## **Issues and Perspectives**

# Travel Management Planning for Wildlife with a Case Study on the Mojave Desert Tortoise

Roy C. Averill-Murray,\* Linda J. Allison†

Desert Tortoise Recovery Office, U.S. Fish and Wildlife Service, Reno, Nevada 89502

#### **Abstract**

Roads are important drivers of habitat loss, degradation, and fragmentation that affect global biodiversity. Detrimental effects of roads include direct mortality of individual animals, spread of habitat-altering invasive plants, and loss of demographic and genetic connectivity of wildlife populations. Various measures address the negative effects of roads on wildlife. However, most strategies for minimizing or mitigating the effects of roads are focused on the actual roads themselves rather than on the collective travel network across landscapes. We summarized a growing body of literature that has documented the effects of road density on wildlife populations and the benefits associated with lower densities. This literature supports the application of limits on road density as a viable tool for managing cumulative effects. Based on these examples, we recommend road densities, including all linear features used for travel, of less than 0.6 km/km<sup>2</sup> as a general target for travel management in areas where wildlife conservation is a priority. Lower densities may be necessary in particularly sensitive areas, whereas higher densities may be appropriate in areas less important to landscape-level conservation and wildlife connectivity. Public policy and funding also are needed to address challenges of enforcing off-highway vehicle regulations. In applying this general overview to a case study of the Mojave desert tortoise Gopherus agassizii, we found that all management plans across the species' range lack considerations of road density and that tortoise populations declined within all conservation areas with road densities of more than 0.75 km/km<sup>2</sup>. From this, we provide several travel management recommendations specific to Mojave desert tortoise conservation beginning with identifying the entire travel network within management areas. Specific actions for managing or setting limits for road density depend on the site-specific biological or management context, for instance relative to habitat quality or proximity to designated tortoise conservation areas. In addition, increasing law enforcement and public outreach will improve enforcement and compliance of travel regulations, and installing tortoise-exclusion fencing along highways will reduce road kills and allow tortoise populations to reoccupy depleted areas adjacent to highways. Implementation of these recommendations would improve the prospects of reversing desert tortoise population declines.

Keywords: population declines; roads; route density; travel network; OHV recreation

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- \* Corresponding author: royaverillmurray@gmail.com
- † Deceased

#### Introduction

Habitat destruction has long been recognized as the greatest threat to global biodiversity (Wilcove et al. 1998; Pimm and Raven 2000; Venter et al. 2006). Roads provide access to natural areas for extractive natural resource use, energy infrastructure, and off-highway vehicle (OHV) recreation. As a result, roads contribute substantially to habitat destruction, degradation, and direct wildlife mortality via vehicle collision, construction, and maintenance operations (Forman and Alexander 1998; Andrews et al. 2008; Fahrig and Rytwinksi 2009; Switalski 2018). Roads also degrade habitat outside their direct footprint, for instance by spreading invasive plant species (Gelbard and Belnap 2003) and facilitating human access deeper into wildlands (McLellan and Shackleton 1988; Trombulak and Frissell 2000).

The extent of collective road networks enhances the magnitude of the effects of individual roads. For example, using effect zones (i.e., the area over which ecological effects extend beyond a road) weighted by the type of road, dated calculations estimated that up to 20% or more of United States land area experienced direct ecological effects from roads (Forman and Alexander 1998; Forman 2000). This estimate likely underestimates road-effect zones and is undoubtedly greater today (Carr and Fahrig 2001), but even at intermediate densities (e.g., 1–1.5 km/km<sup>2</sup>), road-effect zones can saturate a landscape (Frair et al. 2008). In fact, species richness correlates positively with roadless volume (Chen and Roberts 2008), and greater proportions of suitable habitat for species of conservation concern lie within inventoried roadless areas than outside such areas on national forests in the contiguous United States (Dietz et al. 2021).

Here, we summarize measures recommended in the literature and other guidance documents for a variety of North American taxa (and for forests and drylands more generally) to mitigate the effects of individual roads on wildlife. We contrast these measures with documented effects of road networks on wildlife populations and provide recommendations for travel management and road densities for wildlife conservation. Next, we apply this general overview to a case study of the Mojave desert tortoise Gopherus agassizii (hereafter, desert tortoise) by summarizing the specific effects of individual roads on desert tortoises and the existing measures to mitigate those effects. We then compare road densities with documented desert tortoise population trends within conservation areas and use the observed pattern as the basis for extending our general travel management recommendations to specific recommendations for Mojave desert tortoise conservation.

## Measures to Mitigate Effects of Roads on Wildlife

We can divide measures to address negative effects of roads on wildlife into strategies for minimizing impacts through system design and for mitigation and management (Switalski 2018). These measures often differ depending on whether the road is paved or unpaved. Researchers in the road ecology literature variously include roads of different types and use; so herein, we refer to all types of roads collectively as "roads" unless we specifically describe them as paved or unpaved. We generally refer to unpaved roads and other trails used for motorized travel as "routes."

System design recommendations pertinent to paved roads and highways include avoiding new road construction or road redundancy in areas where conservation is a priority and educating transportation planners on road-related impacts (Grandmaison 2016). A major mitigation and management recommendation involves incorporating barrier fencing to reduce wildlife-vehicle collisions and to funnel animals toward road-crossing structures (Huijser et al. 2009). Others include identifying road kill "hot spots"; minimizing use of contaminants such as salts, petrochemicals, and herbicides; and installing educational signs and speed limits (Bailey et al. 2006; Mitchell et al. 2006; Grandmaison 2016).

System design recommendations to minimize impacts from dirt roads and OHV routes begin with minimizing the creation of new routes, especially through interior habitat tracts and in habitat of sensitive species (Bushman and Therres 1988; Halama and Lovich 2016; Switalski 2018). Related recommendations include deactivating routes that are no longer used, incorporating crossing structures into new route plans and designs, avoiding routes that require multiple stream crossings, and locating routes outside riparian areas (Bailey et al. 2006; Mitchell et al. 2006; Switalski and Jones 2012; Halama and Lovich 2016; Switalski 2018). Biologists have recommended seasonal closures, such as those to avoid ungulate wintering habitat, to mitigate the effects of existing routes, for example, Jageman (1984). Additional mitigation and management recommendations include constructing routes outside the active seasons of sensitive wildlife, implementing outreach programs targeted toward OHV users, setting speed limits, and using law enforcement to deter cross-country travel (Bailey et al. 2006; Mitchell et al. 2006; Switalski and Jones 2012; Halama and Lovich 2016; Switalski 2018). Switalski (2018) also provided best management practices to mitigate direct and indirect impacts of OHVs on vegetation; soil compaction and erosion; social impacts, conflicts, and displacement; and impacts on cultural heritage sites.

