University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

USDA National Wildlife Research Center - Staff Publications

U.S. Department of Agriculture: Animal and Plant Health Inspection Service

11-6-2019

Impact of the human footprint on anthropogenic mortality of North American reptiles

Jacob E. Hill
State University of New York College of Environmental Science and Forestry, jehill@esf.edu

Travis L. DeVault
USDA National Wildlife Research Center, Travis.L.DeVault@aphis.usda.gov

Jerrold L. Belant
State University of New York College of Environmental Science and Forestry

Follow this and additional works at: https://digitalcommons.unl.edu/icwdm_usdanwrc

🟠 Part of the Natural Resources and Conservation Commons, Natural Resources Management and Policy Commons, Other Environmental Sciences Commons, Other Veterinary Medicine Commons, Population Biology Commons, Terrestrial and Aquatic Ecology Commons, Veterinary Infectious Diseases Commons, Veterinary Microbiology and Immunobiology Commons, Veterinary Preventive Medicine, Epidemiology, and Public Health Commons, and the Zoology Commons

Short Communication

Impact of the human footprint on anthropogenic mortality of North American reptiles

Jacob E. Hill[a],*, Travis L. DeVault[b,1], Jerrold L. Belant[a]

[a] Camp Fire Program in Wildlife Conservation, State University of New York College of Environmental Science and Forestry, 1 Forestry Dr, Syracuse, NY, 13210, USA
[b] U.S. Department of Agriculture, Animal and Plant Health Inspection Service, National Wildlife Research Center, 6100 Columbus Ave, Sandusky, OH, 44870, USA

ABSTRACT

Human activities frequently result in reptile mortality, but how direct anthropogenic mortality compares to natural morality has not been thoroughly investigated. There has also been a limited examination of how anthropogenic reptile mortality changes as a function of the human footprint. We conducted a synthesis of cause-specific North American reptile mortality studies based on telemetry, documenting 550 mortalities of known cause among 2461 monitored individuals in 57 studies. Overall 78% of mortality was the result of direct natural causes, whereas 22% was directly caused by humans. The single largest source of mortality was predation, accounting for 62% of mortality overall. Anthropogenic mortality did not increase with the human footprint or with species body mass, though predation mortality increased with decreasing human footprint. The relatively low amount of anthropogenic mortality compared to other taxa suggests that reptiles may be more impacted by indirect than direct anthropogenic mortality. As a result, mitigating these indirect impacts, which include habitat loss and introduction of invasive species, is essential for conservation of North American reptiles.

1. Introduction

Humans have substantially altered Earth's surfaces through mechanisms such as land transformation, pollution, and the introduction of invasive species. These changes have resulted in widespread losses of biodiversity, with current extinction rates for vertebrates more than 100 times greater than background levels (Ceballos et al., 2015). Reptiles are particularly prone to such anthropogenically-induced declines due to traits such as small geographic ranges (Böhm et al., 2016), disease susceptibility (Sandmeier et al., 2013), and life history strategies (Heppell, 1998; Tingley et al., 2013; Webb et al., 2002). Consequently, today an estimated 20% of reptile (Böhm et al., 2013) species are threatened with extinction.

Reptiles are negatively impacted by multiple anthropogenic causes. Direct anthropogenic mortality of reptiles occurs through mechanisms such as harvest, vehicle collisions, and nuisance killing (e.g. Colino-Rabanal and Lizana, 2012; Mali et al., 2014; Pitts et al., 2017). However, humans can also cause wildlife mortality indirectly. For example, destruction of habitat can make animals more prone to predation by removing vegetation used for protection from predators (Newell, 1999). Human activities can also supplement predators of reptiles, leading to increased predation rates (Kristan III and Boarman, 2003). Introduction

of invasive species can also indirectly cause mortality of reptiles through predation and increased competition for resources (Doherty et al., 2016). Distinguishing between indirect anthropogenic mortality and natural mortality can thus be difficult when assigning causes of death to animals. However, comparing direct anthropogenic mortality to direct natural sources can be informative for identifying the major mechanisms by which humans cause reptile mortality.

Increases in reptile mortality often occur with increasing human development. Land transformation is the most important cause of extinctions worldwide (Vitousek et al., 1997), with habitat loss and fragmentation the primary threats to reptile and amphibian populations (Gibbons et al., 2000). Increasing human access to formerly inaccessible areas can cause rapid extirpation of reptile populations (Garber and Burger, 1995). Additionally, construction of roads can negatively impact reptiles through facilitating spread of invasive species (Brown et al., 2006), serving as a source of pollution (Reeves et al., 2008), and altering sex ratios (Gibbs and Steen, 2005).

