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Connectivity of Mojave Desert Tortoise Populations: Management Implications for Maintaining a Viable Recovery Network

Introduction

Connectivity of Mojave desert tortoise (*Gopherus agassizii*) populations has become an issue of increasing concern due to recent and proposed development of large tracts of desert tortoise habitat that cross, fragment, and surround designated conservation areas. Much of this development is a result of the recent renewable energy boom, but also the result of long-planned urban expansion and infrastructure projects that are reaching the implementation phase. Researchers have studied the implications of existing tortoise conservation areas becoming isolated from this current and planned development and have also modeled past, current, and potential future population connectivity across the desert tortoise's range (see below). Managers have incorporated much of the available information into individual planning decisions (e.g., Desert Renewable Energy Conservation Plan [DRECP], draft Apple Valley Habitat Conservation Plan). However, general principles for maintaining functionally connected desert tortoise populations have not been synthesized to assist with a comprehensive, species wide analysis, and several existing land-management plans lack the focus on desert tortoise population connectivity present in other plans such as the DRECP. To address this information gap, this white paper summarizes the underlying concepts and importance of population connectivity for Mojave desert tortoise populations by 1) reviewing current information on connectivity, and 2) providing information to managers for maintaining or enhancing desert tortoise population connectivity as they consider future proposals for development and management actions across the landscape.

The framework for Mojave Desert Tortoise recovery

Historic population connectivity

The historic distribution of Mojave desert tortoises was relatively continuous across the range, broken only by major topographic barriers, such as the Baker Sink and Death Valley, California, and the Spring Mountains, Nevada (Germano et al. 1994; Nussear et al. 2009). Although desert tortoises generally do not move long distances over their lifetimes, modest dispersal and connected home ranges occurred over a relatively continuous distribution across the tortoise's range. This contiguous distribution fostered historically high levels of gene flow and a population structure characterized as isolation-by-distance (Murphy et al. 2007; Hagerty and Tracy 2010; Hagerty et al. 2011). Maintaining functionally connected landscapes is necessary to conserve historic genetic gradation (Frankham 2006). Large, connected landscapes are also necessary to facilitate natural range shifts in response to climate change (Hilty et al. 2020; Krosby et al. 2010; National Fish, Wildlife, and Plants Climate Adaptation Partnership 2012). Nevertheless, while gene flow and adaptive capacity are critically important in the long term, the need for extensive, unfragmented habitat is of even more immediate concern for supporting populations that are demographically viable on time scales relative to management (Kuo and Janzen 2004).

Design and goals of the current network of Tortoise Conservation Areas
Tortoise Conservation Areas (TCAs[1]) form the foundation of the desert tortoise recovery strategy and are centered around 12 designated critical habitat units which range in area from approximately 85 to 1595 square miles (1 square mile = 640 acres or 256 hectares; USFWS 2011). Effective conservation areas are designed to support species viability according to ecological concepts of representation, redundancy, and resilience (USFWS 1994, 2016; Shaffer and Stein 2000).

- Representation captures the breadth of genetic or ecological diversity of a species, and recovery units are distributed across the range in a pattern designed to capture this breadth (USFWS 2011).
- Redundancy, having multiple protected populations within representative units, protects against catastrophic loss of any particular population. In the case of the Mojave desert tortoise, each of the recovery units identified in the 2011 recovery plan contains multiple TCAs except the Upper Virgin River Recovery Unit in Utah (USFWS 2011).
- Resilience represents the ability of populations to recover from stochastic setbacks, such as drought-induced population declines or localized disease outbreaks. To maintain resilience, TCAs were envisioned to sustain a population of at least 5000 adult tortoises (USFWS 1994). In situations where a critical habitat unit was smaller than the threshold of 500 square miles (1,295 km^2) or if the number of tortoises was found to be fewer than 5000, land management was expected to maintain connectivity to larger populations outside the critical habitat unit and to other critical habitat units (USFWS 1994).

The importance of tortoise habitat outside of TCAs to recovery has long been recognized for its contributions to supporting gene flow between TCAs and to minimizing impacts and edge effects within TCAs (USFWS 1994, 2011). This dependence on a reserve design of protected areas supported by surrounding areas that are not necessarily protected is considered the linchpin of sustaining a resilient protected area network (USFWS 2011).

Challenges and weaknesses of the current network of Tortoise Conservation Areas
When the original recovery plan was developed, there were no reliable abundance estimates for tortoises in any critical habitat unit. However, one unit in particular, the Upper Virgin River Critical Habitat Unit, was insufficient in size to support the necessary 5000 adult tortoises; thus it was identified as requiring intensive management since its establishment (USFWS 1994). Range-wide monitoring since 2004 (1999 in Upper Virgin River) now provides population estimates for each TCA and recent changes in tortoise density. As of 2014, 11 of 17 TCAs had negative population trends, and 8 of 17 were estimated to contain fewer than 5000 adult tortoises (Allison and McLuckie 2018; Fig. 1).

[1]Tortoise conservation areas include desert tortoise habitat within designated critical habitat, Desert Wildlife Management Areas, Areas of Critical Environmental Concern, Grand Canyon-Parashant National Monument, Desert National Wildlife Refuge, National Park Service lands, Red Cliffs Desert Reserve, and other conservation areas or easements managed for desert tortoises (USFWS 2011).

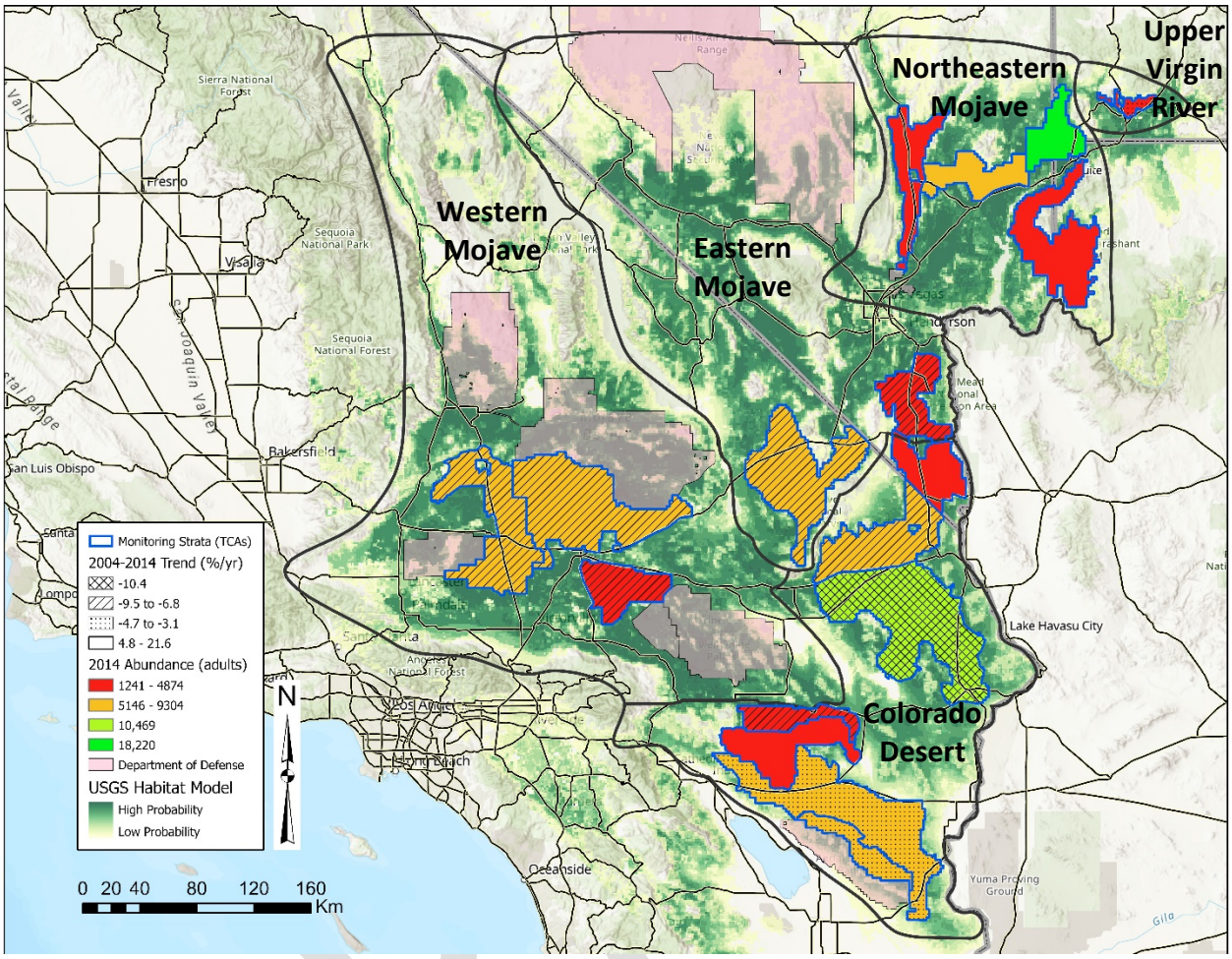

Figure 1. Population trends and abundance of adult Mojave Desert Tortoises within Tortoise Conservation Areas (TCAs). Thick black lines represent recovery unit boundaries (USFWS 2011).

