Herpetological Conservation and Biology 8(1):1 – 15.
Submitted: 7 August 2012; Accepted: 4 March 2013; Published: 30 April 2013.

CONSERVING POPULATION LINKAGES FOR THE MOJAVE DESERT TORTOISE (*GOPHERUS AGASSIZII*)

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***Abstract.*—Conservation of Mojave Desert Tortoises is founded on a set of tortoise conservation areas (TCAs) established across the range of the species. Limitations of the existing reserve design and increasing development pressures on the intervening habitat matrix underscore the need to conserve linkages between existing TCAs. We modeled linkages between TCAs using least-cost corridors based on an underlying model of suitable tortoise habitat. Results indicate that TCAs contain 55% of total historic habitat (45,340 km^2). A minimum linkage network would contain 16,282 km^2 of habitat (20% historic). This combined area of 61,622 km^2 represents an initial framework to develop a conservation network for the species, taking into account large areas of existing high-intensity human uses such as military operations and off-highway-vehicle recreation. Models that assume more permeable habitat to tortoise connectivity reveal much broader linkages, but approximately 700 km^2 of habitat within the minimum linkages are already at risk of permanent habitat loss through solar energy development. Additional conservation of occupied habitat adjacent to the minimum linkages and existing TCAs would provide security against edge effects and population declines within conservation areas, especially given limitations in existing reserve architecture. Application of these linkage models will require refinement at the local level, and questions remain about the ultimate ability of a conservation network based on these models to support viable tortoise populations and accommodate climate change. Nevertheless, conservation decisions cannot be delayed while awaiting final answers to all relevant questions. In areas proposed for permanent habitat conversion, critical linkages may be severed before they are protected.**

Key Words.—connectivity; conservation; habitat fragmentation; least-cost corridor

INTRODUCTION

Habitat loss and fragmentation are prevalent threats to biodiversity (Yiming and Wilcove 2005; Venter et al. 2006). Fragmented, isolated populations are subject to demographic, environmental, and genetic forces that can act independently or together to create a "vortex" of extinction (Wilcox and Murphy 1985; Gilpin and Soulé 1986; Fagan and Holmes 2006). Connecting protected areas with linkages is a way to increase the effective area of reserves and the population size of at-risk species (Crooks and Sanjayan 2006). In addition to the benefits of buffering small or low-density populations in protected areas, preservation of natural levels of connectivity between these areas may be critical to facilitate gene flow and to prevent habitat specialization and genetic divergence between otherwise isolated populations (Frankham 2006). Preserving connectivity also may allow species to adapt to or allow for natural range shifts in response to changing environmental conditions (Meffe and Carroll 1994; Krosby et al. 2010). Therefore, protected areas by themselves may not provide adequate long-term protection to biodiversity without considering the context of the reserve, its shape, and the "matrix" of the surroundings, which may contain a variety of habitats of different quality (Ricketts 2001; Prugh et al. 2008; Prevedello and Vieira 2010). A well-connected network of reserves increases chances of maintaining viable populations of a particular species over a single reserve or isolated reserves (e.g., Carroll et al. 2003).

The Mojave Desert Tortoise (*Gopherus agassizii*) was listed as threatened under the U.S. Endangered Species Act in 1990 due to reports of population declines across the species' distribution (see Berry and Medica [1995] for evidence of declines within local populations, but see also Bury and Corn [1995] for alternative interpretations of widespread declines) and numerous perceived threats across its range (U.S. Fish and Wildlife Service 1990). The historic distribution of the Mojave Desert Tortoise was relatively continuous across its range, broken only by major topographic barriers, such as Death Valley, California, and the Spring Mountains, Nevada (Germano et al. 1994; Nussear et al. 2009). The foundation of desert tortoise conservation and recovery across this landscape consists of 12 designated critical habitat units, which range in area from 221 to 4,130 km^2. Critical habitat, in addition to National Park Service lands and other conservation areas or easements managed for desert tortoises, constitutes the primary component of tortoise conservation areas (TCAs; U.S. Fish and Wildlife Service 2011). The minimum reserve size recommended to preserve viable populations was estimated as 2,590 km^2 (U.S. Fish and Wildlife Service 1994), and only four critical habitat units meet this threshold. Given that the quality of conserved habitat

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can be affected by factors present outside a preserve's boundary (Harrison and Bruna 1999), optimal reserve shape would be circular to minimize the perimeter and potential edge effects relative to the area. However, management practicalities resulted in all critical habitat units having complex perimeters, often with narrow extensions or projections into relatively unprotected habitat.

