurance et al., 2014; Alamgir et al., 2017), proper planning and effective mitigation of their unavoidable impacts is one of the most challenging tasks for conservation biologists today. Addressing this defiance will require changing our conceptual perspective, from current study designs focused on single road sections to studies on large road networks (e.g., Lamb et al., 2018; Grilo et al., 2020). Recording roadkills is a good starting point, but we suggest that the only way to truly limit the impact of roads is to determine whether the population trend is being affected by road mortality. Similarly, passage use is not enough to ensure mitigation effectiveness (Rytwinski et al., 2015). Thus, we suggest that road ecologists should strive to quantify whether functional connectivity is being affected by roads, and whether this has been restored after mitigation actions. We are beginning to have some redundancy in the kinds of studies on large mammals that are carried out in high-income countries, but we know very little about the impact that roads have on the persistence of wildlife populations in most developing countries or on less charismatic species. If we explore road-wildlife conflict with this new aim, we will be better prepared to face one of the most important environmental challenges of our times.

Authors' contributions

RB, FA, MD conceived ideas and wrote the first draft of the manuscript; RB conducted the systematic searches and led the writing of the manuscript. All authors contributed to the writing of the final version of the manuscript.

Data availability statement

All data are available at the Appendix A.

Conflict of interests

The authors declare no conflict of interest.

Acknowledgements

This work was financed by Comunidad de Madrid through 2018T1/AMB10374 to RB and by Infraestructuras de Portugal through Infraestruturas de Portugal Biodiversity Chair (02035004) to HMP. FA and MD were supported by Fundação da Ciência e Tecnologia (FCT, CEECIND/03265/2017 and CEECIND/03798/2017). Thanks are due to FCT/MCTES for the financial support to CESAM (UIDP/50017/2020+UIDB/50017/2020), through national funds. We thank Adam T. Ford for permission to use the elk photo for the graphical abstract. Two anonymous reviewers contributed with their comments to improve the manuscript.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.pecon.2021.07.004.

References

Alamgir, M., Campbell, M.J., Sloan, S., Goosem, M., Clements, G.R., Mahmoud, M.I., Laurance, W.F., 2017. Economic, socio-political and environmental risks of road development in the tropics. Curr. Biol. 27, R1130–R1140, http://dx.doi.org/10.1016/j.cub.2017.08.067.

Ascensão, F., Fahrig, L., Clevenger, A.P., Corlett, R.T., Jaeger, J.A.G., Laurance, W.F., Pereira, H.M., 2018. Environmental challenges for the belt and road initiative. Nat. Sustain. 1, 206–209, http://dx.doi.org/10.1038/s41893-018-0059-3.

Ascensão, F., Kindel, A., Zimmermann Teixeira, F., Barrientos, R., D'Amico, M., Borda-de-Água, L., Pereira, H.M., 2019. Beware that the lack of wildlife mortality records can mask a serious impact of linear infrastructures. Glob. Ecol. Conserv. 19, e00661, http://dx.doi.org/10.1016/j.gecco.2019.e00661.

Benítez-López, A., Alkemade, R., Verweij, P.A., 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biol. Conserv. 143, 1307–1316, http://dx.doi.org/10.1016/j.biocon.2010.02.009.

Bennett, V.J., 2017. Effects of road density and pattern on the conservation of species and biodiversity. Curr. Landsc. Ecol. Rep. 2, 1, http://dx.doi.org/10.1007/s40823-017-0020-6.

Ceia-Hasse, A., Navarro, L.M., Borda-de-Água, L., Pereira, H.M., 2018. Population persistence in landscapes fragmented by roads: disentangling isolation, mortality, and the effect of dispersal. Ecol. Model. 375, 45–53, http://dx.doi.org/10.1016/j.ecolmodel.2018.01.021.

Christie, A.P., Abecasis, D., Adjeroud, M., Alonso, J.C., Amano, T., Antón, A., Baldigo, B.P., Barrientos, R., Bicknell, J.E., Buhl, D.A., Cebrian, J., Ceia, R.S., Cibils-Martina, L., Clarke, S., Claudet, J., Craig, M.D., Davoult, D., De Backer, A., Donovan, M.K., Eddy, T.D., França, F.M., Gardner, J.P.A., Harris, B.P., Huusko, A., Jones, I.L., Kelaher, B.P., Kotiaho, J.S., López-Baucells, A., Major, H.L., Mäki-Petäys, A., Martín, B., Martín, C.A., Martin, P.A., Mateos-Molina, D., McConnaughey, R.A., Meroni, M., Meyer, C.F.J., Mills, K., Montefalcone, M., Noreika, N., Palacín, C., Pande, A., Pitcher, C.R., Ponce, C., Rinella, M., Rocha, R., Ruiz-Delgado, M.C., Schmitter-Soto, J.J., Shaffer, J.A., Sharma, S., Sher, A.A., Stagnol, D., Stanley, T.R., Stokesbury, K.D.E., Torres, A., Tully, O., Vehanen, T., Watts, C., Zhao, Q., Sutherland, W.J., 2020. Quantifying and addressing the prevalence and bias of study designs in the environmental and social sciences. Nat. Commun. 11, 6377, http://dx.doi.org/10.1038/s41467-020-20142-y.