In addition to concerns about the status of tortoise populations within the TCAs, the configuration of several TCAs is inconsistent with optimal reserve design. The theoretically optimal reserve shape would be circular to minimize the perimeter and potential edge effects relative to the area because the quality of habitat within conservation areas can be affected by factors present outside conservation area boundaries (Harrison and Bruna 1999; Environmental Law Institute 2003; Radeloff et al. 2010). For example, subsized predators within the urban-wildland interface can affect tortoise populations well within TCAs (Kristan and Boarman 2003; Esque et al. 2010). However, to capture the actual pattern of suitable habitat while accommodating land ownership considerations, all TCAs have complex perimeters, often with narrow extensions or projections into relatively unprotected habitat (Fig. 1). This is partly because, prior to TCA establishment, the landscape already had many inholdings and disturbances that were avoided because they rendered the habitat incompatible for tortoise use. The result of this configuration is a network of land parcels of variable habitat quality and tortoise permeability (Gray et al. 2019). All of these issues emphasize the importance of maintaining and ideally increasing the availability of habitat connectivity within and among TCAs.

Functional connectivity of desert tortoise populations across the landscape
Connectivity can be viewed as the degree to which regional landscapes, encompassing a variety of natural, semi-natural, and developed land-cover types, are conducive to wildlife movement and to sustaining ecological processes (Ament et al. 2014; Hilty et al. 2020). Functionally, connectivity describes the degree to which landscapes facilitate or impede the movement of organisms and processes (Meiklejohn et al. 2010; Hilty et al. 2020). Decreased connectivity results from various degrees of landscape resistance. For example, natural linear features that entirely preclude movement include impassable vertical cliffs, talus slopes, and large rivers. Equivalent man-made features include walls and fences such as those used to limit highway access fitted with tortoise-proof fencing. Semi-permeable features include natural habitats with questionably sufficient thermal cover, such as burned areas or playa edges, or other features typical of the urban-wildland interface such as ploughed lots, roads, railways, and large berms, all of which can act as filters that reduce connectivity between populations in the absence of appropriate under- or over-passes (e.g., Peaden et al. 2015; Rautsaw et al. 2018; Dutcher et al. 2020a; Hromada et al. 2020a).

The effects listed above are widespread across the Mojave Desert; for example, almost all TCAs are divided internally or separated from adjacent units by major roads and highways (Fig. 1). Many miles of tortoise-barrier fencing have been installed along roads, primarily within TCAs; this fencing reduces mortality in tortoises by reducing or removing movement across dangerous surfaces but thereby also eliminates connectivity between populations. Although individual tortoises cross through culverts (Boarman et al. 1998; Hromada et al. 2020a), the effectiveness of culverts in mitigating the fragmenting effects of highways at a population scale is unknown. Even culverts designed to reduce resistance across linear barriers may be ineffective if materials such as rip-rap of talus-sized rocks prevent access by tortoises.

Structure and dynamics of desert tortoise populations
Desert tortoises do not occur at uniform densities across the landscape (Krzysik 2002). Local population abundances fluctuate asynchronously due to differences in habitat quality, variability in precipitation patterns; to localized declines attributed to drought, disease, or predation events (Peterson 1994; Longshore et al. 2003; Tracy et al. 2004, Esque et al. 2010, Emblidge et al. 2015); or to stochastic population dynamics (USFWS 2011). Adjacent habitat patches of sufficient quality to support healthy tortoise populations are necessary for local population declines or extinctions to be rescued by recolonization (Fahrig and Merriam 1994; see below). As habitat is lost and fragmented, though, habitat patches become smaller, patch populations (e.g., clusters of tortoises) have fewer tortoises and become more disjunct, extinction probabilities within patches increase, and the number of occupied patches decreases (Fahrig 2002; Ovaskainen et al. 2002). As described above, tortoise populations adjacent to and contiguous with populations within TCAs are essential for long-term species viability and recovery given the limitations of the existing TCA reserve design (Fig. 2).

Large expanses of high-quality habitat are necessary to increase the likelihood that tortoises from local areas with higher recruitment will emigrate to and repopulate or "rescue" adjacent areas of suitable habitat (e.g., within TCAs) that may have fewer tortoises due to low recruitment or high mortality (Germano and Joyner 1988; Morafka 1994; Tracy et al. 2004). This rescue effect has

been described and studied using island biogeography principles that lead us to expect that the probability a population will persist is related to the size and isolation of the habitat patch on which it exists (MacArthur and Wilson 1967; Brown and Kodric-Brown 1977). Figure 2B provides an example of the historical relationship between habitat patches for desert tortoises in the Mojave Desert. Patches suffering localized declines in tortoise numbers could be recolonized by tortoises emigrating from adjacent patches. As habitat is degraded or lost, however, inter-patch relationships may break down, resulting in a decreased likelihood that recolonizations will occur. In short, tortoises within remaining patches that have fewer connections are more likely to be extirpated and less likely to be replaced than tortoises inhabiting patches surrounded by permeable habitats with intact connections (Figure 2C; cf. Lefkovitch and Fahrig 1985). Such fragmentation could isolate and reduce the viability of regional populations, including those within TCAs, creating an "extinction debt" (Kuussaari et al. 2009; Hylander and Ehrlén 2013) that extends well beyond the perimeters of parcels of lost habitats. Rescue of unoccupied habitat patches may not occur, or may be delayed, if few tortoises disperse from nearby small or declining populations (Adler and Nuernberger 1994). Unoccupied patches present a special problem if the source of the decline is unknown because evidence is lacking to indicate whether the decline was due to temporary conditions for the occupants or if the site can no longer sustain tortoises. Obtaining better information about habitat quality requirements may resolve some of this uncertainty.

Effectively connecting current desert tortoise habitat to recover populations

The patterns of population distribution and dynamics described above represent those of a "patchy" metapopulation (Harrison 1991). For species with this type of metapopulation dynamics to persist over the long term, connectivity between patches must be provided through contiguous viable habitat. The Mojave desert tortoise requires inter-connected habitat across its range to sustain populations within and outside of TCAs over multiple generations (Tracy et al. 2004). Low-mobility species such as the desert tortoise are considered "corridor dwellers" that may spend entire life-times within corridors (Beier and Loe 1992). In effect, low mobility of the species means that inter-connected local populations of tortoises must persist across the landscape to ensure overall species persistence (Fig. 2B).

In contrast, passage species may move through corridors between protected areas in days or weeks, even at large spatial scales (Beier and Loe 1992). Though individual desert tortoises can move many kilometers in one season (Berry 1986; Edwards et al. 2004), this type of movement has been observed in large open areas rather than a long (e.g., tens of kilometers), narrow strip of habitat a few meters – or even a few hundred meters – wide. Tortoises may traverse short culverts and thereby navigate the otherwise absolute barrier of a fenced road (Boarman et al. 1998) or may occupy narrow mountain passes (Dutcher et al. 2020b; Hromada et al. 2020a), but tortoise movement patterns do not lead us to expect that a tortoise in one TCA would traverse a long narrow strip of preserved desert vegetation to another TCA many kilometers distant in its lifetime. For all these reasons, habitat linkages among TCAs must be wide enough to sustain multiple home ranges or local clusters of resident tortoises (Beier et al. 2008; Morafka 1994) in order to sustain regional tortoise populations.