Despite a long list of recommendations, most strategies for minimizing or mitigating the effects of roads are focused on the actual roads themselves rather than on the collective travel network across entire landscapes. Higher densities of roads reduce the probability that any given area will escape detrimental effects of human access, and higher road density will also fragment habitat more severely. For example, Mech (1989) showed that female gray wolves Canus lupus had reduced replacement rates in an area of Minnesota with road densities of more than 0.58 km/km<sup>2</sup>. In Wisconsin, gray wolves were eliminated from counties with road densities of more than 0.58 km/km<sup>2</sup> (Thiel 1985), packs were more likely to occupy areas with densities of less than 0.45 km/km<sup>2</sup> (Mladenoff et al. 1995, 1999), and 60% of human-induced mortality occurred at densities of more than 0.63 km/km<sup>2</sup> (Wydeven et al. 2001). Areas with road densities of more than 0.75 km/km<sup>2</sup> had declining populations of grizzly bears Ursus arctos horribilis in western Alberta, Canada (Boulanger and Stenhouse 2014; Proctor et al. 2019). Among smaller species, moor frogs Rana arvalis had smaller population sizes and lower probability of pond occupancy (more likely to be extirpated and less likely to recolonize) with increasing density of roads of all types within 750 m of ponds (Vos and Chardon 1998). Fishers *Pekania pennanti* had the highest probability of occurrence when road densities were less than 1 km/km<sup>2</sup> (Fuller et al. 2016).

Whereas direct mortality affects individuals immediately, a network of roads impacts wildlife populations and biodiversity by decreasing habitat area with fragmentation and reducing habitat quality; road networks also disrupt horizontal landscape processes, such as groundwater flow, spread of species tolerant of human-disturbed environments, and fire spread (Harris et al. 1996; Forman and Alexander 1998; Fahrig 2002). Therefore, density limits on road networks constitute a viable tool for managing cumulative effects, especially for land managers seeking to support healthy wildlife populations across large landscapes (van der Marel et al. 2020). For example, where construction of routes for timber access led to increased elk Cervus elaphus mortality, management that included seasonal closures (i.e., temporarily reducing effects of route density) became an important part of hunting and poacher management. Route management for elk was directed at regulating hunter densities, at maintaining adequate habitat for elk, and at limiting movement of elk populations due to road avoidance (Rowland et al. 2000). Gratson and Whitman (2000) suspected that higher elk densities in areas with road densities of less than 0.56 km/km<sup>2</sup> (presumably unpaved) contributed to greater hunter success in Idaho.

We believe that establishing road density limits in travel management plans will enable managers to more effectively implement regulations intended to protect resources on public lands. For example, Bureau of Land Management regulations require that where OHVs "are causing or will cause considerable adverse effects upon soil, vegetation, wildlife, wildlife habitat, ..., threatened or endangered species, wilderness suitability, other authorized uses, or other resources," the areas will be closed until the adverse effects are eliminated (43 CFR Subpart 8341.2). The regulations further stipulate that "areas and trails shall be located to minimize harassment of wildlife or significant disruption of wildlife habitats," with special attention to threatened and endangered species (43 CFR Subpart 8342.1). Consequently, given the relationships between road density and wildlife populations described above, consideration of road densities by the Bureau of Land Management could contribute to the reduction of adverse effects upon wildlife on public land. A relevant example comes from the U.S. Forest Service, which implemented travel management regulations to benefit grizzly bears in the Flathead National Forest. These regulations stipulate that 55–68% of the planning area be more than 500 m from an open route (i.e., a route without restriction to motorized vehicle use), 19-33% should have a route density of less than 0.6 km/km<sup>2</sup>, and 19–26% may have a total route density of more than 1.2 km/km<sup>2</sup> (USFS 1995; Proctor et al. 2019). Despite this example, cumulative effects of road networks are rarely

considered in land-use planning (van der Marel et al. 2020). Plans often do not explicitly describe road densities or do not quantify the length of roads covered by the plan (Table S1, Supplemental Material). Of those plans that do quantify road lengths, most exclude paved roads on federal land and all roads on nonfederal land within the plan area.

## **Recommendations for Travel Management** and Road Densities

Forman and Alexander (1998) suggested a road density of 0.6 km/km<sup>2</sup> as the maximum that would support a naturally functioning landscape containing sustained populations of large predators and other species. We recommend this road density as a general target for travel management in areas where wildlife conservation is a priority. The first step in effectively achieving this or any target road density is to quantify roads across the entire travel network, including paved roads, designated unpaved and user-created routes, and any other linear features used for travel within the area of concern (Switalski 2018). Note that the travel network includes land both under the management jurisdiction of the agency implementing travel management and on any other interspersed land of differing management authority, such as private inholdings. Road density is a function of the total conservation area of interest, not parcel-specific management jurisdiction.

Road densities of less than 0.6 km/km<sup>2</sup> may be necessary in areas with particularly sensitive, declining, or threatened species, whereas higher densities may be appropriate in areas less important to landscape-level conservation and wildlife connectivity. For example, the Livingstone-Porcupine Hills Land Footprint Management Plan limited publicly accessible roads in management zones with the highest values and sensitivity to disturbance to 0.4 km/km<sup>2</sup> in Alberta, Canada (van der Marel et al. 2020). Finally, public land management officials across the United States identified that financial and staff resources were insufficient to meet the challenge of enforcing OHV regulations (U.S. Government Accountability Office 2009), suggesting that public policy and funding to address this challenge will be critical to achieving conservation and management objectives associated with maintaining appropriate cumulative road densities.

## **Mojave Desert Tortoise Case Study**

#### **Effects of roads**

Mojave desert tortoises occur across a large geographic area in the Mojave Desert and the Lower Colorado River Valley subdivision of the Sonoran Desert of the southwestern United States (Figure 1). The species was federally listed as Threatened under The U.S. Endangered Species Act in 1990 (ESA 1973, as amended; 55 FR 12178, Apr. 2, 1990), and populations have continued to decline across much of the species' range (Allison and McLuckie 2018). Roads are particular threats

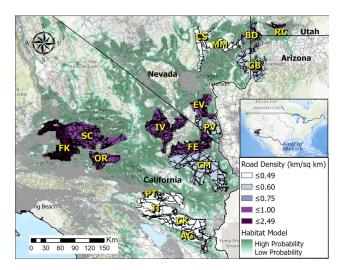


Figure 1. Density of roads (black lines) within Mojave desert tortoise Gopherus agassizii monitoring strata in 2014. Roads between strata are shown in gray. The underlying habitat model is from Nussear et al. (2009). The strata occur in California, Nevada, Utah, and Arizona in the southwestern United States and are labelled as follows: AG = Chocolate Mountain Aerial Gunnery Range; BD = Beaver Dam Slope; CK = Chuckwalla; CM = Chemehuevi; CS = Coyote Springs; EV = Eldorado Valley; FE = Fenner; FK = Fremont-Kramer; GB = Gold Butte-Pakoon; IV = Ivanpah; JT = Joshua Tree National Park; MM = Mormon Mesa; OR = Ord-Rodman; PT = Pinto Mountains; PV = Piute Valley; RC = Red Cliffs Desert Reserve; SC = Superior-Cronese.

because direct mortality from vehicles on paved roads and highways can create population depression zones up to 0.4 km from the roads themselves (von Seckendorff Hoff and Marlow 2002; Nafus et al. 2013; Peaden et al. 2015). This single effect can severely reduce both demographic and genetic connectivity of tortoise populations across the range (Averill-Murray et al. 2021).