Population viability analyses indicate that, while focused management to improve adult tortoise survival could be effective in reversing population declines, the loss of large blocks of habitat in adjacent areas would be a major setback for population recovery (Doak et al. 1994; see also Reed et al. 2009). Similar analyses led to the recommendation that reserves should contain at least 10,000 adult tortoises to allow persistence > 350 y (U.S. Fish and Wildlife Service 1994). During the three most recent years of monitoring for which data are available, estimated abundances in only three (in 2009 and 2010) to five (in 2008) of the critical habitat units met this target (McLuckie et al. 2010; U.S. Fish and Wildlife Service, unpubl. data). However, some units share boundaries and form contiguous blocks (Fig. 1), and three such blocks in California include combined abundances of over 10,000 adult tortoises (Fremont-Kramer/Superior-Cronese, Fenner/Chemehuevi, and Pinto Mountains/ Joshua Tree National Park/Chuckwalla).

Concentrated management of protected areas, especially those that fail to meet minimum area or abundance guidelines, has been recommended to increase desert tortoise populations, but managing the habitat matrix between protected areas is also important (U.S. Fish and Wildlife Service 1994, 2011). Habitat loss within the matrix has been increasing recently from anthropogenic pressures such as utility-scale renewable energy development (Lovich and Ennen 2011), and proposals exist for other habitat-destructive activities such as expansion of military training lands, high-speed rail lines, and new airport construction. Low-mobility species like the Mojave Desert Tortoise require corridors that contain habitat attributes within the matrix for sustaining individuals for extended periods or even multi-generational populations ("corridor dwellers"), in contrast to species that may pass through corridors between protected areas in days or weeks, especially at large spatial scales (Beier and Loe 1992). As a result, even though individual desert tortoises can make long-distance movements (Berry 1986; Edwards et al. 2004), we rarely expect desert tortoises in one protected area to traverse a long, narrow "green strip" (e.g., more narrow than that necessary to support an individual's annual activity) of "preserved" Mojave Desert habitat, with potentially habitat-degrading edge effects, to another protected area several kilometers distant (as opposed to tortoises moving several meters through a narrow barrier, such as through a culvert below a highway; Boarman et al. 1998). In this study, we integrated assessments of habitat potential and anthropogenic effects to model existing suitable habitat for the Mojave Desert Tortoise. We used this suitable habitat layer to model linkages between TCAs using least-cost corridor analysis.

MATERIALS AND METHODS

Data.—All data used in our analyses came from previously published sources: 1) TCAs (U.S. Fish and Wildlife Service 2011; compiled from multiple sources including the U.S. Fish and Wildlife Service, Bureau of Land Management, and Clark County, Nevada); 2) U.S.

TABLE 1. Pairs of conservation areas between which habitat linkages for the Mojave Desert Tortoise (*Gopherus agassizii*) were identified with least-cost corridor models.

1	Ord-Rodman	Joshua Tree National Park
2	Fremont-Kramer	Ord-Rodman
3	Superior-Cronese	Ord-Rodman
4	Ord-Rodman	Mojave National Preserve
5	Superior-Cronese	Ivanpah
6	Superior-Cronese	Death Valley National Park (west)
7	Pinto Mountains	Chemehuevi
8	Chuckwalla	Chemehuevi
9	Chemehuevi	Ivanpah
10	Ivanpah	Death Valley National Park (Greenwater Valley)
11	Ivanpah	Piute-El Dorado
12	Ivanpah	Desert Tortoise Conservation Center
13	Desert Tortoise Conservation Center	Desert National Wildlife Refuge
14	Desert Tortoise Conservation Center	Piute-Eldorado
15	Death Valley National Park (Greenwater Valley)	Mormon Mesa
16	Mormon Mesa	Lake Mead National Recreation Area
17	Desert National Wildlife Refuge	Lake Mead National Recreation Area
18	Beaver Dam Slope	Gold Butte-Pakoon
19	Beaver Dam Slope	Upper Virgin River

Geological Survey's (USGS) desert tortoise habitat potential model (Nussear et al. 2009); 3) The Nature Conservancy's Mojave Ecoregional Assessment (Randall et al. 2010. Mojave Desert Ecoregional Assessment. Available from http://conserveonline.org/workspaces/mojave/documents/mojave-desertecoregional-2010/@@view.html [Accessed 10 January 2012]); 4) The Nature Conservancy's Sonoran Desert Ecoregional Assessment (Conservation Biology Institute. 2009. A framework for effective conservation management of the Sonoran Desert in California. Available from http://static.consbio.org/media/reports/files/Sonoran Framework January 20091.pdf [Accessed 10 January 2012]); and 5) the Multi-Resolution Land Characteristics Consortium's National Landcover Dataset: 2006 (NLCD; Fry et al. 2011).