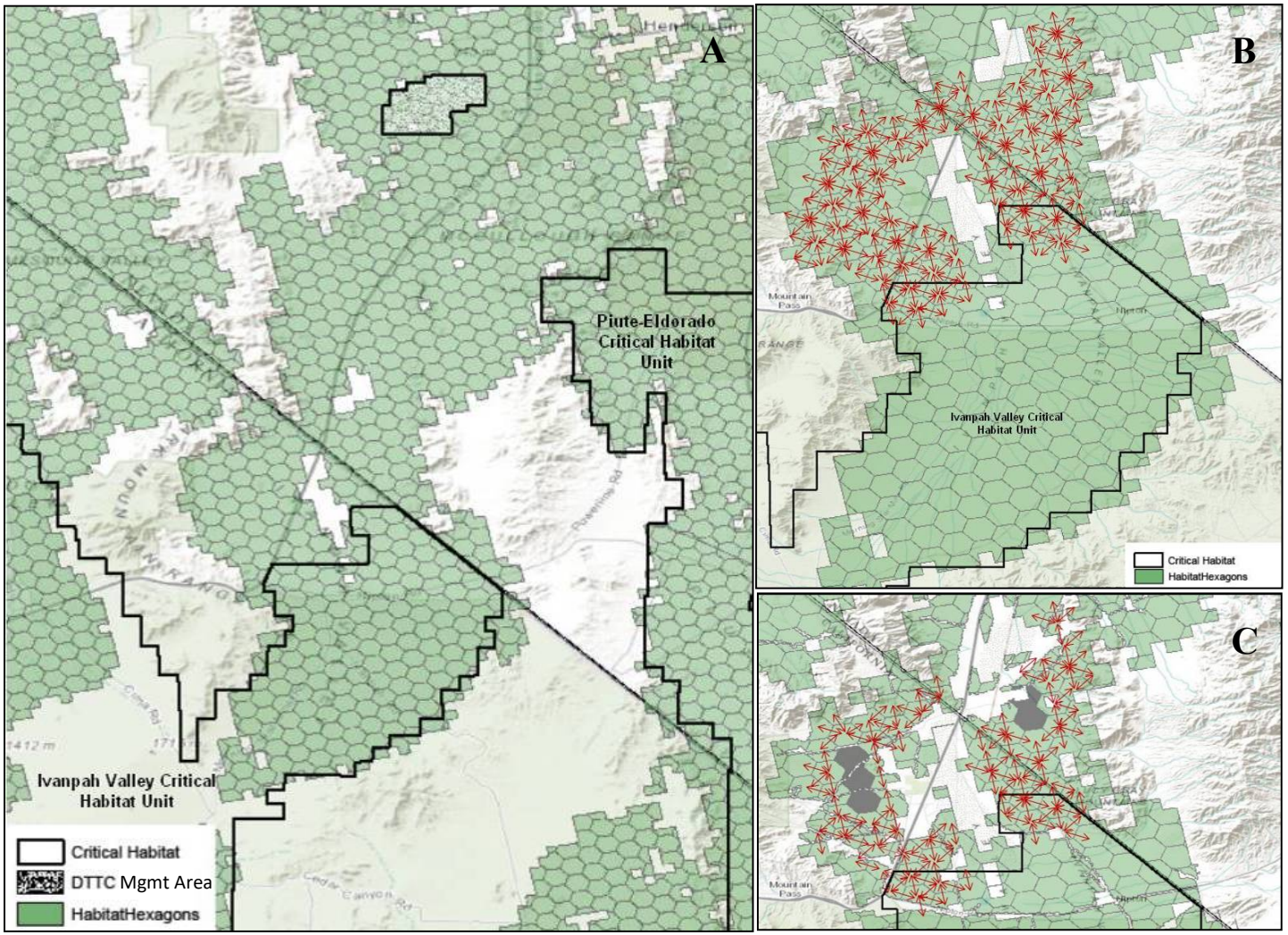

Figure 2. Diagrammatic representation of inter-patch habitat connectivity of Mojave desert tortoises. Each hexagon represents a 259-hectare (640-acre) habitat patch. A: Historically interconnected habitat constrained by major topographic barriers. B: Inter-patch relationships across a portion of the landscape are represented by red arrows. C: Reduction in patch connections occurs with habitat loss and fragmentation, conceptually represented by gray patches.

Recent research relevant to desert tortoise habitat and connectivity
A variety of spatial habitat models have been developed for the management of desert tortoise habitat, including models describing habitat suitability, levels of development within modeled habitat, landscape genetics, tortoise habitat linkages, and connectivity (Appendix 1). These models have been used for project-proponent and regulatory planning, establishing survey requirements, evaluating reports for project compliance, and as base inputs for subsequent spatial models. Furthermore, many of the natural resource layers developed for these models (e.g., soil texture layer by Nowicki et al. 2019; wash layers by Gray et al. 2019) have been applied to understand habitats for other species of management concern across the southwestern U.S. (e.g., Mohave Ground Squirrel by Inman et al. 2013; multiple species and energy development by Vandergast et al. 2013).

Spatial models focusing on habitat connectivity that are currently in development were presented at the annual symposium of the Desert Tortoise Council in February 2020 (https://deserttortoise.org/wp-content/uploads/ABSTRACTS_2020-DTC-FINAL-Feb72020.pdf), including syntheses of habitat status (Nussear et al. 2020), genetic responses to landscape disturbances (Dutcher et al. 2020b), desert tortoise movements (Hromada et al. 2020b), demographics (Shoemaker et al. 2020), and alternative future habitat scenarios (Bassett et al. 2020). The development of these models is ongoing and dynamic. For example, two of the 'working' models have been published since their presentation in February (Dutcher et al. 2020b, Carter et al. 2020a) and another is in press (Hromada et al. 2020a). In particular, these studies reinforced evidence of reduced movements and gene flow across linear barriers (highways and railroads), while reporting movements and gene flow across mountain passes, and documented limited tortoise occupancy in areas with >5% surface disturbance per square kilometer (Fig. 3), respectively.

Several additional models are still in development but can be accessed as they become ready for distribution. Available data and modelling, along with the those still in development, will further inform management agencies seeking to address connectivity issues for the Mojave desert tortoise.

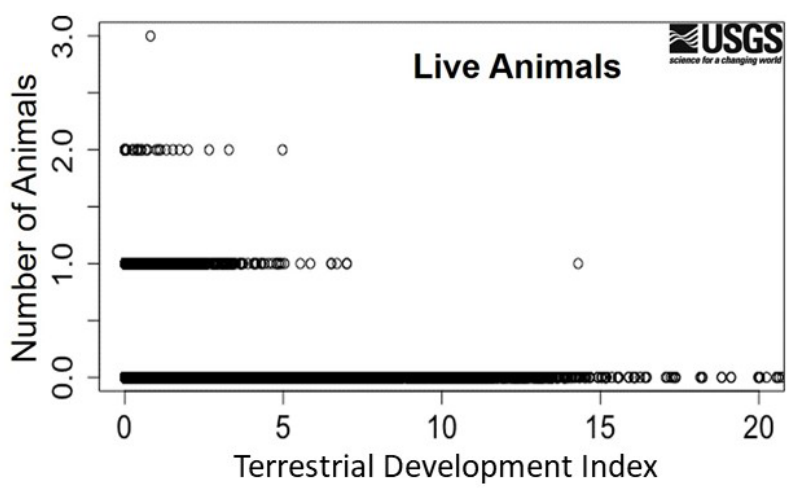

Figure 3. Observations of live Mojave Desert Tortoises from the USFWS range-wide monitoring program relative to the proportion of development in the surrounding landscape within 1km of the observation location (Terrestrial Development Index). A development index value of 5 indicates that 5% of the area within 1 km of that location has been altered by development. From Carter et al. (2020a).

Management implications

Maintaining an ecological network (i.e., recovery network) for the Mojave desert tortoise with a system of core habitats (TCAs) connected by linkages (Hilty et al. 2020) could support demographically viable populations and long-term gene flow within and between TCAs. Below are four points for wildlife and management agencies to consider to help maintain functional connectivity of Mojave desert tortoise populations (e.g., in reviewing resource management plans or amendments in light of the latest information on connectivity).

1) ***Management of all desert tortoise habitat for connectivity.*** Narrowly delineated corridors may not allow for natural population dynamics if they do not accommodate overlapping home ranges along most of their widths so that tortoises reside, grow, find mates, and produce offspring that can replace older tortoises (Beier and Loe 1992; Beier 2018). In addition, most habitat outside TCAs includes more multiple uses and landscape-level disturbance from development than areas within TCAs (Carter et al. 2020a). Therefore, managing the entire remaining matrix of desert tortoise habitat for permeability may be better than delineating fixed corridors (Beier 2018; cf. Gray et al. 2019). These concepts apply especially given uncertainty about long-term condition of habitat within and outside of TCAs under a changing climate.
   - Questions such as "*What are the critical linkages that need to be protected?*" may be better framed as "*How can we manage the remaining habitat matrix in ways that sustain ecological processes and habitat suitability for special status species?*". Land-management decisions made in the context of the latter question may be more conducive to maintenance of a functional ecological network.