As discussed above, paved and unpaved roads can also serve as corridors for nonnative weed dispersal (Gelbard and Belnap 2003; Brooks and Lair 2005; Brooks 2009), and nonnative plant species cover and richness are greater closer to roads (Boarman and Sazaki 2006). This is a particular concern for desert tortoises because nonnative plants affect the quality and quantity of forage and the ability of tortoises to acquire important nutrients (Nagy et al. 1998; Oftedal 2002; Hazard et al. 2010). Further, many of these nonnative plants are fire adapted and contribute to increases in unnatural fire regimes, including extent and frequency (Brown and Minnich 1986; Brooks and Esque 2002; Brooks et al. 2004). Direct mortality of desert tortoises increases with more frequent or widespread fires (Esque et al. 2003).

Vehicle travel can also adversely affect dry washes, which are used by tortoises for travelling, burrowing, and foraging (Jennings 1997; Todd et al. 2016; Peaden et al. 2017). Custer et al. (2017) reported greater degradation from OHV use in designated open wash zones (those open to motorized travel if that travel will not result in unavoidable disturbance to the wash bank, vegetation, or soil) near access roads than in washes in designated closed areas. Finally, the potential for negative impacts to desert tortoise populations exists from collection, deliberate maiming, or killing by humans as a result of road access, vehicles on paved and unpaved roads, and nonmotorized recreation (Grandmaison and Frary 2012). In sum, road-related threats contributed  $\sim$ 22% of the total impacts to the Mojave desert tortoise in an aspatial conceptual model of risk to the species, not including effects of population fragmentation (Darst et al. 2013).

## Existing measures to mitigate the effects of roads

The U.S. Fish and Wildlife Service recovery plan for the Mojave desert tortoise contains a suite of recommendations aimed at improving the status of the species so it can be removed from the list of threatened species. Recommendations specific to roads include restricting, designating, closing, and fencing roads and restricting OHV events within desert tortoise habitat (USFWS 2011). More specifically, these recommendations suggest that new roads should not be established within tortoise conservation areas (TCAs), with a goal of "no net gain" of roads. In addition, the recovery plan recommends formally designating the conditions of use of existing roads, closing nonessential routes, establishing 40-kph speed limits on unpaved and rural paved roads, maintaining berms along graded dirt roads so that tortoises do not get trapped in the roadbed, and identifying hot spots of mortality and installing tortoise barrier fencing along highways in desert tortoise habitat. Several of these recommendations have been applied to individual land-use plans as well as other actions, such as limiting the distance from the road centerline within which parking and camping is authorized (BLM 2019a).

Brooks and Berry (2006) suggested that minimizing the density of unpaved roads across the Mojave desert tortoise's range reduces dominance, richness, and biomass of invasive annual plants and helps reduce the frequency and size of fires facilitated by these plants. Reducing the density of unpaved roads would also improve the habitat used by desert tortoises to move between locations, because even though they are not completely averse to crossing dirt roads, desert tortoises generally avoid moving through areas close to roads (Hromada et al. 2020). However, existing recommendations and land-use plans lack consideration of the current or desired density of roads within desert tortoise habitat. For example, of 19 federal land-use plans that overlap the range of the Mojave desert tortoise, none explicitly describe road densities (Table S1, Supplemental Material). Consequently, densities of approved routes within desert tortoise conservation areas vary widely, with means of 0.09–1.36 km/km<sup>2</sup> where we could calculate them. However, most plans did not quantify paved roads on federal land or any roads on nonfederal land within the planning areas, so these calculated densities underestimate true road densities within the TCAs.

#### Road networks and population trends

We compared estimated annual trends in tortoise density within 17 TCAs between 2004 and 2014 (from Allison and McLuckie 2018) with the density of all roads in each TCA using data from the 2014 TIGER/Line layers (U.S. Census Bureau 2014a), including primary roads, secondary roads, local neighborhood roads, rural roads, city streets, vehicular trails (four-wheel drive), ramps, service drives, walkways, stairways, alleys, and private roads (U.S. Census Bureau 2014b). We used ArcGis Pro 2.6.2 (Esri Inc.) to clip the roads layer to the TCAs, from which we then calculated the total length of roads within each TCA. We estimated road density by dividing the total road length by the area of each TCA. Road density ranged from 0.29 to 2.49 km/km<sup>2</sup> (Table 1; Figure 1). At low road densities, trends in tortoise populations vary widely, but all TCAs with road densities of more than  $0.75 \text{ km/km}^2$  (n = 7) had declining tortoise population trends (Table 1; Figure 2).

Previous studies indicate that desert tortoises do not coexist well with human development and disturbances. For example, tortoises are essentially absent from habitats within 1 km of areas with more than 5% development, including urban development, cultivated agriculture, energy development, surface mines and quarries, pipelines and transmission lines, and roads and railroads (Carter et al. 2020). More specific to the impact of roads, an unused, natural plot in southern California had 1.7 times the number of live plants, 3.9 times the plant cover, 3.9 times the number of desert tortoise detections, and 4.0 times the active tortoise burrows compared with a nearby area heavily used by OHVs (Bury and Luckenbach 2002). The demographic and movement traits of tortoises place them in the company of grizzly bears and gray wolves as fauna for which road networks may be an important limiting factor to population recovery (Gibbs and Shriver 2002).

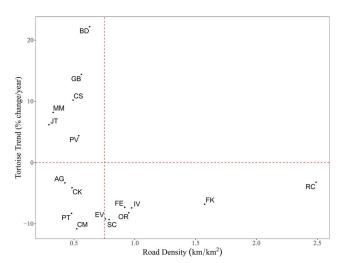


Figure 2. Mojave desert tortoise Gopherus agassizii population trends, 2004-2014, plotted against road density within monitoring strata. The vertical line indicates 0.75 km/km<sup>2</sup>. The strata occur in California, Nevada, Utah, and Arizona in the southwestern United States and are labelled as follows: AG = Chocolate Mountain Aerial Gunnery Range; BD = Beaver Dam Slope; CK = Chuckwalla; CM = Chemehuevi; CS = Coyote Springs; EV = Eldorado Valley; FE = Fenner; FK = Fremont-Kramer; GB = Gold Butte-Pakoon; IV = Ivanpah; JT = Joshua Tree National Park; MM = Mormon Mesa; OR = Ord-Rodman; PT = Pinto Mountains; PV = Piute Valley; RC = Red Cliffs Desert Reserve; SC = Superior-Cronese.

As noted previously, unpaved route proliferation and compliance with OHV travel regulations remain an ongoing challenge even in the absence of road density limits (U.S. Government Accountability Office 2009). Federal regulations define designated open routes as those on which all types of vehicle use are permitted at all times and define designated limited routes as those restricted at certain times, in certain areas, or to certain vehicular use (43 CFR Subpart 8340.0-5). In California, for

Table 1. Annual trends in Mojave desert tortoise Gopherus agassizii populations between 2004 and 2014 (Allison and McLuckie 2018), total road length in 2014 (U.S. Census Bureau 2014a), and road density within 17 monitoring strata in California, Nevada, Utah, and Arizona of the southwestern United States.