Crawford, B.A., Moore, C.T., Norton, T.M., Maerz, J.C., 2018. Integrated analysis for population estimation, management impact evaluation, and decision-making for a declining species. Biol. Conserv. 222, 33–43, http://dx.doi.org/10.1016/j.biocon.2018.03.023.

Cullen Jr., L., Stanton, J.C., Lima, F., Uezu, A., Perilli, M.L.L., Akçakaya, H.R., 2016. Implications of fine-grained habitat fragmentation and road mortality for jaguar conservation in the Atlantic Forest, Brazil. PLoS One 11, e0167372, http://dx.doi.org/10.1371/journal.pone.0167372.

Dwinnell, S.P.H., Sawyer, H., Randall, J.E., Beck, J.L., Forbey, J.S., Fralick, G.L., Monteith, K.L., 2019. Where to forage when afraid: does perceived risk impair use of the foodscape? Ecol. Appl. 29, e01972, http://dx.doi.org/10.1002/eap.1972.

Grilo, C., Koroleva, E., Andrášik, R., Bíl, M., González-Suárez, M., 2020. Roadkill risk and population vulnerability in European birds and mammals. Front. Ecol. Environ. 18, 323–328, http://dx.doi.org/10.1002/fee.2216.

Hill, J.E., DeVault, T.L., Belant, J.L., 2019. Cause-specific mortality of the world's terrestrial vertebrates. Glob. Ecol. Biogeogr. 28, 680–689, http://dx.doi.org/10.1111/geb.12881.

Howell, H.J., Seigel, R.A., 2019. The effects of road mortality on small, isolated turtle populations. J. Herpetol. 53, 39–46, http://dx.doi.org/10.1670/18-022.

Lamb, C.T., Mowat, G., Reid, A., Smit, L., Proctor, M., Mclellan, B.N., Nielsen, S.E., Boutin, S., 2018. Effects of habitat quality and access management on the density of a recovering grizzly bear population. J. Appl. Ecol. 55, 1406–1417, http://dx.doi.org/10.1111/1365-2664.13056.

Laurance, W.F., Reuben Clements, G., Sloan, S., O'Connell, C.S., Mueller, N.D., Goosem, M., Venter, O., Edwards, D.P., Phalan, B., Balmford, A., van der Ree, R., Burgues Arrea, I., 2014. A global strategy for road building. Nature 513, 229–232, http://dx.doi.org/10.1038/nature13717.

Lesbarrères, D., Fahrig, L., 2012. Measures to reduce population fragmentation by roads: what has worked and how do we know? Trends Ecol. Evol. 27, 374–380, http://dx.doi.org/10.1016/j.tree.2012.01.015.

Lyons, A.L., Gaines, W.L., Singleton, P.H., Kasworm, W.F., Proctor, M.F., Begley, J., 2018. Spatially explicit carrying capacity estimates to inform species specific recovery objectives: grizzly bear (*Ursus arctos*) recovery in the North Cascades. Biol. Conserv. 222, 21–32, http://dx.doi.org/10.1016/j.biocon.2018.03.027.

Polak, T., Rhodes, J.R., Jones, D., Possingham, H.P., 2014. Optimal planning for mitigating the impacts of roads on wildlife. J. Appl. Ecol. 51, 726–734, http://dx.doi.org/10.1111/1365-2664.12243.

Polak, T., Nicholson, E., Grilo, C., Bennett, J.R., Possingham, H.P., 2019. Optimal planning to mitigate the impacts of roads on multiple species. J. Appl. Ecol. 56, 201–213, http://dx.doi.org/10.1111/1365-2664.13258.

Rytwinski, T., Fahrig, L., 2012. Do species life history traits explain population responses to roads? A meta-analysis. Biol. Conserv. 147, 87–98, http://dx.doi.org/10.1016/j.biocon.2011.11.023.

Rytwinski, T., van der Ree, R., Cunnington, G.M., Fahrig, L., Findlay, C.S., Houlahan, J., Jaeger, J.A.G., Soanes, K., van der Grift, E.A., 2015. Experimental study designs to improve the evaluation of road mitigation measures for wildlife. J. Environ. Manage. 154, 48–64, http://dx.doi.org/10.1016/j.jenvman.2015.01.048.

Sawaya, M.A., Kalinowski, S.T., Clevenger, A.P., 2014. Genetic connectivity for two bear species at wildlife crossing structures in Banff National Park. Proc. R. Soc. B 281, 20131705, http://dx.doi.org/10.1098/rspb.2013.1705.

Soanes, K., Taylor, A.C., Sunnucks, P., Vesk, P.A., Cesarini, S., van der Ree, R., 2018. Evaluating the success of wildlife crossing structures using genetic approaches and an experimental design: lessons from a gliding mammal. J. Appl. Ecol. 55, 129–138, http://dx.doi.org/10.1111/1365-2664.12966.

Sterrett, S.C., Katz, R.A., Fields, W.R., Campbell Grant, E.H., 2019. The contribution of road-based citizen science to the conservation of pond-breeding amphibians. J. Appl. Ecol. 56, 988–995, http://dx.doi.org/10.1111/1365-2664.13330.

van der Ree, R., Smith, D.J., Grilo, C. (Eds.), 2015. Handbook of Road Ecology. John Wiley and Sons, Hoboken, http://dx.doi.org/10.1002/9781118568170.