2) ***Limitations on landscape-level disturbance across habitat managed for the desert tortoise.*** Even with a shifted focus on managing the entire habitat matrix for permeability as described above, clearly delineating linkages and differentiating them from non-delineated areas by uses that are allowed or prohibited within them by proper management guidelines can help achieve functional connectivity (Hilty et al. 2020). For example, in California suitable linkages were delineated in the DRECP (Fig. 4; U.S. Bureau of Land Management 2016). Elsewhere, linkages modeled by Averill-Murray et al. (2013; Fig. A-1) provide a framework for connecting designated TCAs.
   a) In California, the Bureau of Land Management established 0.1-1.0% new surface-disturbance caps for TCAs and mapped linkages that address the issues described in #1 above (Fig. 4, Table 1; U.S. Bureau of Land Management 2016).
   b) Nevada, Utah and Arizona currently do not have surface-disturbance limits. Limits comparable to those in the DRECP would be 0.5% within TCAs and 1% within the linkages modeled by Averill-Murray et al. (2013). Limits in some areas of California within the DRECP, such as Ivanpah Valley, are more restrictive at 0.1% (Fig. 4, Table 1). Continuity across the state line in Nevada could be achieved with comparable limits in the adjacent portion of Ivanpah Valley, as well as the Greater Trout Canyon Translocation Area and the Stump Springs Regional Augmentation Site (Fig. 5).These more restrictive limits help protect remaining habitat in the major inter-state connectivity pathway through Ivanpah Valley (Hagerty et al. 2011) and focal areas of population

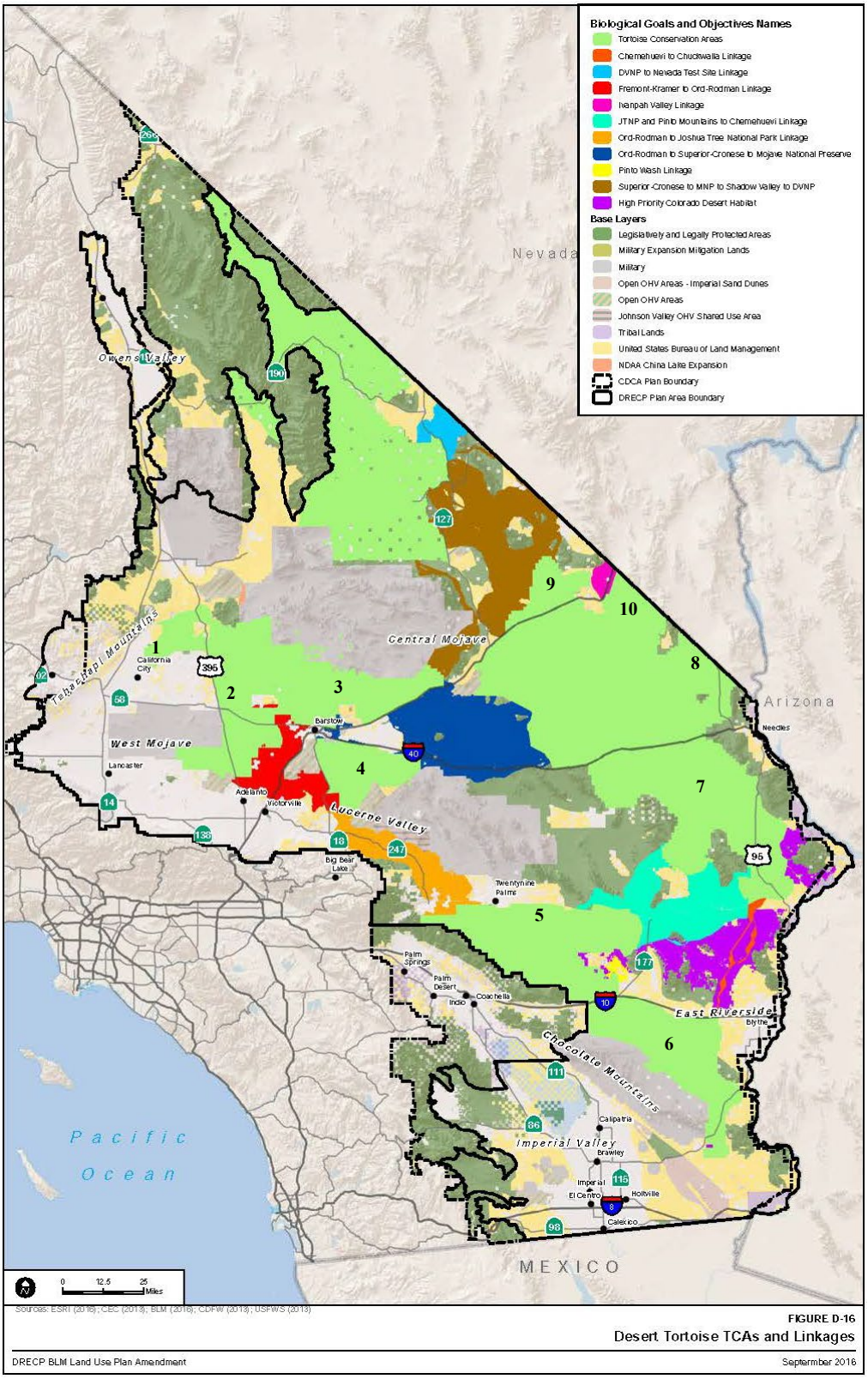

Figure 4. Desert Tortoise Conservation Areas and Linkages in the California Desert Renewable Energy Conservation Plan (U.S. Bureau of Land Management 2016). Tortoise Conservation Areas are labelled according to Table 1.

Table 1. Surface-disturbance caps in Desert Tortoise Conservation Areas and linkages in the California Desert Renewable Energy Conservation Plan (U.S. Bureau of Land Management 2016). ACEC = Area of Critical Environmental Concern; CHU = critical habitat unit.

Tortoise Conservation Area (numbers correspond to Fig. 4)	**Disturbance Cap**
1) Desert Tortoise Research Natural Area	0.1%
2) Fremont-Kramer ACEC and CHU	0.5%
3) Superior-Cronese ACEC and CHU	0.5%
4) Ord-Rodman ACEC and CHU	0.5%
5) Pinto Mountains ACEC and CHU	0.5%
6) Chuckwalla ACEC and CHU	0.5%
7) Chemehuevi Desert ACEC and CHU	0.5%
8) Piute Valley ACEC and CHU	0.5%
9) Shadow Valley ACEC	0.5%
10) Ivanpah Valley ACEC (includes critical habitat on BLM land)	0.1%
Desert Tortoise Linkages (see legend in Fig. 4)	
Ord-Rodman to Superior-Cronese to Mojave National Preserve	1%
Superior-Cronese to Mojave National Preserve to Shadow Valley to Death Valley National Park	1%
Joshua Tree National Park and Pinto Mountains to Chemehuevi	1%
Death Valley National Park to Nevada National Security Site	1%
Ivanpah Valley	0.1%
Chemehuevi to Chuckwalla	0.1%
Pinto Wash	0.1%
Ord-Rodman to Joshua Tree National Park	0.5%
Fremont-Kramer to Ord-Rodman	0.5%
High-value Colorado Desert Habitat	1%

augmentation that provide additional population connectivity along the western flank of the Spring Mountains.

c) To help maintain tortoise occupancy and permeability across all other non-conservation-designated tortoise habitat, surface disturbance could be limited to <5% development per square kilometer (Carter et al. 2020a; Fig. 3). This would be particularly useful in areas within the upper 5th percentile of connectivity values modeled by Gray et al. (2019; Fig. A-3; Fig. 5).

d) Reducing ancillary threats in places where connectivity is restricted to narrow strips of habitat, e.g., narrow mountain passes or vegetated strips between solar development, could enhance the functionality of these vulnerable linkages. In such areas, maintaining multiple, redundant linkages could further enhance overall connectivity.