Despite these relationships between human development and reptile declines, there has been no large-scale assessment of how reptile mortality sources change as a function of human impacts to the landscape. This understanding is important for managing reptile populations across human-dominated landscapes. Additionally, there has been no

---

* Corresponding author.
  E-mail address: jehill@esf.edu (J.E. Hill).
[1] University of Georgia, Savannah River Ecology Laboratory, PO Drawer E, Aiken, SC 29802, USA.

assessment of direct anthropogenic mortality of reptiles compared to direct natural mortality. Understanding the proximate causes of mortality can lend insight into how reptiles are primarily affected by human activities, which is important in the formulation of mitigation efforts.

To investigate these questions, we conducted a synthesis of cause-specific mortality studies of North American reptiles based on telemetry. We first compared overall direct anthropogenic mortality to direct natural mortality. We then tested the hypothesis that human impacts to the landscape influence anthropogenic reptile mortality. We tested this hypothesis using the Human Footprint Index (HFI), which quantifies human impacts by combining measures of road infrastructure, human access, and human population density (Sanderson et al., 2002). Specifically, we predicted that direct anthropogenic reptile mortality would increase as the human footprint increased.

2. Methods

We searched the following databases for studies of reptile cause-specific mortality: JSTOR, BioOne, EBSCO Host, Google Scholar, Web of Science, ProQuest Dissertations and Theses, and SCOPUS. We searched documents for the terms 'cause-specific mortality', or 'telemetry' and 'mortality' or 'telemetry' and 'survival.' We only selected papers that implemented telemetry to determine cause-specific mortality because this technique produces less-biased estimates of mortality than other methods such as mark-recapture (Naef-Daenzer et al., 2017).

The date range of studies began at 1970, roughly the date when radio telemetry became common, and continued through March 2019. The first version of the HFI was created in 1993 (Sanderson et al., 2002) and an updated version was produced in 2009 (Venter et al., 2016). We calculated the midpoint of the range of years over which each study was completed and used the study year to assign them the appropriate HFI version. Our delineation between the two HFI datasets was midway between them such that studies up to 2001 were assigned the 1993 version, while those subsequent to 2001 were assigned to the 2009 version. As the midpoints in the dataset ranged 1987–2009, no study had a time difference of more than 6 years between study year and the HFI version that was used. Because the precise boundaries of a study site were rarely provided, we estimated the geographic center of the study area, constructed a circle with a radius of 3 km around that point, and averaged HFI values within this area.

For each study, we documented the number of mortalities due to direct human causes (e.g. harvest, vehicle collision), the number of mortalities due to direct natural causes (e.g. predation, disease, starvation), and the number of individuals that were monitored. Though our search included all age classes, we limited our statistical analysis to adults due to the low number of juvenile studies. We also determined the average adult body mass for each species (Myhrvold et al., 2015). We incorporated this variable because body mass may influence susceptibility to vehicle collisions for reptiles (Andrews et al., 2005) and has been shown to influence anthropogenic mortality of other taxa (Hill et al., 2019).

We used linear mixed effects models to determine the best set of predictor variables for proportion of anthropogenic mortality (i.e. number dying from anthropogenic causes/number dying from all known causes) and magnitude of mortality (i.e. number dying of any cause/number monitored). Our largest mortality sources were vehicle collision and predation, and we also modelled proportion of mortality due to these causes. Models of mortality proportion were weighted by the number of mortalities of known cause for each study, whereas models of magnitude of mortality were weighted by number of individuals monitored in the study. We included species body mass and HFI as fixed effects, accounted for phylogeny by using taxonomy as a nested random effect (order:family:genus:species) (Tucker et al., 2018), and incorporated a Gaussian spatial autocorrelation structure (Dormann et al., 2007).