Name	Trend (%/y)	Stratum area (km²)	Road length (km)	Road density (km/km²)
Chocolate Mountain Aerial Gunnery Range	-3.3	754.6	321	0.43
Beaver Dam Slope	22.2	828.3	521	0.63
Chuckwalla	-4.1	3,508.7	1,699	0.48
Chemehuevi	-10.8	4,037.5	2,113	0.52
Coyote Springs	10.2	1,116.5	550	0.49
Eldorado Valley	-9.2	1,152.6	875	0.76
Fenner	-7.3	1,841.4	1,689	0.92
Fremont-Kramer	-6.8	2,416.8	3,804	1.57
Gold Butte-Pakoon	14.4	1,976.6	1,109	0.56
Ivanpah	-7.4	2,566.9	2,500	0.97
Joshua Tree National Park	6.2	1,566.6	461	0.29
Mormon Mesa	8.2	968.1	319	0.33
Ord-Rodman	-8.2	1,124.3	1,069	0.95
Pinto Mountains	-8.3	751.1	361	0.48
Piute Valley	4.4	1,070.4	578	0.54
Red Cliffs Desert Reserve	-3.2	115.0	286	2.49
Superior-Cronese	-9.3	3,331.7	2,628	0.79

example, the West Mojave Route Network Project designated 10,051 km of unpaved routes as open or limited; however, 24,518 km of ground transportation linear features (254% of the designated total) were mapped on the ground (BLM 2019a, 2019b). The total length of currently identified, unpaved routes across the entire planning area (which includes several TCAs and land between these units; Figure 1) equates to a density of 1.95 km/km<sup>2</sup>, and the 10.051 km of unpayed routes actually designated as open or limited equates to a density of 0.80 km/km<sup>2</sup>, noting again that these calculations underestimate true road density due to the exclusion of paved and nonfederal roads from the plan (Table S1, Supplemental Material). Both calculated route densities exceed the published recommended maximum density of all roads (0.6 km/km<sup>2</sup>) and the density above which our results found only declining populations (0.75 km/km<sup>2</sup>). Before publication of the final plan, the Bureau of Land Management considered specific limits of 29.0-38.6 km of routes per township ( $\sim$ 93.2 km<sup>2</sup>) for desert tortoise habitat areas in the western Mojave Desert, which would have corresponded to 0.3–0.4 km/km<sup>2</sup>. However, the Bureau of Land Management dismissed the suggested density caps, stating that they were arbitrary (BLM 2005:2-226, 2019a:2-58).

#### Recommendations

Our analysis, existing literature, and established federal precedent (USFS 1995) provide justification for establishing clear road density limits on public land within the range of the Mojave desert tortoise. We make the following specific recommendations:

- 1) Identify the entire travel network, including paved, designated unpaved, and user-created routes, and open wash zones on all federal and nonfederal land within management areas.
- 2) Reduce total road density within the travel network to less than 0.6 km/km<sup>2</sup> in TCAs that currently exceed this threshold by administratively closing, signing, physically blocking, obscuring, and restoring excess unpaved routes.
- 3) Stratify road density thresholds in large TCAs based on habitat quality (Proctor et al. 2019; van der Marel et al. 2020). Many of the TCAs cover large landscapes (up to almost 4,100 km<sup>2</sup>; Table 1) composed of areas with different road densities and variable habitat quality. Impacts to tortoises and their habitats within particular areas of a TCA that contain higher than the average recommended road density could compromise healthy population dynamics of the larger population. Nussear et al. (2009) modeled desert tortoise habitat probability based on several environmental variables. Using this model, managers could apply a maximum road density of 0.6 km/km<sup>2</sup> to areas predominately containing lower-probability habitat (e.g., probability values of less than 0.6 [Nussear et al. 2009, figure 6]) and further reduce road densities in

- higher-probability habitats (e.g., probability values of more than 0.6).
- 4) Recognize that wholesale reduction of road densities across the entire landscape of some TCAs may be impractical within a short time frame. Reducing road densities to recommended levels initially within smaller focal areas in which managers are implementing other conservation actions, possibly in conjunction with the stratification recommendation above, could help more quickly stabilize tortoise populations in those areas.
- 5) Maintain population connectivity within habitat linkages between TCAs (Averill-Murray et al. 2021) by limiting road densities to less than 0.75 km/km<sup>2</sup> in large areas of potential tortoise habitat between TCAs.
- 6) Strategically acquire private inholdings not needed for public access to reduce road density and improve management capability of the surrounding area (USFWS 2011). Many routes on public land exist primarily as access roads to private lands and may not be intended for public use (BLM 2019a:1-4).
- 7) Increase law enforcement staff and patrols where necessary to enforce travel regulations (USFWS 2011). Managers also could increase the use of innovative means, such as the use of free mapping software and mobile apps, to disseminate information about route status to increase compliance even where signs are vandalized (Custer et al. 2017).
- 8) Install tortoise-exclusion fencing along paved highways within tortoise habitat to eliminate road kills and to allow tortoise populations to reoccupy depleted areas adjacent to the highways (USFWS 2011; Peaden et al. 2015). Exclusion fencing should connect to passages to prevent roads from becoming absolute barriers to population connectivity (Boarman et al. 1997; Averill-Murray et al. 2021).

#### **Conclusions**

Roads pose significant direct and indirect threats to the Mojave desert tortoise, and the magnitude of effort required to address these threats is daunting but not impossible. The Livingstone-Porcupine Hills Land Footprint Management Plan reduced approved road densities from an average of 2.34 km/km<sup>2</sup> to 0.6 km/km<sup>2</sup> or less within its 1,793-km<sup>2</sup> plan area (van der Marel et al. 2020). Reducing excessive road densities will be necessary for the continued persistence of Mojave desert tortoise populations and populations of other sensitive species. Nevertheless, variability in population trends in areas with low road densities (Figure 2) indicates that where road densities are lower, many other unaddressed threats continue to reduce population numbers and contribute to the threatened status of Moiave desert tortoise populations (Tracy et al. 2004; USFWS 2011; Darst et al. 2013). A next step for Mojave desert tortoise conservation efforts, in general, is to look at TCAs with declining populations despite having road densities of less than 0.60 to 0.75 km/km<sup>2</sup> to identify threats that might be more prevalent there than in TCAs with increasing trends.

## **Supplemental Material**

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**Table S1.** Approved route densities calculated from information in federal land management plans published between 1997 and 2021 in the Mojave Desert and the Lower Colorado River Valley subdivision of the Sonoran Desert, United States.

Available: https://doi.org/10.3996/JFWM-22-030.S1 (21 KB XLSX)

Reference S1. Averill-Murray RC, Esque TC, Allison LJ, Bassett S, Carter SK, Dutcher KE, Hromada SJ, Nussear KE, Shoemaker K. 2021. Connectivity of Mojave desert tortoise populations—management implications for maintaining a viable recovery network. Reston, Virginia: U.S. Geological Survey Open-File Report 2021–1033.

Available: https://pubs.usgs.gov/of/2021/1033/ ofr20211033.pdf (July 2022) and https://doi.org/10. 3996/JFWM-22-030.S2 (7.875 MB PDF)

Reference S2. Brooks ML, Lair B. 2005. Ecological effects of vehicular routes in a desert ecosystem. Henderson, Nevada: U.S. Geological Survey Report for the Recoverability and Vulnerability of Desert Ecosystems Program.