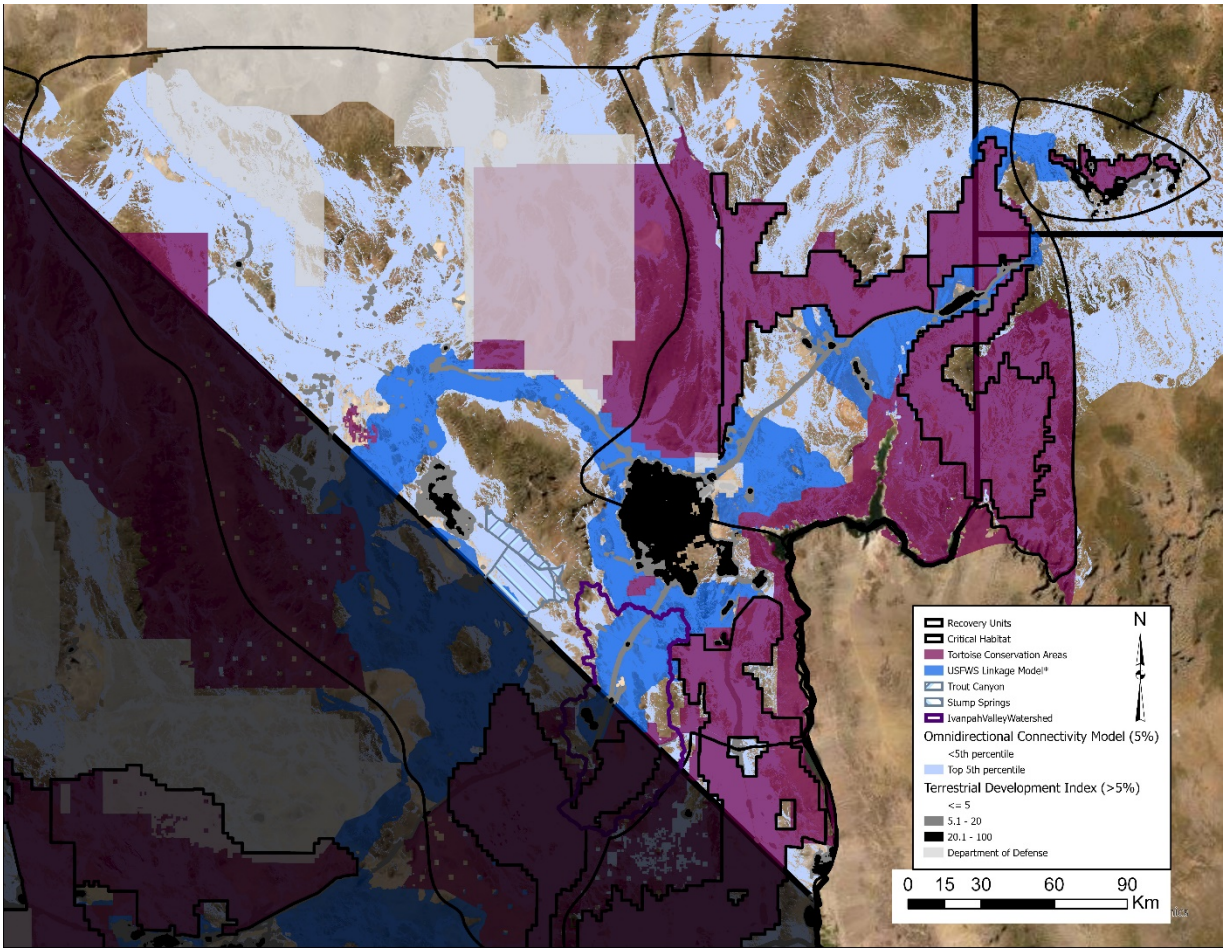

Figure 5. Tortoise Conservation Areas, linkages, and other habitat managed for desert tortoise population connectivity in Nevada, Utah, and Arizona.

3) ***Minimization of mortality from roads and maximization of passage under roads.*** Three points pertain to maintaining a minimal level of permeability across the many roads that cross desert tortoise habitat and to reducing direct mortality of tortoises on these roads.
   a) Tortoise-exclusion fencing tied into culverts, under- or over-passes, or other passages below roads in desert tortoise habitat would limit vehicular mortality of tortoises.
   b) Passages below highways could be maintained or retro-fitted to ensure safe tortoise access, e.g., by filling eroded drop-offs or by modifying erosion-control features such as rip-rap to make them safer and more passable for tortoises. Wildlife management agencies could work with transportation departments to develop construction standards that are consistent with hydrologic/erosion management goals while also maximizing the potential for tortoise survival and passage and to make the standards widely available. The process would be most effective if the status of passages was regularly monitored and built into management plans.
   c) Healthy tortoise populations along fenced highways could be supported by ensuring that land inside tortoise-exclusion fences is not so degraded that it leads to degradation of tortoise habitat outside the exclusion areas (e.g., high-density incursions of invasive plant species along the roadway).

4) ***Adaptation of management based on new information.*** The models described here have already been useful for informing management of tortoise habitat to support population recovery and connectivity. Future research will continue to build upon and refine these models and to develop new ones. New models could consider landscape levels of development and be constructed such that they share common foundations to support future synthesis efforts. If model development was undertaken in partnership with entities having major responsibility for management of desert tortoise habitat, it would facilitate incorporation of current and future modeling results into their land management decisions (Carter et al. 2020b). Specific topics that may be clarified with further evaluation include:

- The ability of solar energy facilities or similar developments to support tortoise movement and occupancy by leaving washes intact; leaving native vegetation intact whenever possible, or if not possible, mowing the site, allowing vegetation to re-sprout, and managing weeds; and allowing tortoises to occupy the sites.
- The design and frequency of underpasses necessary to maintain functional demographic and genetic connectivity across linear features like highways.

Literature Cited

Adler, F.R., and B. Nuernberger. 1994. Persistence in patchy irregular landscapes. Theoretical Population Biology 45:41-75.

Allison, L.J., and A.M. McLuckie. 2018. Population trends in Mojave Desert Tortoises (*Gopherus agassizii*). Herpetological Conservation and Biology 13:433–452.

Ament, R., R. Callahan, M. McClure, M. Reuling, and G. Tabor. 2014. Wildlife Connectivity: Fundamentals for Conservation Action. Center for Large Landscape Conservation: Bozeman Montana.

Averill-Murray, R.C., C.R. Darst, N. Strout, and M. Wong. 2013. Conserving population linkages for the Mojave Desert Tortoise (*Gopherus agassizii*). Herpetological Conservation and Biology 8:1–15.

Bassett, S.D., D.A. Friend, S.A. Wright, K.E. Nussear, T.C. Esque, D.P. Boyle, and J.S. Heaton. 2020. Land use futures for the Mojave Desert, USA: implications for the Mojave Desert Tortoise. Presented at a special invited session on Connectivity and the Desert Tortoise. 45th annual symposium of the Desert Tortoise Council. Las Vegas, NV. 22 February.

Beier, P. 2018. A rule of thumb for widths of conservation corridors. Conservation Biology 33:976–978.

Beier, P., and S. Loe. 1992. A checklist for evaluating impacts to wildlife movement corridors. Wildlife Society Bulletin 20:434-440.

Beier, P., D.R. Majka, and W.D. Spencer. 2008. Forks in the road: choices in procedures for designing wildland linkages. Conservation Biology 22:836-851.

Berry, K.H. 1986. Desert tortoise (*Gopherus agassizii*) relocation: implications of social behavior and movements. Herpetologica 42:113-125.

Boarman, W.I., M.L. Beigel, G.C. Goodlett, and M. Sazaki. 1998. A passive integrated transponder system for tracking animal movements. Wildlife Society Bulletin 26:886-891.

Brown, J.H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445-449.

Carter, S.K., I.I.F. Leinwand, K.E. Nussear, T.C. Esque, E. Masters, R.D. Inman, N.B. Carr, and L.J. Allison. 2020a. Quantifying development to inform management of Mojave and Sonoran desert tortoise habitat. Endangered Species Research 42:167-184.

Carter, S.K., D.S. Pilliod, T. Haby, K.L. Prentice, C.L. Aldridge, P.J. Anderson, Z.H. Bowen, J.B. Bradford, S.A. Cushman, J.C. DeVivo, M.C. Duniway, R.S. Hathaway, L. Nelson, C.A. Schultz, R.M. Schuster, E.J. Trammell, and J.F. Weltzin. 2020b. Bridging the research-management gap: landscape science in practice on public lands in the western United States. Landscape Ecology 35:545-560.

Dutcher, K.E., A.G. Vandergast, T.E. Esque, M.D. Matocq, J.S. Heaton, and K.E. Nussear. 2020a. Connecting the plots: anthropogenic disturbance and Mojave Desert Tortoise genetic connectivity. Presented at a special invited session on Connectivity and the Desert Tortoise. 45th annual symposium of the Desert Tortoise Council. Las Vegas, NV. 22 February.