Modeling suitable habitat.—The USGS model of historical habitat probability for the Mojave Desert Tortoise used presence data and a set of environmental variables to predict potential areas of desert tortoise habitat on a scale of 0–1 throughout its geographic range at 1 km^2 resolution. The model did not account for anthropogenic changes that have altered relatively high-potential habitat into areas with lower potential. We therefore used the NLCD developed-areas layer and The Nature Conservancy's "Highly Converted Areas" for the Mojave ecoregion (Randall et al. *op. cit.*) and "Conservation Category D" areas for the Sonoran ecoregion (Conservation Biology Institute *op. cit.*) to reclassify developed areas where tortoises cannot or are less likely to occur to a lower habitat potential, as described below. The "highly converted" and "category D" layers depict urban, suburban, and agricultural lands that have been heavily altered. The Nature Conservancy's ecoregional assessments were done as hexagon rasters of approximately 2.6 km^2, which are appropriate at scales greater than 1:250,000 (Randall et al. op. cit; Conservation Biology Institute op. cit).

To make the three primary datasets analytically comparable, we resampled all datasets to the same 100 m grid-cell resolution, as is commonly done with GIS datasets. We resampled the USGS habitat potential model from its 1 km grid-cell size to a 100 m grid cell with a nearest-neighbor approach using the Resample tool in ArcGIS (ESRI, Redlands, California, USA). The Nature Conservancy's Ecoregional Assessment dataset was available as hexagonal units approximately 2.5 km^2 in area as vector (polygon) files. To be compatible with our analysis, we rasterized the output to a 100 m grid cell. We downsampled the NLCD from 30 m using ArcGIS's Aggregate tool, setting the aggregation technique to Maximum. This setting took the maximum cell value from the source when determining the new value for the output cell.

We reclassified habitat potential values based on anthropogenic features from the datasets described above. We assigned areas within the NLCD as 0 habitat potential using a series of ArcGIS conditional (if/else "Con") statements if they were classified as high-intensity developed or medium-intensity developed. The high-intensity developed category includes highly developed areas where impervious surfaces account for 80–100% of the total cover. The medium-intensity developed category includes areas where impervious surfaces account for 50–79% of the total cover; these areas most commonly include single-family housing units. We assumed that the low-intensity developed category, which includes areas where impervious surfaces account for 20–49% percent of total cover, reduces tortoise occupancy potential below the baseline threshold for natural habitat without necessarily eliminating all use, so we assigned scores of 0.3 to these areas if the USGS habitat potential value was greater than or equal to 0.3. We reclassified areas categorized by The Nature Conservancy as "highly converted" and "category D" to 0 habitat potential; the highly converted layer depicts urban, suburban, and agricultural lands that have been heavily altered. Areas not affected by these anthropogenic features retained their underlying score from the USGS habitat model.

We also identified areas of contiguous non-zero cells less than a cumulative area of 1 km^2. We classified these areas as 0 habitat potential because they are isolated patches that are disconnected from contiguous habitat and are capable of supporting few tortoises (e.g., fewer than 14 adult tortoises on average; U.S. Fish and Wildlife Service, unpubl. data). Figure 1 depicts the resulting "Suitable Habitat" model. For discrete estimations of habitat area (i.e., to convert the probability model to presence/absence), we clipped the model to the 0.5 habitat-probability threshold based on 0.5 prevalence in the model dataset (Liu et al. 2005; Ken Nussear, pers. comm. 2009).