Available: https://doi.org/10.3996/JFWM-22-030.S3 (114 KB PDF)

**Reference S3.** [BLM] Bureau of Land Management. 1997. Approved Tonopah resource management plan and record of decision. Battle Mountain, Nevada: Bureau of Land Management (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S4 (17.113 MB PDF)

**Reference S4.** [BLM] Bureau of Land Management. 1998. Record of decision for the approved Las Vegas resource management plan and final environmental impact statement. Reno, Nevada: Bureau of Land Management. BLM/LV/LP-99/002+1610 (cited in Table

Available: https://doi.org/10.3996/JFWM-22-030.S5 (11.953 MB PDF)

Reference S5. [BLM] Bureau of Land Management. 2000. Proposed general management plan and final environmental impact statement for Red Rock Canyon National Conservation Area. Las Vegas, Nevada: Bureau of Land Management. BLM/LV/PL-01/006+8322 (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S6 (3.069 MB PDF)

Reference S6. [BLM] Bureau of Land Management. 2002a. Proposed Northern & Eastern Colorado Desert coordinated management plan and final environmental impact statement. Riverside: Bureau of Land Management, California Desert District and California Department of Fish and Game, Inland, Deserts, and Eastern Sierra Region (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S7 (1.621 MB PDF)

**Reference S7.** [BLM] Bureau of Land Management. 2002b. Proposed Northern & Eastern Mojave Desert coordinated management plan and final environmental impact statement. Riverside: Bureau of Land Management, California Desert District (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S8 (13.167 MB PDF)

**Reference S8.** [BLM] Bureau of Land Management. 2005. Final environmental impact report and statement for the West Mojave Plan: a habitat conservation plan and a California Desert conservation area plan amendment. Volume 1. Moreno Valley: Bureau of Land Management, California Desert District. BLM/CA/ES-2004-005+1790-1600 (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S9 (2.990 MB PDF)

Reference S9. [BLM] Bureau of Land Management. 2006. The Sloan Canyon National Conservation Area record of decision for the approved resource management plan/final environmental impact statement and approval of the North McCullough Wilderness Management Plan. Las Vegas, Nevada: Bureau of Land Management, Las Vegas Field Office. BLM/LV/PL-06/016+1610 (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S10 (2.079 MB PDF)

**Reference S10.** [BLM] Bureau of Land Management. 2007. Arizona Strip Field Office approved resource management plan. St. George, Utah: Bureau of Land Management, Arizona Strip Field Office (cited in Table

Available: https://doi.org/10.3996/JFWM-22-030.S11 (80.211 MB PDF)

Reference S11. [BLM] Bureau of Land Management. 2008. Ely District record of decision and approved resource management plan. Ely, Nevada: Bureau of Land Management, Ely District Office. BLM/NV/EL/PL-GI08/ 25+1793 (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S12 (10.526 MB PDF)

Reference S12. [BLM] Bureau of Land Management. 2016a. St. George Field Office record of decision and approved resource management plan amendment. St. George, Utah: Bureau of Land Management, St. George Field Office (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S13 (9.751 MB PDF)

**Reference S13.** [BLM] Bureau of Land Management. 2016b. Beaver Dam Wash National Conservation Area record of decision and approved resource management plan. St. George, Utah: Bureau of Land Management, St. George Field Office (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S14 (13.530 MB PDF)

Reference S14. [BLM] Bureau of Land Management. 2019a. West Mojave Route Network Project final California Desert conservation plan amendment and supplemental environmental impact statement for the California Desert District. Moreno Valley: Bureau of Land Management, California Desert District. BLM/CA/DOI-BLM-CA-D080-2018-0008-EIS (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S15 (5.574 MB PDF)

**Reference S15.** [BLM] Bureau of Land Management. 2019b. Record of decision: West Mojave Route Network Project decision to amend California Desert conservation area plan and implement nine travel management plans. Moreno Valley: Bureau of Land Management, California Desert District (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S16 (90 KB PDF)

Reference S16. [BLM] Bureau of Land Management. 2021. Record of decision and approved resource management plan amendments for the Northern Corridor right-of-way, Red Cliffs National Conservation Area resource management plan, and St. George Field Office resource management plan. St. George, Utah: Bureau of Land Management, St. George Field Office (cited in Table

Available: https://doi.org/10.3996/JFWM-22-030.S17 (10.094 MB PDF)

Reference \$17. [BLM/NPS] Bureau of Land Management and National Park Service. 2008. Grand Canyon-Parashant National Monument approved management plan. St. George, Utah: Bureau of Land Management and National Park Service (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S18 (71.166 MB PDF)

Reference S18. Bushman ES, Therres GD. 1988. Habitat management guidelines for forest interior breeding birds of coastal Maryland. Annapolis: Maryland Department of Natural Resources. Wildlife Technical Publication 88-1.

Available: https://doi.org/10.3996/JFWM-22-030.S19 (2.288 MB PDF)

Reference S19. Jageman H. 1984. White-tailed deer habitat management guidelines. Moscow: Forest, Wildlife, and Range Experiment Station, University of Idaho.

Available: https://doi.org/10.3996/JFWM-22-030.S20 (4.746 MB PDF)

Reference S20. [NPS] National Park Service. 2000. General management plan development concept plans environmental impact statement. Twentynine Palms, California: Joshua Tree National Park (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S21 (9.065 MB PDF)

Reference S21. [NPS] National Park Service. 2002a. Mojave National Preserve general management plan. Essex, California: Mojave National Preserve (cited in Table

Available: https://doi.org/10.3996/JFWM-22-030.S22 (4.229 MB PDF)

**Reference S22.** [NPS] National Park Service. 2002b. Death Valley National Park general management plan. Essex, California: Mojave National Preserve (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S23 (3.866 MB PDF)

Reference S23. [NPS] National Park Service. 2005. General Management Plan amendment/environmental assessment. Boulder City, Nevada: Lake Mead National Recreation Area (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S24 (4.696 MB PDF)

Reference S24. Nussear KE, Esque TC, Inman RD, Gass L, Thomas KA, Wallace CSA, Blainey JB, Miller DM, Webb RH. 2009. Modeling habitat of the desert tortoise (Gopherus agassizii) in the Mojave and parts of the Sonoran deserts of California, Nevada, Utah, and Arizona. Reston, Virginia: U.S. Geological Survey Open-File Report 2009-1102.

Available: https://doi.org/10.3996/JFWM-22-030.S25 (1.484 MB PDF) and https://pubs.usgs.gov/of/2009/ 1102/ofr20091102.pdf (July 2022)

**Reference S25.** Tracy CR, Averill-Murray R, Boarman WI, Delehanty D, Heaton J, McCoy E, Morafka D, Nussear K, Hagerty B, Medica P. 2004. Desert tortoise recovery plan assessment. Washington, D.C.: Report to U.S. Fish and Wildlife Service.

Available: https://doi.org/10.3996/JFWM-22-030.S26 (9.926 MB PDF)

Reference S26. [USFWS] U.S. Fish and Wildlife Service. 2009. Desert National Wildlife Refuge Complex Ash Meadows, Desert, Moapa Valley, and Pahranagat National Wildlife Refuges final comprehensive conservation plan and environmental impact statement. Sacramento, California: U.S. Fish and Wildlife Service, Pacific Southwest Region (cited in Table S1).

Available: https://doi.org/10.3996/JFWM-22-030.S27 (12.289 MB PDF)

Reference S27. [USFWS] U.S. Fish and Wildlife Service. 2011. Revised recovery plan for the Mojave population of the desert tortoise (Gopherus agassizii). Sacramento, California: U.S. Fish and Wildlife Service, Pacific Southwest Region.