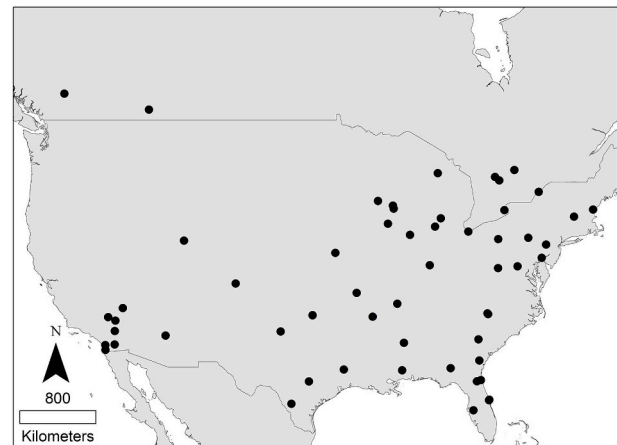We calculated sample size corrected Akaike's information criterion

Fig. 1. Locations of reptile study sites across North America used in analysis.

(AIC$_c$) for each candidate model. For each model set we considered the best approximating model as the model with the lowest AIC$_c$ and calculated the difference in AIC$_c$ values between this model and all additive model combinations (represented by Δ_i) (Burnham and Anderson, 2002). Only models with $\Delta_i \leq 2$ were selected for further consideration (Burnham and Anderson, 2002). We calculated Akaike weights (w_i) for candidate models to examine the relative weight of evidence for each model. We used multi-model inference to calculate a weighted average of parameter estimates with 85% confidence intervals across competing models (Arnold, 2010; Burnham and Anderson, 2002).

3. Results

We compiled 57 studies which reported 550 mortalities of known cause among 2461 monitored individuals representing 28 reptile species (Fig. 1). Overall 78% of mortality was the result of direct natural causes, whereas 22% was directly caused by humans (Table 1). The single largest source of mortality was predation, accounting for 62% of mortality overall. The predator was not identified in 75% of mortality events and coyotes were the most common identified predator, responsible for 8% of predation mortality and reported in 4 studies (Supplemental Table 1). Vehicle collisions were the second largest cause, accounting for 9% of total mortality (Table 1).

Our dataset of adults for analysis consisted of 48 studies that monitored 2166 individuals and recorded 393 deaths of known cause. Proportion of anthropogenic mortality was not influenced by body mass ($\beta = 0.479$, $p = 0.213$) or HFI ($\beta = 0.019$, $p = 0.370$; Supplemental Table 2; Supplemental Table 3). Predation mortality decreased with increasing HFI ($\beta = -0.051$, $p = 0.003$; Fig. 2), but was not influenced by body mass ($\beta = -0.773$, $p = 0.245$). Body mass also did not influence proportion of vehicle mortality ($\beta = 0.343$, $p = 0.342$) and HFI was not included in top models for the mortality source. Neither body mass nor HFI were in top models for magnitude of mortality.

Table 1
Mortality sources of North American reptiles.

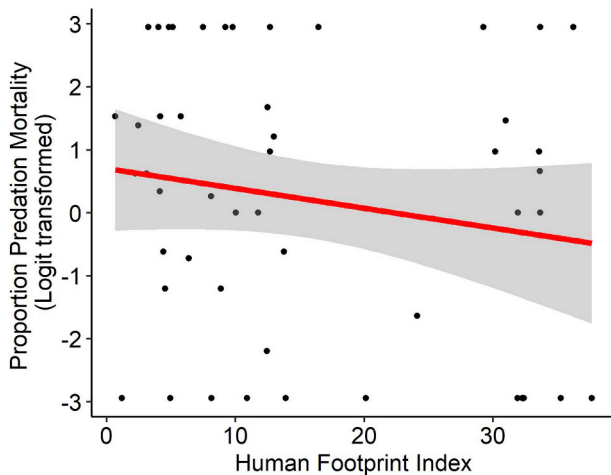| Mortality source	Number of mortalities	Proportion of mortalities
Harvest	4	0.007
Vehicle	50	0.091
Agriculture	22	0.040
Other human causes	45	0.082
Predation	341	0.620
Disease	2	0.004
Accident/Injury	4	0.007
Other natural causes	82	0.149
Total mortalities	**550**	

Fig. 2. Change in proportion of predation mortality as a function of Human Footprint Index.

4. Discussion

We found that direct natural mortality of North American reptiles was more than 3 times greater than direct anthropogenic mortality. This pattern is different from that of mammals, in which natural mortality was less than 2 times greater than direct anthropogenic mortality (Hill et al., 2019). These dissimilarities reflect differences in how humans influence these taxonomic classes. High rates of anthropogenic mammal mortality were largely driven by harvest, which accounted for 23% of overall mortality (Hill et al., 2019). By contrast, harvest was only present in 1 reptile study and accounted for less than 1% of reptile mortality. These differences between taxa are even more pronounced when considering only adult mammals, in which anthropogenic and natural mortality are nearly equal and harvest accounts for 33% of mortality (Hill et al., 2019).