Least-cost corridor model simulation.—Least-cost path analysis uses a raster-based algorithm that weighs the minimal cost distance between source and target cells. We used five basic steps to finding least-cost corridor networks in our study landscape (cf. Sawyer et al. 2011): (1) Select the specific source and destination points; (2) create a spatially-explicit resistance surface that is weighted according to facilitating or hindering effects on the movement process; (3) calculate a minimum accumulated cost surface over the resistance surface from all cells in the study area for both the source and destination features (treating each feature as a source), creating two raster maps where every cell is assigned a value that represents the lowest possible accumulative cost from the feature to each cell; (4) use these two accumulative cost outputs to find the sum of

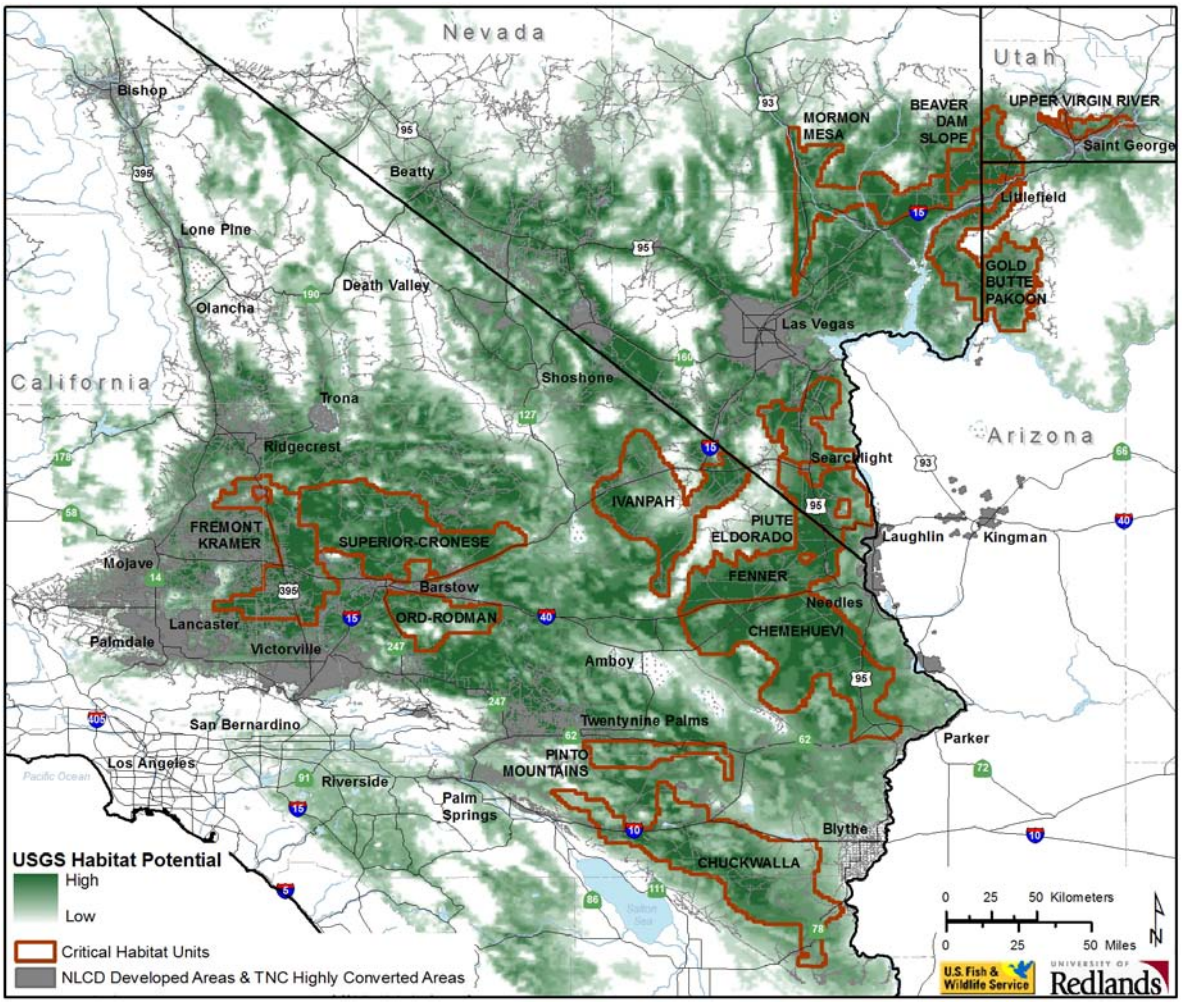

FIGURE 1. Current predicted Mojave Desert Tortoise (*Gopherus agassizii*) habitat adapted from Nussear et al. (2009).

the two surfaces at each cell. The sum of the two raster costs identifies for each cell location the least-cost path from one source to another source that passes through the cell location (ESRI. 2011. Creating a least cost corridor. ArcGIS Desktop Help 10.0. Available from http://help.arcgis.com/en/arcgisdesktop/10.0/help/index.html#//009z00000024000000.htm [Accessed 9 April 2012]); and (5) apply a maximum accumulated distance threshold to define a corridor (as opposed to a single line resulting from a least-cost path analysis).