Available: https://doi.org/10.3996/JFWM-22-030.S28 (11.803 MB PDF) and https://www.fws.gov/sites/default/ files/documents/USFWS.2011.RRP%20for%20the% 20Mojave%20Desert%20Tortoise.pdf (July 2022)

Reference S28. [USFS] U.S. Forest Service. 1995. Decision notice: allowable sale quantity and objectives and standards for grizzly bear habitat management. Kalispell, Montana: USDA National Forest Service, Flathead National Forest.

Available: https://doi.org/10.3996/JFWM-22-030.S29 (2.501 MB PDF)

Reference S29. U.S. Government Accountability Office. 2009. Enhanced planning could assist agencies in managing increased use of off-highway vehicles. Washington, D.C.: House of Representatives. Report to the Subcommittee on National Parks, Forests and Public Lands, Committee on Natural Resources, GAO-09-509.

Available: https://doi.org/10.3996/JFWM-22-030.S30 (3.708 MB PDF)

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## References

- Allison LJ, McLuckie AM. 2018. Population trends in Mojave desert tortoises (Gopherus agassizii). Herpetological Conservation and Biology 13:433–452.
- Andrews KM, Gibbons JW, Jochimsen DM. 2008. Ecological effects of roads on amphibians and reptiles: a literature review. Pages 121-143 in Mitchell JC, Jung Brown RE, Bartholomew B, editors. Urban herpetology. Salt Lake City, Utah: Society for the Study of Amphibians and Reptiles.
- Averill-Murray RC, Esque TC, Allison LJ, Bassett S, Carter SK, Dutcher KE, Hromada SJ, Nussear KE, Shoemaker K. 2021. Connectivity of Mojave desert tortoise populations—management implications for maintaining a viable recovery network. Reston, Virginia: U.S. Geological Survey Open-File Report 2021-1033. Available:

- https://pubs.usgs.gov/of/2021/1033/ofr20211033.pdf (July 2022) (see Supplemental Material, Reference S1).
- Bailey MA, Holmes JN, Buhlmann KA, Mitchell JC. 2006. Habitat management guidelines for amphibians and reptiles of the southeastern United States. Montgomery, Alabama: Partners in Amphibian and Reptile Conservation. Technical Publication HMG-2.
- Boarman WI, Sazaki M. 2006. A highway's road-effect zone for desert tortoises (Gopherus agassizii). Journal of Arid Environments 65:94-101.
- Boarman WI, Sazaki M, Jennings WB. 1997. The effect of roads, barrier fences, and culverts on desert tortoise populations in California, USA. Pages 54-58 in Abbema JV, editor. Proceedings: Conservation, restoration, and management of tortoises and turtles: an international conference. Purchase: State University of New York, New York Turtle and Tortoise Society.
- Boulanger J, Stenhouse GB. 2014. The impact of roads on the demography of grizzly bears in Alberta. PLoS ONE 9:e115535.
- Brooks ML. 2009. Spatial and temporal distribution of nonnative plants in upland areas of the Mojave Desert. Pages 101–124 in Webb R, Fenstermaker LF, Heaton JS, Hughson DL, McDonald EV, Miller DM, editors. The Mojave Desert: ecosystem processes and sustainability. Reno: University of Nevada.
- Brooks ML, Berry KH. 2006. Dominance and environmental correlates of alien annual plants in the Mojave Desert, USA. Journal of Arid Environments 67:100–124.
- Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D. 2004. Effects of invasive alien plants on fire regimes. BioScience 54:677-688.
- Brooks ML, Esque TC. 2002. Alien plants and fire in desert tortoise (Gopherus agassizii) habitat of the Mojave and Colorado deserts. Chelonian Conservation and Biology 4:330-340.
- Brooks ML, Lair B. 2005. Ecological effects of vehicular routes in a desert ecosystem. Henderson, Nevada: U.S. Geological Survey Report for the Recoverability and Vulnerability of Desert Ecosystems Program (see Supplemental Material, Reference S2).
- Brown DE, Minnich RA. 1986. Fire and changes in creosote bush scrub of the western Sonoran Desert, California. American Midland Naturalist 116:411-422.
- [BLM] Bureau of Land Management. 1997. Approved Tonopah resource management plan and record of decision. Battle Mountain, Nevada: Bureau of Land Management (see Supplemental Material, Reference S3, cited in Table S1).
- [BLM] Bureau of Land Management. 1998. Record of decision for the approved Las Vegas resource management plan and final environmental impact statement. Reno, Nevada: Bureau of Land Management. BLM/LV/LP-99/002+1610 (see Supplemental Material, Reference S4, cited in Table S1).

- [BLM] Bureau of Land Management. 2000. Proposed general management plan and final environmental impact statement for Red Rock Canyon National Conservation Area. Las Vegas, Nevada: Bureau of Land Management. BLM/LV/PL-01/006+8322 (see Supplemental Material, Reference S5, cited in Table S1).
- [BLM] Bureau of Land Management, 2002a, Proposed Northern & Eastern Colorado Desert coordinated management plan and final environmental impact statement. Riverside: Bureau of Land Management, California Desert District and California Department of Fish and Game, Inland, Deserts, and Eastern Sierra Region (see Supplemental Material, Reference S6, cited in Table S1).
- [BLM] Bureau of Land Management. 2002b. Proposed Northern & Eastern Mojave Desert coordinated management plan and final environmental impact statement. Riverside: Bureau of Land Management, California Desert District (see Supplemental Material, Reference S7, cited in Table S1).
- [BLM] Bureau of Land Management. 2005. Final environmental impact report and statement for the West Mojave Plan: a habitat conservation plan and a California Desert conservation area plan amendment. Volume 1. Moreno Valley: Bureau of Land Management, California Desert District. BLM/CA/ES-2004-005+1790-1600 (see Supplemental Material, Reference S8, cited in Table S1).
- [BLM] Bureau of Land Management. 2006. The Sloan Canyon National Conservation Area record of decision for the approved resource management plan/final environmental impact statement and approval of the North McCullough Wilderness Management Plan. Las Vegas, Nevada: Bureau of Land Management, Las Vegas Field Office. BLM/LV/PL-06/016+1610 (see Supplemental Material, Reference S9, cited in Table S1).
- [BLM] Bureau of Land Management. 2007. Arizona Strip Field Office approved resource management plan. St. George, Utah: Bureau of Land Management, Arizona Strip Field Office (see Supplemental Material, Reference S10, cited in Table S1).
- [BLM] Bureau of Land Management. 2008. Ely District record of decision and approved resource management plan. Ely, Nevada: Bureau of Land Management, Ely District Office. BLM/NV/EL/PL-GI08/25+1793 (see Supplemental Material, Reference S11, cited in Table S1).
- [BLM] Bureau of Land Management. 2016a. St. George Field Office record of decision and approved resource management plan amendment. St. George, Utah: Bureau of Land Management, St. George Field Office (see Supplemental Material, Reference S12, cited in Table S1).
- [BLM] Bureau of Land Management. 2016b. Beaver Dam Wash National Conservation Area record of decision and approved resource management plan. St. George, Utah: Bureau of Land Management, St. George Field