Differences in harvest intensity among taxa may account for the lack of relationship between body mass and anthropogenic mortality. An increase in anthropogenic mortality with body mass has been reported for mammals and this likely occurs because larger species provide more meat per unit effort and larger trophies (Collins and Kays, 2011; Hill et al., 2019; Jerozolimski and Peres, 2003; Johnson et al., 2010). However, with harvest mortality nearly absent, the drivers behind the increase in anthropogenic mortality with body mass reported for mammals were not present, leading to no effect of body mass on anthropogenic mortality for reptiles. Furthermore, larger mammals are more likely to be killed through management removal when they are deemed a threat to human life or property and this mortality source was also not present in our dataset (Linnell et al., 1999).

Another difference between taxa is that HFI did not influence susceptibility of reptiles to vehicle mortality, although it did for mammals (Collins and Kays, 2011). These dissimilarities may be due to differences in mobility among taxa. Mammals are endothermic with a field metabolic rate 12–20 times greater than that of an equivalent-sized ectothermic reptile (Nagy, 2005). As larger home ranges are typically required for animals with higher metabolism to meet their increased energetic needs, a mammal would be expected to have a larger home range than a similarly sized reptile (Lindstedt et al., 1986; McNab, 1963). This discrepancy could result in increased mobility of mammals, potentially increasing their risk of encountering roads and dying from vehicle mortality (Bonnet et al., 1999; Schwab and Zandbergen, 2011). As a result, vehicle mortality may be largely dependent on animal movement patterns.

Similarly, vehicle mortality of snakes was positively associated with movement patterns (DeGregorio et al., 2010; Meek, 2009). During periods of higher ambient temperature, snakes were inactive and there

was a low level of vehicle mortality, despite high traffic volume at the time. However, there were peaks in activity during egg-laying migrations and juvenile dispersals, resulting in greater road mortality despite lower traffic volume during these periods (DeGregorio et al., 2010). For ectothermic animals, seasonal activity patterns may be the predominate driver of vehicle mortality, which may account for the lack of relationship between vehicle mortality and human development. The differences between the influence of HFI on vehicle mortality of reptiles and mammals suggest that a taxa-specific approach is required for predicting the influence of HFI on vehicle mortality of terrestrial vertebrates.

Overall anthropogenic mortality also did not increase with HFI. Similar to vehicle mortality, activity patterns may influence susceptibility to overall anthropogenic mortality. Additionally, reptiles in areas with HFI values may have become adapted to living in anthropogenically-modified areas, reducing the amount of direct anthropogenic mortality. Only predation was influenced by HFI, which decreased with increasing HFI. In areas with high HFI values, predators of reptiles may consume anthropogenic food subsidies and prey on reptiles less often. For example, some facultative scavengers will stop killing their own prey when other more easily accessible food resources such as carrion become available (Van Dijk et al., 2008). Urbanization may also change the predator community such that there are less predators in areas with high HFI values or predators less adept at consuming reptiles, but we were unable to assess this because the predator was not determined in most predation events.

Overall, we found that vehicle collision was responsible for 9% of reptile mortality in North America and comprised the single largest direct cause of anthropogenic mortality. This is a higher percentage than reported for North American mammals (Collins and Kays, 2011; Hill et al., 2019). Reptiles may be particularly prone to vehicle mortality due to traits such as movement speed, locomotion, and response to vehicles (Andrews et al., 2005). This mortality can have a number of consequences such as decreasing genetic diversity (Clark et al., 2010) and altering sex ratios (Gibbs and Steen, 2005). These results suggest that vehicle mortality is a major mortality factor for reptiles and we reiterate the need for appropriate mitigation measures such as road crossing structures or habitat management to ensure the viability of North American reptile populations (Glista et al., 2009; Meek, 2015; Shoemaker et al., 2009).

Although telemetry offers less-biased estimates of mortality than other techniques such as opportunistic encounters of dead individuals, there are still caveats that should be considered. Carcasses could have been scavenged, leading the mortality to be classified as predation when it was actually the result of other causes. Many animals scavenge along roads (e.g. Hill et al., 2018) and removal of carcasses from roads by scavengers may have led to a vehicle mortality being classified as predation. Additionally, many individuals go missing during telemetry studies, meaning they cannot be relocated and cause of death cannot be determined. If certain mortality sources such as predation or vehicle mortality routinely result in the destruction of transmitters, estimates of cause-specific mortality may be biased.