Nineteen pairs of TCAs served as source/destination polygons for our least-cost corridor analysis (Table 1). We modeled connectivity between TCA pairs through cells of habitat capable of supporting tortoise occupancy under the premise that the Mojave Desert Tortoise is a corridor dweller. High-probability habitat corresponds to "low cost" for tortoise occupancy, so we inverted the habitat suitability surface using ESRI's Spatial Analyst arithmetic functions for use as a cost surface. Using the source polygons and the cost surface, we created a cost-distance surface for each of the source polygons defined in a pair (two surfaces per pair). These surfaces represent the accumulative cost of "traveling" over the cost surface from each cell back to the edge of the source polygon. We created these surfaces with ESRI's Spatial Analyst CostDistance function. We used ESRI's Spatial Analyst Corridor function to sum the two accumulative costs for the two input accumulative-cost rasters, thereby identifying, for each cell location, the least-cost path from the source to the destination that passes through that cell location. Because of the varying cost between each TCA pair (one pair might be geographically adjacent to one another while another pair might be separated by > 100 km), we applied a standard threshold percentage to normalize the outputs. Through an iterative process of reviewing threshold outputs, we chose a standard distance threshold of 1% for each corridor output. The associated range of cost-distance values were calculated from the total range of corridor values and applied using ESRI's Spatial Analyst Con