Dutcher, K., K.E. Nussear, A. Vandergast, T.C. Esque, A. Mitelberg, and J. Heaton. 2020b. Genes in space: what Mojave Desert tortoise genetic relationship can tell us about landscape connectivity. Conservation Genetics DOI 10.1007/s10592-020-01251-z.

Edwards, T., E.W. Stitt, C.R. Schwalbe, and D.E. Swann. 2004. *Gopherus agassizii* (desert tortoise). Movement. Herpetological Review 35:381-382.

Emblidge, P.G., K.E. Nussear, T.C. Esque, C.M. Aiello, and A.D. Walde. 2015. I. Severe predation on a population of threatened desert tortoises: The American Badger as a novel predator. Endangered Species Research 28: 109-116. doi: 10.3354/esr00680.

Environmental Law Institute. 2003. Conservation thresholds for land use planners. Environmental Law Institute, Washington, D.C.

Esque, T.C., K.E. Nussear, K.K. Drake, A.D. Walde, K.H. Berry, R.C. Averill-Murray, A.P. Woodman, W.I. Boarman, P.A. Medica, J. Mack, and J.S. Heaton. 2010. Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave Desert. Endangered Species Research 12(2):167-177. doi 10.3354/esr00298.

Fahrig, L. 2002. Effect of habitat fragmentation on the extinction threshold: a synthesis. Ecological Applications 12:346-353.

Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8:50-59.

Frankham, R. 2006. Genetics and landscape connectivity. Pages 72-96 *in* K.R. Crooks and M. Sanjayan (eds.), Connectivity Conservation. Cambridge University Press, Cambridge, U.K.

Germano, D.J., and M.A. Joyner. 1988. Changes in a desert tortoise (*Gopherus agassizii*) population after a period of high mortality. Pages 190-198 *in* R.C. Szaro, K.E. Severson, and D.R. Patton (technical coordinators), Management of Amphibians, Reptiles, and Small Mammals in North America: Proceedings of the Symposium. U.S.D.A. Forest Service General Technical Report RM-166, Fort Collins, Colorado.

Germano, D.J., R.B. Bury, T.C. Esque, T.H. Fritts, and P.A. Medica. 1994. Range and habitat of the desert tortoise. Pages 57-72 *in* R.B. Bury and D.J. Germano (eds.), Biology of the North American Tortoises. National Biological Survey, Fish and Wildlife Research 13, Washington, D.C.

Gray, M.E., B.G. Dickson, K.E. Nussear, T.C. Esque, and T. Chang. 2019. A range-wide model of contemporary, omnidirectional connectivity for the threatened Mojave desert tortoise. Ecosphere 10(9):e02847. 10.1002/ecs2.2847

Hagerty, B.E., and C.R. Tracy. 2010. Defining population structure for the Mojave desert tortoise. Conservation Genetics 11:1795-1807.

Hagerty, B.E., K.E. Nussear, T.C. Esque, and C.R. Tracy. 2011. Making molehills out of mountains: landscape genetics of the Mojave Desert Tortoise. Landscape Ecology 26:267–280.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42:73-88.

Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography 22:225-232.

Hilty, J., G.L. Worboys, A. Keeley, S. Woodley, B. Lausche, H. Locke, M. Carr, I. Pulsford, J. Pittock, J.W. White, D.M. Theobald, J. Levine, M. Reuling, J.E.M. Watson, R. Ament, and G.M. Tabor. 2020. Guidelines for conserving connectivity through ecological networks and corridors. Best Practice Protected Area Guidelines Series No. 30. Gland, Switzerland: IUCN.

Hromada, S.J., T.C. Esque, A.G. Vandergast, K.E. Dutcher, C.I. Mitchell, M.E. Gray, T. Chang, B.G. Dickson, and K.E. Nussear. 2020a. Using movement to inform conservation corridor design for Mojave desert tortoise. Movement Ecology *in press*.

Hromada, S.J., T.C. Esque, A.G. Vandergast, C.I. Mitchell, K.E. Dutcher, K.E. Nussear. 2020b. Using movement to inform conservation corridors for Mojave desert tortoises. 45th annual symposium of the Desert Tortoise Council. Las Vegas, NV. 22 February.

Hylander, K., and J. Ehrlén. 2013. The mechanisms causing extinction debts. Trends in Ecology and Evolution in press. http://dx.doi.org/10.1016/j.tree.2013.01.010.

Inman, R.D., K.E. Nussear, M. Matocq, T. Dilts, P. Weisberg, A. Vandergast, and T.C. Esque. 2013. Potential Habitat for the Mohave Ground Squirrel (*Xerospermophilus mohavensis*): Is there room for all of us? Featured Article. *Endangered Species Research* 20:1-18. doi: 10.3354/esr00487.

Krosby, M., J. Tewksbury, N.M. Haddad, and J. Hoekstra. 2010. Ecological connectivity for a changing climate. Conservation Biology 24:1686-1689.

Kuussaari, M., R. Bommarco, R.K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, and I. Steffan-Dewenter. 2009. Extinction debt: a challenge for biodiversity conservation. Trends in Ecology and Evolution 24:564-571.

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

Krzysik, A.J. 2002. A landscape sampling protocol for estimating distribution and density patterns of desert tortoises at multiple spatial scales. Chelonian Conservation and Biology 4:366-379.

Kuo, C.H., and F.J. Janzen. 2004. Genetic effects of a persistent bottleneck on a natural population of ornate box turtles (*Terrapene ornata*). Conservation Genetics 4:425-437.

Lefkovitch, L.P., and L. Fahrig. 1985. Spatial characteristics of habitat patches and population survival. Ecological Modelling 30:297-308.

Longshore, K.M., J.R. Jaeger, and J.M. Sappington. 2003. Desert tortoise (*Gopherus agassizii*) survival at two eastern Mojave Desert sites: death by short-term drought? Journal of Herpetology 37:169-177.

MacArthur, R.H., and E.O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press.

Meiklejohn, K., R. Ament, and G. Tabor. 2010. Landscape Corridors and Habitat Connectivity: Clarifying the Terminology. Center of Large Landscape Conservation. 6pp.

Morafka, D.J. 1994. Neonates: missing links in the life histories of North American tortoises. Pages 161-173 *in* R.B. Bury and D.J. Germano (eds.), Biology of North American Tortoises. National Biological Survey, Fish and Wildlife Research 13, Washington, D.C.

Murphy, R.W., K.H. Berry, T. Edwards, and A.M. McLuckie. 2007. A genetic assessment of the recovery units for the Mojave population of the desert tortoise, *Gopherus agassizii*. Chelonian Conservation and Biology 6:229-251.

National Fish, Wildlife, and Plants Climate Adaptation Partnership. 2012. National Fish, Wildlife and Plants Climate Adaptation Strategy. Association of Fish and Wildlife Agencies, Council on Environmental Quality, Great Lakes Indian Fish and Wildlife Commission, National Oceanic and Atmospheric Administration, and U.S. Fish and Wildlife Service. Washington, D.C. 112pp.

Nowicki, S.A., R.D. Inman, T.C. Esque, K.E. Nussear, and C.S. Edwards. 2019. Spatially consistent high-resolution land surface temperature mosaics for thermophysical mapping of the Mojave Desert. *Sensors* 2019, 19, 2669; doi:10.3390/s19122669.

Nussear, K.E., T.C. Esque, R.D. Inman, L. Gass, K.A. Thomas, C.S.A. Wallace, J.B. Blainey, D.M. Miller, and R.H. Webb. 2009. Modeling habitat of the Desert Tortoise (*Gopherus agassizii*) in the Mojave and parts of the Sonoran deserts of California, Nevada, Utah, and Arizona. U.S. Geological Survey Open-file Report 2009–1102. 18 p.

Nussear, K., J. Heaton, S. Bassett, D. Boyle, M. Matocq, A. Parandhaman, D. Friend, S. Wright, K. Dutcher, S. Hromada, C. Mitchell, A. Vandergast, and T. Esque. 2020. Progress toward understanding the impacts of land use and climate change on Desert Tortoise structural genetics and corridor functionality. Presented at a special invited session on Connectivity and the Desert Tortoise. 45th annual symposium of the Desert Tortoise Council. Las Vegas, NV. 22 February.