The high number of reptile species threatened with extinction but relatively low amount of direct anthropogenic mortality suggests that humans mainly influence reptiles through indirect mortality. The ways in which humans may impact wildlife indirectly are diverse, but include habitat loss, pollution and introduction of invasive species (Gibbons et al., 2000). For some mammal populations, which are generally subject to high levels of direct anthropogenic mortality, conservation measures may include restrictions on harvest or limiting harvest in certain areas (Hill et al., 2019). However, the low anthropogenic mortality of reptiles we found suggests that conserving North American reptiles populations will require a larger focus on mitigating these indirect human impacts.

Author contributions

All authors conceived the idea and designed the methodology. JEH collected the data. JEH and JLB analyzed the data. JEH led the writing of the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actao.2019.103486.

References

Andrews, K.M., Gibbons, J.W., Reeder, T., 2005. How do highways influence snake movement? Behavioral responses to roads and vehicles. Copeia 2005 772–782.

Arnold, T.W., 2010. Uninformative parameters and model selection using Akaike's Information Criterion. J. Wildl. Manag. 74, 1175–1178.

Böhm, M., Collen, B., Baillie, J.E., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R., Ram, M., 2013. The conservation status of the world's reptiles. Biol. Conserv. 157, 372–385.

Böhm, M., Williams, R., Bramhall, H.R., McMillan, K.M., Davidson, A.D., Garcia, A., Bland, L.M., Bielby, J., Collen, B., 2016. Correlates of extinction risk in squamate reptiles: the relative importance of biology, geography, threat and range size. Glob. Ecol. Biogeogr. 25, 391–405.

Bonnet, X., Naulleau, G., Shine, R., 1999. The dangers of leaving home: dispersal and mortality in snakes. Biol. Conserv. 89, 39–50.

Brown, G.P., Phillips, B.L., Webb, J.K., Shine, R., 2006. Toad on the road: use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. Biol. Conserv. 133, 88–94.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: a Practical Information-Theoretical Approach. Springer, New York.

Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human–induced species losses: entering the sixth mass extinction. Sci. Adv. 1, e1400253.

Clark, R.W., Brown, W.S., Stechert, R., Zamudio, K.R., 2010. Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. Conserv. Biol. 24, 1059–1069.

Colino-Rabanal, V.J., Lizana, M., 2012. Herpetofauna and roads: a review. Basic Appl. Herpetol. 26, 5–31.

Collins, C., Kays, R., 2011. Causes of mortality in North American populations of large and medium-sized mammals. Anim. Conserv. 14, 474–483.

DeGregorio, B.A., Nordberg, E.J., Stepanoff, K.E., Hill, J.E., 2010. Patterns of snake road mortality on an isolated barrier island. Herpetol. Conserv. Biol. 5, 441–448.

Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G., Dickman, C.R., 2016. Invasive predators and global biodiversity loss. Proc. Natl. Acad. Sci. 113, 11261–11265.

Dormann, C.F., M McPherson, J., B Araújo, M., Bivand, R., Bolliger, J., Carl, G., G Davies, R., Hirzel, A., Jetz, W., Daniel Kissling, W., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30, 609–628.

Garber, S.D., Burger, J., 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. Ecol. Appl. 5, 1151–1162.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., 2000. The global decline of reptiles, Déjà Vu Amphibians. Bioscience 50, 653–666.

Gibbs, J.P., Steen, D.A., 2005. Trends in sex ratios of turtles in the United States: implications of road mortality. Conserv. Biol. 19, 552–556.

Glista, D.J., DeVault, T.L., DeWoody, J.A., 2009. A review of mitigation measures for reducing wildlife mortality on roadways. Landsc. Urban Plan. 91, 1–7.

Heppell, S.S., 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998 367–375.

Hill, J.E., DeVault, T.L., Beasley, J.C., Rhodes, O.E., Belant, J.L., 2018. Roads do not increase carrion use by a vertebrate scavenging community. Sci. Rep. 8, 16331.

Hill, J., DeVault, T.L., Belant, J.L., 2019. Cause-specific mortality of the world's terrestrial vertebrates. Glob. Ecol. Biogeogr. 28, 680–689.