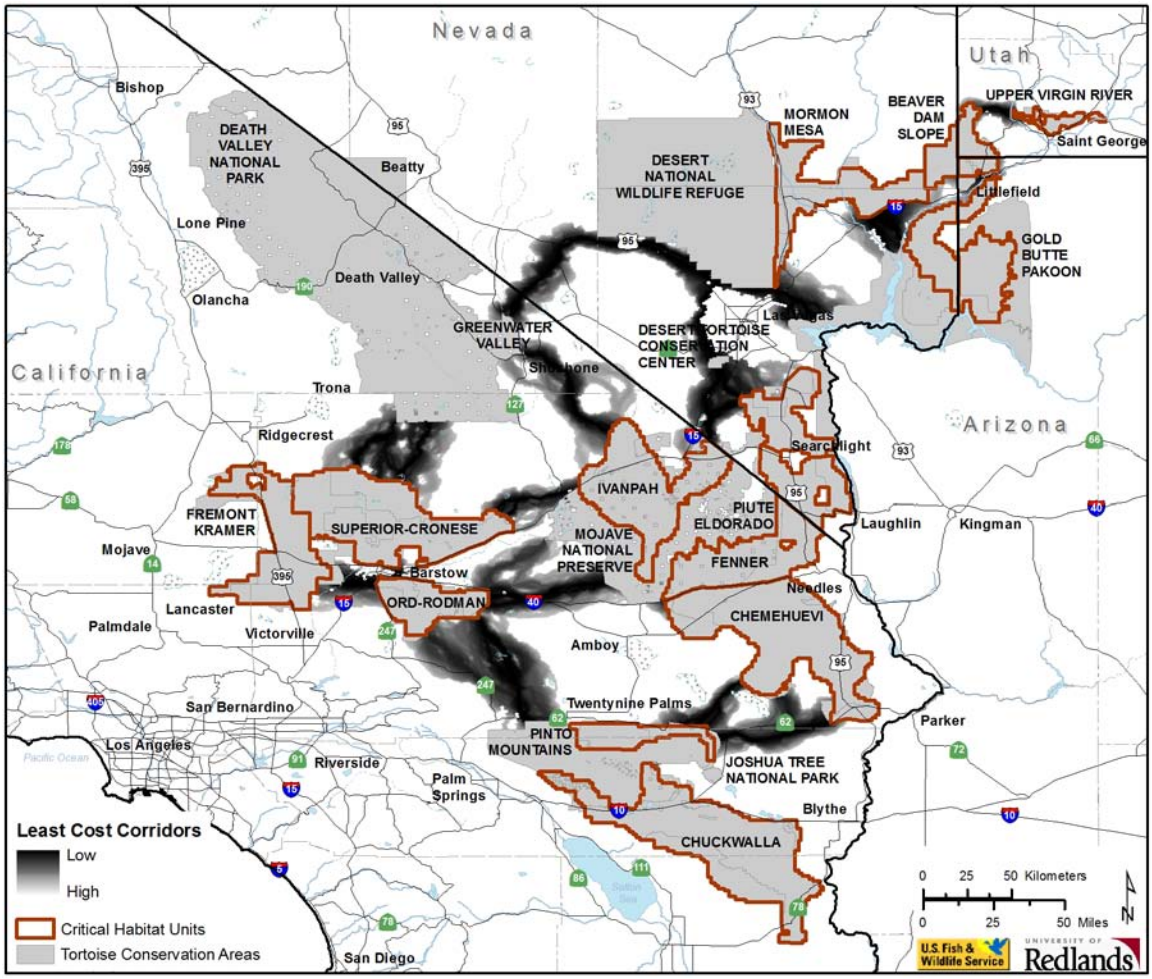

FIGURE 2. Least-cost corridors between tortoise conservation areas (Base model). Each corridor includes the lowest 1% cost-distance paths between tortoise conservation areas (TCAs), where the relative cost to tortoises increases from black to white. White patterns within TCAs are private inholdings within federal lands.

function. The output of this series of operations was a raster of the corridor from/to each TCA polygon, which includes the lowest 1% cost paths from one TCA to another.

While overall movement resistance may be higher between two TCAs than between another pair, corridors between each TCA pair are important to population connectivity range-wide. Therefore, we normalized all corridors from 0–1 using a custom script written in Python. We also inverted these rescaled corridor values to represent importance for connectivity rather than cost.

We refer to the output from this process using the Suitable Habitat model as the "Base" model. The movement cost surface in the Base model assumes a 1:1 relationship between probability of tortoise occurrence in each pixel and resistance to connectivity. However, a

TABLE 2. Overlap (km^2, %) of Mojave Desert Tortoise (*Gopherus agassizii*) habitat in four least-cost corridor models with Department of Defense (DOD) lands, designated open off-highway-vehicle (OHV) recreation areas, and designated wilderness areas or Bureau of Land Management National Conservation Areas (NCAs).

	DOD	OHV	Wilderness/NCA
Base	2,375 (13%)	875 (5%)	2,952 (17%)
Base2	0 --	0 --	4,260 (26%)
Binned	7,165 (16%)	1,200 (3%)	6,985 (16%)
Binned2	0 --	0 --	7,145 (20%)