Ovaskainen, O., K. Sato, J. Bascompte, and I. Hanski. 2002. Metapopulation models for extinction threshold in spatially correlated landscapes. Journal of Theoretical Biology 215:95-108.

Peaden, J.M., T.D. Tuberville, K.A. Buhlmann, M.G. Nafus, and B.D. Todd. 2015. Delimiting road-effect zones for threatened species: implications for mitigation fencing. Wildlife Research 42:650–659.

Peterson, C.C. 1994. Different rates and causes of high mortality in two populations of the threatened desert tortoise *Gopherus agassizii*. Biological Conservation 70:101-108.

Radeloff, V.C., S.I. Stewart, T.J. Hawbaker, U. Gimmi, A.M. Pidgeon, C.H. Flather, R.B. Hammer, and D.P. Helmers. 2010. Housing growth in and near United States protected areas limits their conservation value. Proceedings of the National Academy of Sciences of the U.S. 107:940-945.

Rautsaw, R.M., S.A. Martin, B.A. Vincent, K. Lanctot, M.R. Bolt, R.A. Seigel, and C.L. Parkinson. 2018. Stopped dead in their tracks: the impact of railways on gopher tortoise (*Gopherus polyphemus*) movement and behavior. Copeia 2018:135–143.

Shaffer, M.L., and B.A. Stein. 2000. Safeguarding our precious heritage. Pages 301–321 *in* B.A. Stein, L.S. Kutner, and J.S. Adams (eds.), Precious Heritage: The Status of Biodiversity in the United States. Oxford University Press, New York.

Shoemaker, K.T., M. Walden, E. Hunter, T.C. Esque, and K.E. Nussear. 2020. Modeling critical habitat for Mojave Desert Tortoises in a non-stationary world. Presented at a special invited session on Connectivity and the Desert Tortoise. 45th annual symposium of the Desert Tortoise Council. Las Vegas, NV. 22 February.

Tracy, C.R., R.C. Averill-Murray, W.I. Boarman, D. Delehanty, J.S. Heaton, E.D. McCoy, D.J. Morafka, K.E. Nussear, B.E. Hagerty, and P.A. Medica. 2004. Desert Tortoise Recovery Plan Assessment. Report to the U.S. Fish and Wildlife Service, Reno, Nevada.

U.S. Bureau of Land Management. 2016. Desert Renewable Energy Conservation Plan Land Use Plan Amendment to the California Desert Conservation Area Plan, Bishop Resource Management Plan, and Bakersfield Resource Management Plan. BLM/CA/PL-2016/03+1793+8321.

U.S. Fish and Wildlife Service. 1994. Desert Tortoise (Mojave Population) Recovery Plan. U.S. Fish and Wildlife Service, Portland, Oregon.

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

U.S. Fish and Wildlife Service. 2016. USFWS Species Status Assessment Framework: an integrated analytical framework for conservation. Version 3.4 dated August 2016.

Vandergast, A.G., R.D. Inman, K.R. Barr, K.E. Nussear, T.C. Esque, S.A. Hathaway, D.A. Wood, P.A. Medica, J.W. Breinholt, C.L. Stephen, A.D. Gottscho, S.B. Marks, W.B. Jennings, R.N. Fisher. 2013. Evolutionary Hotspots in the Mojave Desert. *Diversity 5*:293-319.

Appendix 1
Recent Desert Tortoise Habitat and Connectivity Models

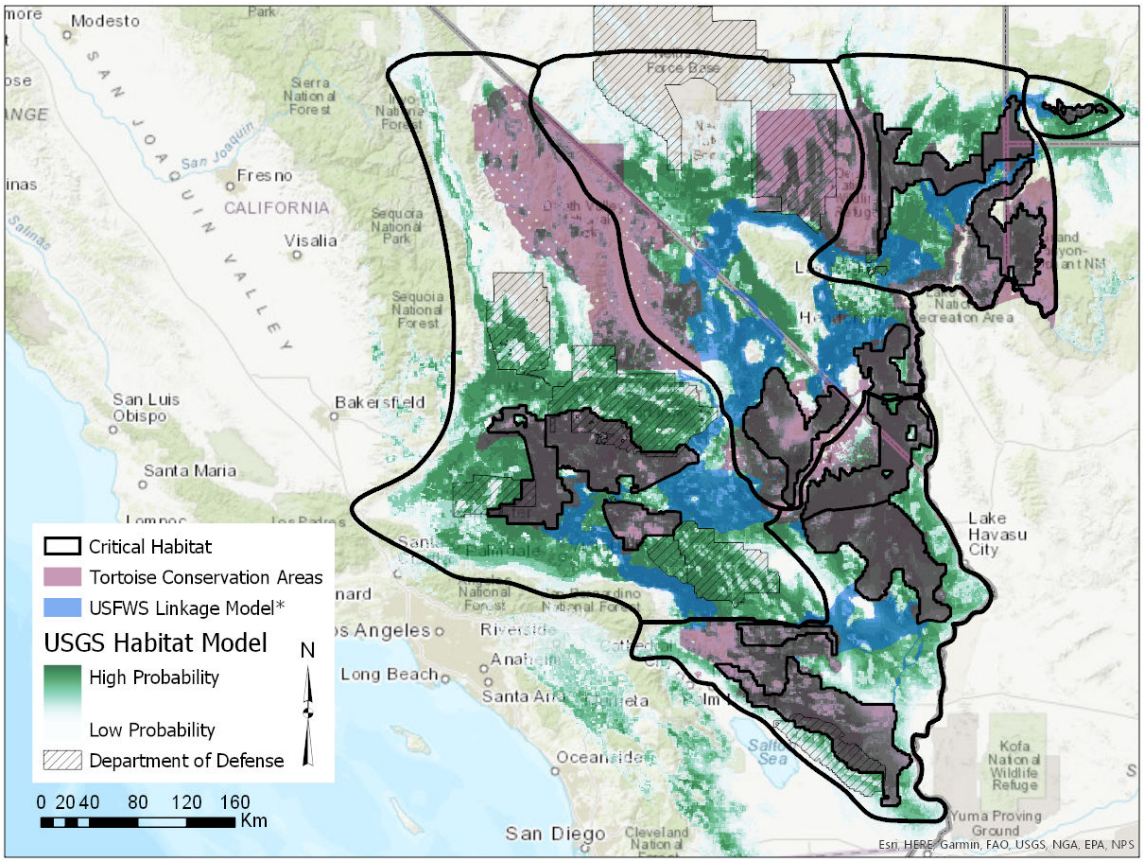

Figure A - 1. Range-wide Mojave Desert Tortoise habitat probability model (Nussear et al. 2009) overlain by the U.S. Fish and Wildlife Service linkage model (Averill-Murray et al. 2013) that connects designated Tortoise Conservation Areas. Black lines subdivide the range into five recovery units (USFWS 2011).