Jerozolimski, A., Peres, C.A., 2003. Bringing home the biggest bacon: a cross-site analysis of the structure of hunter-kill profiles in Neotropical forests. Biol. Conserv. 111, 415–425.

Johnson, P.J., Kansky, R., Loveridge, A.J., Macdonald, D.W., 2010. Size, rarity and charisma: valuing African wildlife trophies. PLoS One 5, e12866.

Kristan III, W.B., Boarman, W.I., 2003. Spatial pattern of risk of common raven predation on desert tortoises. Ecology 84, 2432–2443.

Lindstedt, S.L., Miller, B.J., Buskirk, S.W., 1986. Home range, time, and body size in mammals. Ecology 67, 413–418.

Linnell, J.D., Odden, J., Smith, M.E., Aanes, R., Swenson, J.E., 1999. Large carnivores that kill livestock: do" problem individuals" really exist? Wildl. Soc. Bull. 27, 698–705.

Mali, I., Vandewege, M.W., Davis, S.K., Forstner, M.R., 2014. Magnitude of the freshwater turtle exports from the US: long term trends and early effects of newly implemented harvest management regimes. PLoS One 9, e86478.

McNab, B.K., 1963. Bioenergetics and the determination of home range size. Am. Nat. 97, 133–140.

Meek, R., 2009. Patterns of reptile road-kills in the Vendée region of western France. Herpetol. J. 19, 135–142.

Meek, R., 2015. Where do snakes cross roads? Habitat associated road crossings and mortalities in a fragmented landscape in western France. Herpetol. J. 25, 15–19.

Myhrvold, N.P., Baldridge, E., Chan, B., Sivam, D., Freeman, D.L., Ernest, S.M., 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. Ecology 96 3109-3109.

Nagy, K.A., 2005. Field metabolic rate and body size. J. Exp. Biol. 208, 1621–1625.

Naef-Daenzer, B., Korner-Nievergelt, F., Fiedler, W., Grüebler, M.U., 2017. Bias in ring-recovery studies: causes of mortality of little owls Athene noctua and implications for population assessment. J. Avian Biol. 48, 266–274.

Newell, G.R., 1999. Responses of Lumholtz's tree-kangaroo (*Dendrolagus lumholtzi*) to loss of habitat within a tropical rainforest fragment. Biol. Conserv. 91, 181–189.

Pitts, S.L., Hughes, B.D., Mali, I., 2017. Rattlesnake nuisance removals and urban expansion in phoenix, Arizona. West. N. Am. Nat. 77, 309–317.

Reeves, M.K., Dolph, C.L., Zimmer, H., Tjeerdema, R.S., Trust, K.A., 2008. Road proximity increases risk of skeletal abnormalities in wood frogs from National Wildlife Refuges in Alaska. Environ. Health Perspect. 116, 1009–1014.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The human footprint and the last of the wild. Bioscience 52, 891–904.

Sandmeier, F.C., Tracy, C.R., Hagerty, B.E., DuPré, S., Mohammadpour, H., Hunter, K., 2013. Mycoplasmal upper respiratory tract disease across the range of the threatened Mojave Desert tortoise: associations with thermal regime and natural antibodies. EcoHealth 10, 63–71.

Schwab, A.C., Zandbergen, P.A., 2011. Vehicle-related mortality and road crossing behavior of the Florida panther. Appl. Geogr. 31, 859–870.

Shoemaker, K.T., Johnson, G., Prior, K.A., 2009. Habitat manipulation as a viable conservation strategy. In: Mullin, S.J., Seigel, R.A. (Eds.), Snakes: Ecology and Conservation. Cornell University Press, Ithaca.

Tingley, R., Hitchmough, R.A., Chapple, D.G., 2013. Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards. Biol. Conserv. 165, 62–68.

Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. Science 359, 466–469.

Van Dijk, J., Gustavsen, L., Mysterud, A., May, R., Flagstad, Ø., Brøseth, H., Andersen, R., Andersen, R., Steen, H., Landa, A., 2008. Diet shift of a facultative scavenger, the wolverine, following recolonization of wolves. J. Anim. Ecol. 77, 1183–1190.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M., Watson, J., 2016. Global terrestrial Human Footprint maps for 1993 and 2009. Scientific Data 3, 160067.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. Science 277, 494–499.

Webb, J.K., Brook, B.W., Shine, R., 2002. What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. Ecol. Res. 17, 59–67.