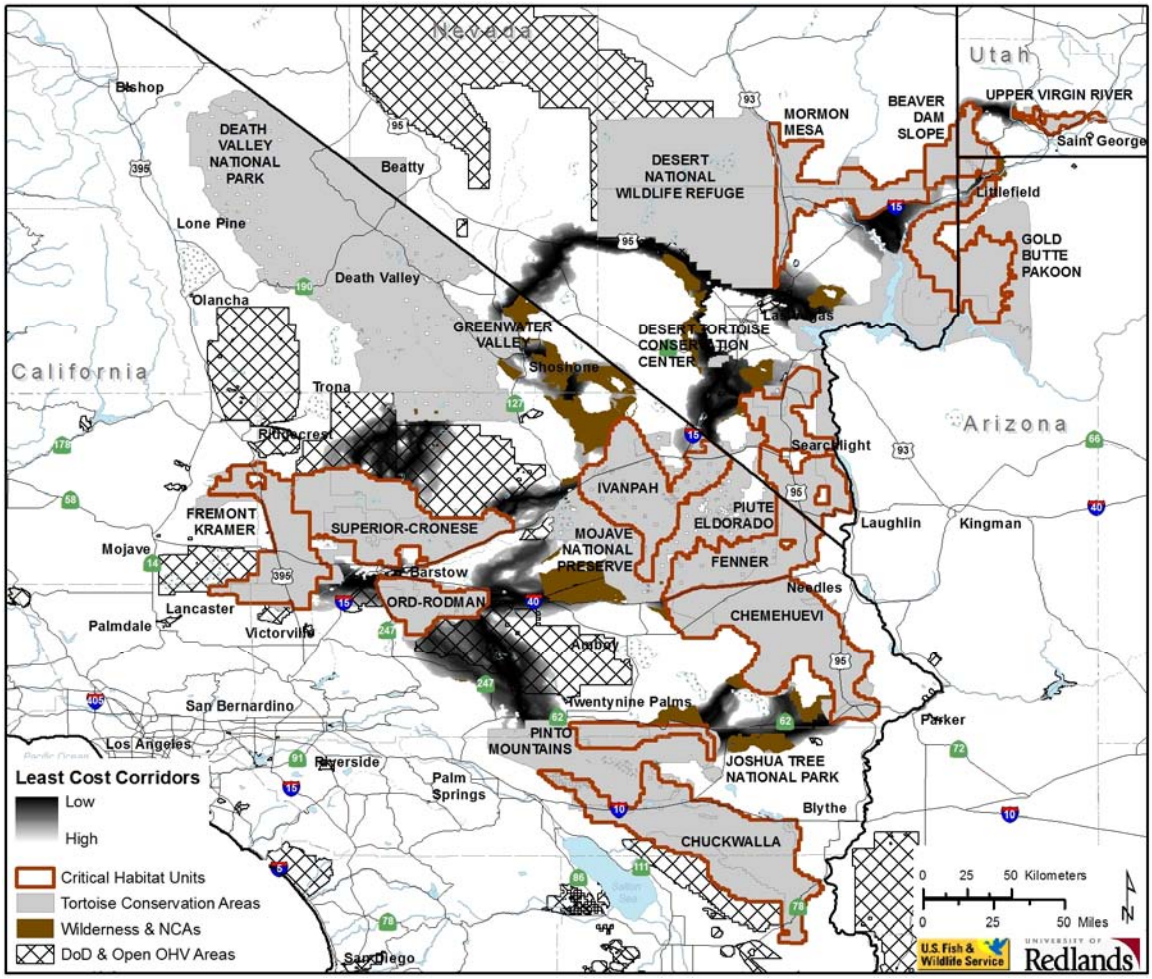

FIGURE 3. Least-cost corridors between tortoise conservation areas (TCAs; Base model), overlaid with Department of Defense (DoD) lands and open off-highway vehicle (OHV) areas, and showing designated wilderness areas and National Conservation Areas (NCAs) clipped to the linkages. Each corridor includes the lowest 1% cost-distance paths between TCAs, where the relative cost to tortoises increases from black to white. White patterns within TCAs are private inholdings within federal lands.

pixel of moderate probability (e.g., 0.7) may contribute equally to connectivity as a pixel of high probability (0.9) if both pixels allow some degree of population presence or individual movement, especially at a temporal scale of a tortoise generation (about 25 y). For example, 95% of cells with known presence in the USGS habitat model had scores greater than 0.7 (Nussear et al. 2009). Therefore, we compared the Base model to a "Binned" model in order to evaluate uncertainty in our choice of resistance values, as recommended by Beier et al. (2009) and Sawyer et al. (2011). We developed the cost surface for the Binned model by re-scoring all pixels ≥ 0.7 in the Base model to 1.0, values 0.50–0.69 to 0.6, values 0.10–0.49 to 0.3, and values < 0.1 to 0. Other land uses also may affect desert tortoise connectivity, but are not captured by NLCD's developed areas of The Nature Conservancy's highly converted areas. Military training maneuvers and open-access off- highway-vehicle (OHV) recreation are high-impact activities that limit tortoise abundance, especially in the long term with increasing use (Bury and Luckenbach 2002; Berry et al. 2006). Therefore, we assessed effects on linkages of converting all Department of Defense (DOD) lands and open OHV areas to 0 habitat probability (models "Base2" and "Binned2").

RESULTS

Suitable Habitat (i.e., current estimated habitat) for the Mojave Desert Tortoise totals 67,000 km^2, 81% of the historic (i.e., unmanipulated USGS habitat model) estimated total of 83,138 km^2. The area of Suitable Habitat within TCAs, including areas of overlap with DOD lands, is 45,340 km^2 (68% of total current, 55% of total historic). Suitable Habitat within linkages connecting the TCAs in the Base model totals17,831 km^2

TABLE 3. Percentage overlap of least-cost corridors based on four connectivity models between Mojave Desert Tortoise (*Gopherus agassizii*) conservation areas. Total habitat area within each linkage is given along the diagonal.

	Base	Base2	Binned	Binned2
Base	17,831 km^2	81%	38%	35%
Base2	74%	16,282 km^2	34%	41%
Binned	92%	90%	43,597 km^2	97%
Binned2	70%	90%	79%	35,629 km^2

(27% current, 21% historic; Fig. 2). Several linkages are already severely constrained or impacted by DOD and open OHV area designations (Fig. 3, Table 2). Military training operations or high-intensity OHV recreation affect up to 18% of Suitable Habitat within linkages in the Base model. On the other hand, portions of some linkages (17%) are protected by wilderness or U.S. Bureau of Land Management (BLM) National Conservation Area (NCA) designations (Fig. 3, Table 2).