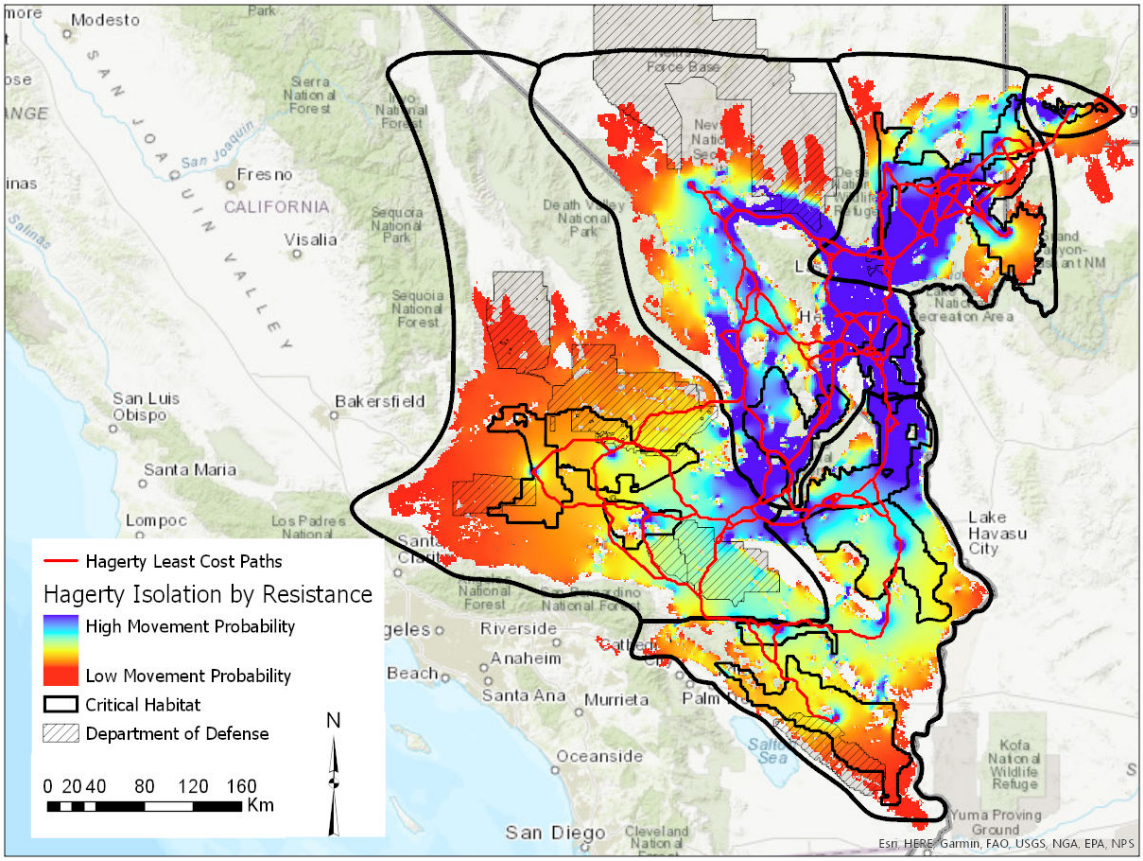

Figure A - 2. Mojave Desert Tortoise landscape genetics modeled by Hagerty et al. (2011) showing least-cost paths between sampled population centroids overlying an isolation-by-resistance surface. Black lines subdivide the range into five recovery units (USFWS 2011).

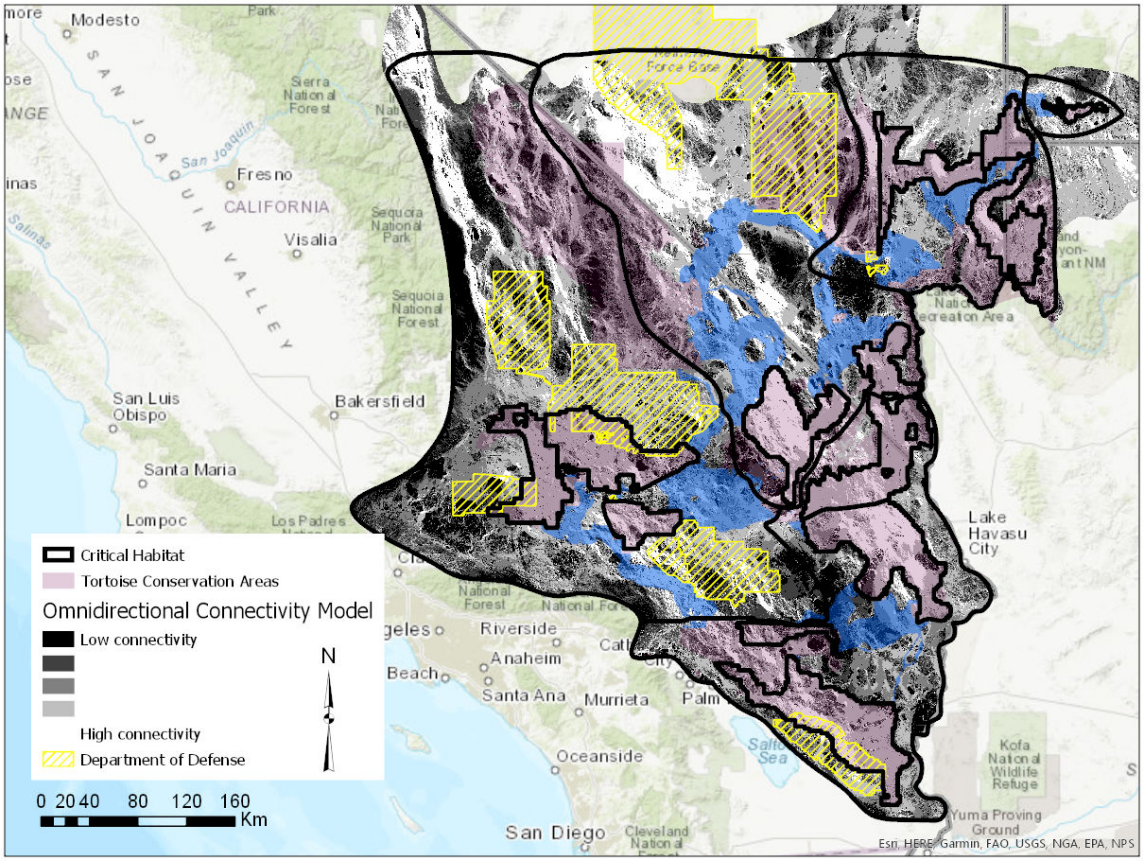

Figure A - 3. Range-wide omnidirectional connectivity model (Gray et al. 2019) for the Mojave Desert Tortoise overlain by the U.S. Fish and Wildlife Service linkage model (blue) that connects designated Tortoise Conservation Areas (Averill-Murray et al. 2013). Black lines subdivide the range into five recovery units (USFWS 2011).

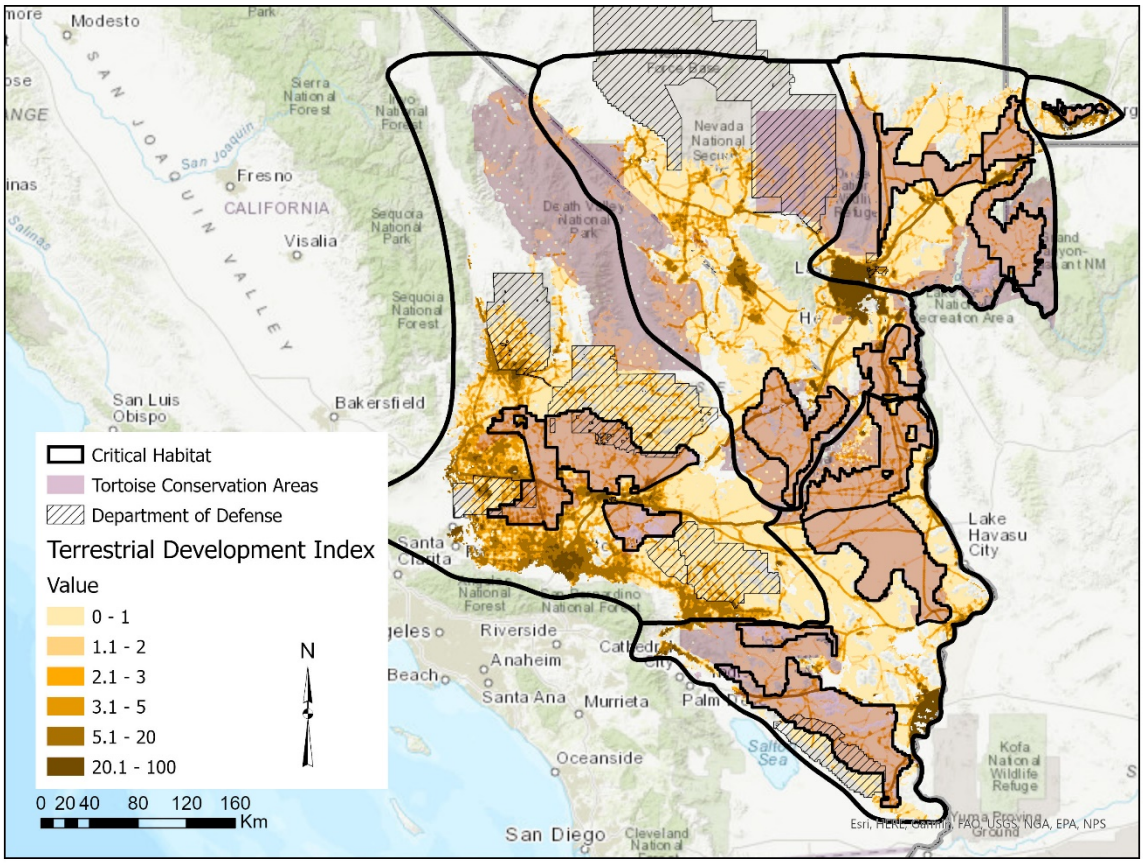

Figure A - 4. Terrestrial development index modeled by Carter et al. (2020a). Black lines subdivide the range into five recovery units (USFWS 2011).