- Office (see Supplemental Material, Reference S13, cited in Table S1).
- [BLM] Bureau of Land Management. 2019a. West Mojave Route Network Project final California Desert conservation plan amendment and supplemental environmental impact statement for the California Desert District. Moreno Valley: Bureau of Land Management, California Desert District. BLM/CA/DOI-BLM-CA-D080-2018-0008-EIS (see Supplemental Material, Reference S14).
- [BLM] Bureau of Land Management. 2019b. Record of decision: West Mojave Route Network Project decision to amend California Desert conservation area plan and implement nine travel management plans. Moreno Valley: Bureau of Land Management, California Desert District (see Supplemental Material, Reference S15).
- [BLM] Bureau of Land Management. 2021. Record of decision and approved resource management plan amendments for the Northern Corridor right-of-way, Red Cliffs National Conservation Area resource management plan, and St. George Field Office resource management plan. St. George, Utah: Bureau of Land Management, St. George Field Office (see Supplemental Material, Reference S16, cited in Table S1).
- Bureau of Land Management and National Park Service. 2008. Grand Canyon-Parashant National Monument approved management plan. St. George, Utah: Bureau of Land Management and National Park Service (see Supplemental Material, Reference S17, cited in Table S1).
- Bury RB, Luckenbach RA. 2002. Comparison of desert tortoise (Gopherus agassizii) populations in an unused and off-road vehicle area in the Mojave Desert. Chelonian Conservation and Biology 4:457–463.
- Bushman ES, Therres GD. 1988. Habitat management guidelines for forest interior breeding birds of coastal Maryland. Annapolis: Maryland Department of Natural Resources. Wildlife Technical Publication 88-1 (see Supplemental Material, Reference S18).
- Carr LW, Fahrig L. 2001. Effect of road traffic on two amphibian species of differing vagility. Conservation Biology 15:1071-1078.
- Carter SK, Nussear KE, Esque TC, Leinwand IAF, Masters E, Inman RD, Carr NB, Allison LJ. 2020. Quantifying development to inform management of Mojave and Sonoran desert tortoise habitat in the American Southwest. Endangered Species Research 42:167–184.
- Chen X, Roberts KA. 2008. Roadless areas and biodiversity: a case study in Alabama, USA. Biodiversity and Conservation 17:2013-2022.
- Custer NA, DeFalco LA, Nussear KE, Esque TC. 2017. Drawing a line in the sand: effectiveness of offhighway vehicle management in California's Sonoran Desert. Journal of Environmental Management 193:448-457.
- Darst CR, Murphy PJ, Strout NW, Campbell SP, Field KJ, Allison L, Averill-Murray RC. 2013. A strategy for

- prioritizing threats and recovery actions for at-risk species. Environmental Management 51:786-800.
- Dietz MS, Barnett K, Belote RT, Aplet GH. 2021. The importance of U.S. national forest roadless areas for vulnerable wildlife species. Global Ecology and Conservation 32:e01943.
- Esque TC, Schwalbe CR, DeFalco LA, Duncan RB, Hughes TJ. 2003. Effects of desert wildfires on desert tortoise (Gopherus agassizii) and other small vertebrates. The Southwestern Naturalist 48:103-111.
- Fahrig L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecological Applications 12:346-353.
- Fahrig L, Rytwinksi T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14(1):21. Available: http://www. ecologyandsociety.org/vol14/iss1/art21/ (July 2022)
- Forman RTT. 2000. Estimate of the area affected ecologically by the road system in the United States. Conservation Biology 14:31-35.
- Forman RTT, Alexander LE. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207-231.
- Frair JL, Merrill EH, Beyer HL, Morales JM. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. Journal of Applied Ecology 45:1504–1513.
- Fuller AK, Linden DW, Royal JA. 2016. Management decision making for fisher populations informed by occupancy modeling. Journal of Wildlife Management 80:794-802.
- Gelbard JL, Belnap J. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conservation Biology 17:420-432.
- Gibbs JP, Shriver WG. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16:1647-1652.
- Grandmaison D. 2016. Major roads and highways. Pages 21-23 in Jones LLC, Halama KJ, Lovich RE, editors. Habitat management guidelines for amphibians and reptiles of the southwestern United States. Birmingham, Alabama: Partners in Amphibian and Reptile Conservation. Technical Publication HMG-5.
- Grandmaison DD, Frary VJ. 2012. Estimating the probability if illegal desert tortoise collection in the Sonoran Desert. Journal of Wildlife Management 76:262–268.
- Gratson MW, Whitman CL. 2000. Road closures and density and success of elk hunters in Idaho. Wildlife Society Bulletin 28:302-310.
- Halama KJ, Lovich RE. 2016. Dirt roads and trails. Pages 19-21 in Jones LLC, Halama KJ, Lovich RE, editors. Habitat management guidelines for amphibians and reptiles of the southwestern United States. Birmingham, Alabama: Partners in Amphibian and Reptile Conservation. Technical Publication HMG-5.
- Harris LD, Hoctor TS, Gergel SE. 1996. Landscape processes and their significance to biodiversity con-

- servation, Pages 319–347 in Rhodes OE, Chesser RK, Smith MH, editors. Population dynamics in space and time. Chicago: University of Chicago.
- Hazard LC, Shemanski DR, Nagy KA. 2010. Nutritional quality of natural foods of juvenile and adult desert tortoises (Gopherus agassizii): calcium, phosphorous, and magnesium digestibility. Journal of Herpetology 44:135-147.
- Hromada SJ, Esque TC, Vandergast AG, Dutcher KE, Mitchell CI, Gray ME, Chang T, Dickson BG, Nussear KE. 2020. Using movement to inform conservation corridor design for Mojave desert tortoise. Movement Ecology 8:38.
- Huijser MP, Duffield JW, Clevenger AP, Ament RJ, McGowen PT. 2009. Cost-benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada: a decision support tool. Ecology and Society 14(2):15. Available: http://www.ecologyandsociety.org/vol14/iss2/art15/ (September 2022)
- Jageman H. 1984. White-tailed deer habitat management guidelines. Moscow, Idaho: Forest, Wildlife, and Range Experiment Station, University of Idaho (see Supplemental Material, Reference S19).
- Jennings WB. 1997. Habitat use and food preferences of the desert tortoise, Gopherus agassizii, in the western Mohave Desert and impacts of off-road vehicles. Pages 42-45 in Abbema JV, editor. Proceedings: Conservation, restoration, and management of tortoises and turtles: an international conference. Purchase: State University of New York, New York Turtle and Tortoise Society.
- McLellan BN, Shackleton DM. 1988. Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat, and demography. Journal of Applied Ecology 25:451-460.
- Mech LD. 1989. Wolf population survival in an area of high road density. American Midland Naturalist 121:387-389.
- Mitchell JC, Breisch AR, Buhlmann KA. 2006. Habitat management guidelines for amphibians and reptiles of the northeastern United States. Montgomery, Alabama: Partners in Amphibian and Reptile Conservation. Technical Publication HMG-3.
- Mladenoff DJ, Sickley TA, Haight RG, Wydeven AP. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the Northern Great Lakes region. Conservation Biology 9:279-294.
- Mladenoff DJ, Sickley TA, Wydeven AP. 1999. Predicting gray wolf landscape recolonization: logistic regression models vs. new field data. Ecological Applications
- Nafus MG, Tuberville TD, Buhlmann KA, Todd BD. 2013. Relative abundance and demographic structure of Agassiz's desert tortoise (Gopherus agassizii) along roads of varying size and traffic volume. Biological Conservation 162:100-106.

- Nagy KA, Henen BT, Vyas DB. 1998. Nutritional quality of native and introduced food plants of wild desert tortoises. Journal of Herpetology 32:260-267.
- [NPS] National Park Service. 2000. General management plan development concept plans environmental impact statement. Twentynine Palms, California: Joshua Tree National Park (see Supplemental Material, Reference S20, cited in Table S1).
- [NPS] National Park Service. 2002a. Mojave National Preserve general management plan. Essex, California: Mojave National Preserve (see Supplemental Material, Reference S21, cited in Table S1).
- [NPS] National Park Service. 2002b. Death Valley National Park general management plan. Essex, California: Mojave National Preserve (see Supplemental Material, Reference S22, cited in Table S1).
- [NPS] National Park Service. 2005. General Management Plan amendment/environmental assessment. Boulder City, Nevada: Lake Mead National Recreation Area (see Supplemental Material, Reference S23, cited in Table S1).
- Nussear KE, Esque TC, Inman RD, Gass L, Thomas KA, Wallace CSA, Blainey JB, Miller DM, Webb RH. 2009. Modeling habitat of the desert tortoise (Gopherus agassizii) in the Mojave and parts of the Sonoran deserts of California, Nevada, Utah, and Arizona. Reston, Virginia: U.S. Geological Survey Open-File Report 2009–1102. Available: https://pubs.usgs.gov/ of/2009/1102/ofr20091102.pdf (July 2022) (see Supplemental Material, Reference S24).
- Oftedal OT. 2002. Nutritional ecology of the desert tortoise in the Mojave and Sonoran deserts. Pages 194–241 in Van Devender TR, editor. The Sonoran desert tortoise: natural history, biology, and conservation. Tucson: University of Arizona.
- Peaden JM, Nowakowski AJ, Tuberville TD, Buhlmann KA, Todd BD. 2017. Effects of roads and roadside fencing on movements, space use, and carapace temperatures of a threatened tortoise. Biological Conservation 214:13-22.
- Peaden JM, Tuberville TD, Buhlmann KA, Nafus MG, Todd BD. 2015. Delimiting road-effect zones for threatened species: implications for mitigation fencing. Wildlife Research 42:650-659.
- Pimm SL, Raven P. 2000. Extinction by numbers. Nature 403:843-845.
- Proctor MF, McLellan BN, Stenhouse GB, Mowat G, Lamb CT, Boyce MS. 2019. Effects of roads and motorized human access on grizzly bear populations in British Columbia and Alberta, Canada. Ursus 30(e2):16-39.
- Rowland MM, Wisdom MJ, Johnson BK, Kie JG. 2000. Elk distribution and modeling in relation to roads. Journal of Wildlife Management 64:672–684.
- Switalski A. 2018. Off-highway vehicle recreation in drylands: a literature review and recommendations for best management practices. Journal of Outdoor Recreation and Tourism 21:87-96.

- Switalski TA, Jones A. 2012. Off-road vehicle best management practices for forestlands: a review of scientific literature and guidance for managers. Journal of Conservation Planning 8:12-24.
- Thiel RP. 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. American Midland Naturalist 113:404-407.
- Todd BD, Halstead BJ, Chiquoine LP, Peaden JM, Buhlmann KA, Tuberville TD, Nafus MG. 2016. Habitat selection by juvenile Mojave desert tortoises. Journal of Wildlife Management 80:720-728.
- Tracy CR, Averill-Murray R, Boarman WI, Delehanty D, Heaton J, McCoy E, Morafka D, Nussear K, Hagerty B, Medica P. 2004. Desert tortoise recovery plan assessment. Washington, D.C.: Report to U.S. Fish and Wildlife Service (see Supplemental Material, Reference S25).
- Trombulak SC, Frissel CA. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18-30.
- U.S. Census Bureau. 2014a. 2014 TIGER/Line Shapefiles (machine-readable data files). Available: https://www. census.gov/geographies/mapping-files/time-series/ geo/tiger-line-file.html (April 2021)
- U.S. Census Bureau. 2014b. 2014 TIGER/Line Shapefiles Technical Documentation. Available: https://www. census.gov/programs-surveys/geography/technicaldocumentation/complete-technical-documentation/ tiger-geo-line.html (April 2021)
- [ESA] U.S. Endangered Species Act of 1973, as amended, Pub. L. No. 93-205, 87 Stat. 884 (Dec. 28, 1973). Available: https://www.fws.gov/sites/default/files/ documents/endangered-species-act-accessible.pdf (July 2022)
- [USFWS] U.S. Fish and Wildlife Service. 2009. Desert National Wildlife Refuge Complex Ash Meadows, Desert, Moapa Valley, and Pahranagat National Wildlife Refuges final comprehensive conservation plan and environmental impact statement. Sacramento, California: U.S. Fish and Wildlife Service, Pacific Southwest Region (see Supplemental Material, Reference 26, cited in Table S1).
- [USFWS] U.S. Fish and Wildlife Service. 2011. Revised recovery plan for the Mojave population of the desert tortoise (Gopherus agassizii). Sacramento, California: U.S. Fish and Wildlife Service, Pacific Southwest Region. Available: https://www.fws.gov/sites/default/ files/documents/USFWS.2011.RRP%20for%20the% 20Mojave%20Desert%20Tortoise.pdf (July 2022) (see Supplemental Material, Reference S27).
- [USFS] U.S. Forest Service. 1995. Decision notice: allowable sale quantity and objectives and standards for grizzly bear habitat management. Kalispell, Montana: USDA National Forest Service, Flathead National Forest (see Supplemental Material, Reference S28).
- U.S. Government Accountability Office. 2009. Enhanced planning could assist agencies in managing increased

- use of off-highway vehicles. Washington, D.C.: House of Representatives. Report to the Subcommittee on National Parks, Forests and Public Lands, Committee on Natural Resources, GAO-09-509 (see Supplemental Material, Reference S29).
- van der Marel RC, Holroyd PC, Duinker PN. 2020. Managing human footprint to achieve large-landscape conservation outcomes: establishing density limits on motorized route-user networks in Alberta's Eastern Slopes. Global Ecology and Conservation 22:e00901.
- Venter O, Brodeur NN, Nemiroff L, Belland B, Dolinsek IJ, Grant JWA. 2006. Threats to endangered species in Canada. BioScience 56:903-910.
- von Seckendorff Hoff K, Marlow RW. 2002. Impacts of vehicle road traffic on desert tortoise populations with consideration of conservation of tortoise habitat in

- southern Nevada. Chelonian Conservation and Biology 4:449-456.
- Vos CC, Chardon JP. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog Rana arvalis. Journal of Applied Ecology
- Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E. 1998. Quantifying threats to imperiled species in the United States: assessing the relative importance of habitat destruction, alien species, pollution, overexploitation, and disease. BioScience 48:607-615.
- Wydeven AP, Mladenoff DJ, Sickley TA, Kohn BE, Thiel RP, Hansen JL. 2001. Road density as a factor in habitat selection by wolves and other carnivores in the Great Lakes Region. Endangered Species UPDATE 18:110-114.