The Binned model had the effect of greatly lowering the resistance to tortoise occupancy, thereby increasing the amount of area included in the lowest 1% cost paths between TCAs (Fig. 4). Linkages in the Base model included only 38% of Suitable Habitat in the Binned model, while the Binned linkages included 92% of Base linkage habitat (Table 3). The total area of habitat within

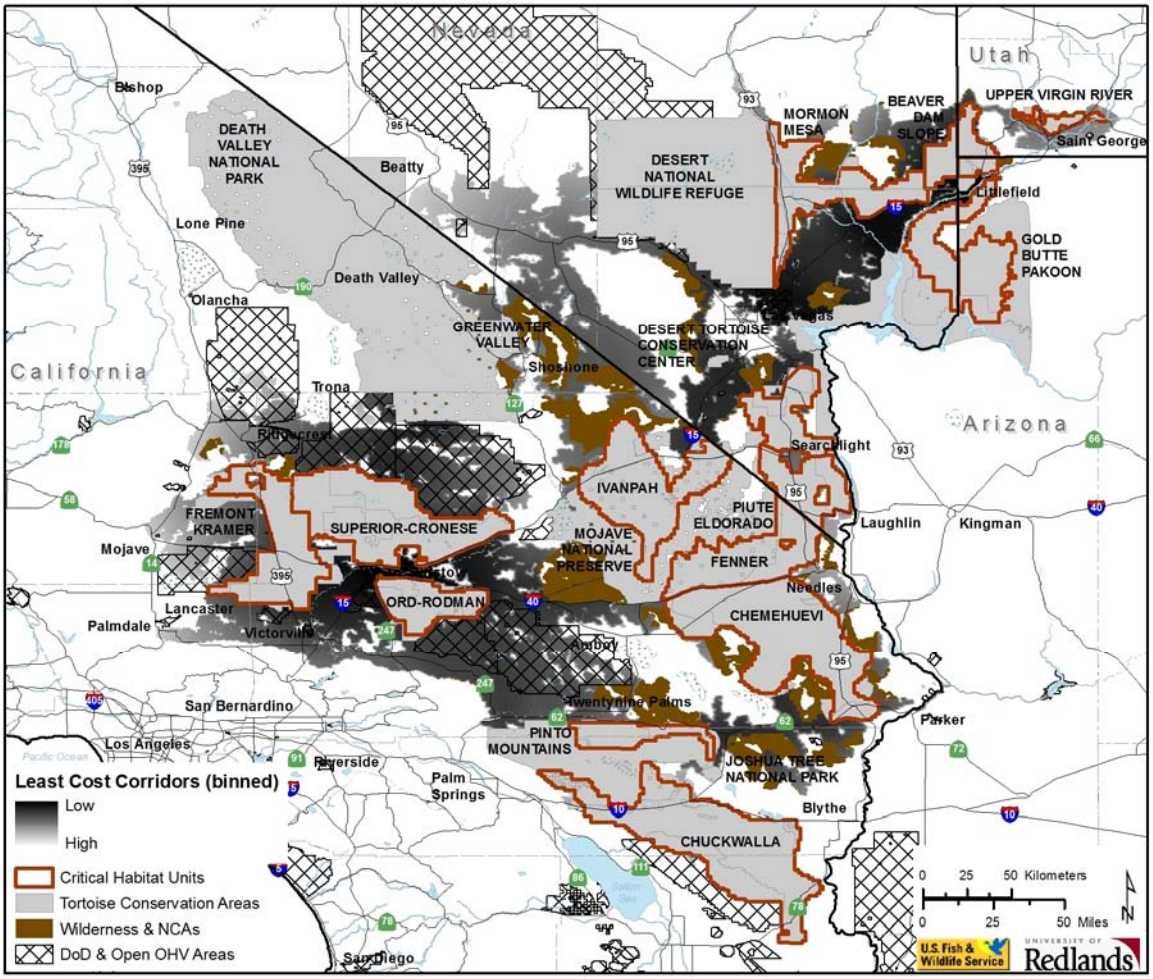

FIGURE 4. Binned model: least-cost corridors between tortoise conservation areas (TCAs), overlaid with Department of Defense (DoD) lands and open off-highway vehicle (OHV) areas, and showing designated wilderness areas and National Conservation Areas (NCAs) clipped to the linkages. Each corridor includes the lowest 1% cost-distance paths between TCAs, where the relative cost to tortoises increases from black to white. White patterns within TCAs are private inholdings within federal lands.

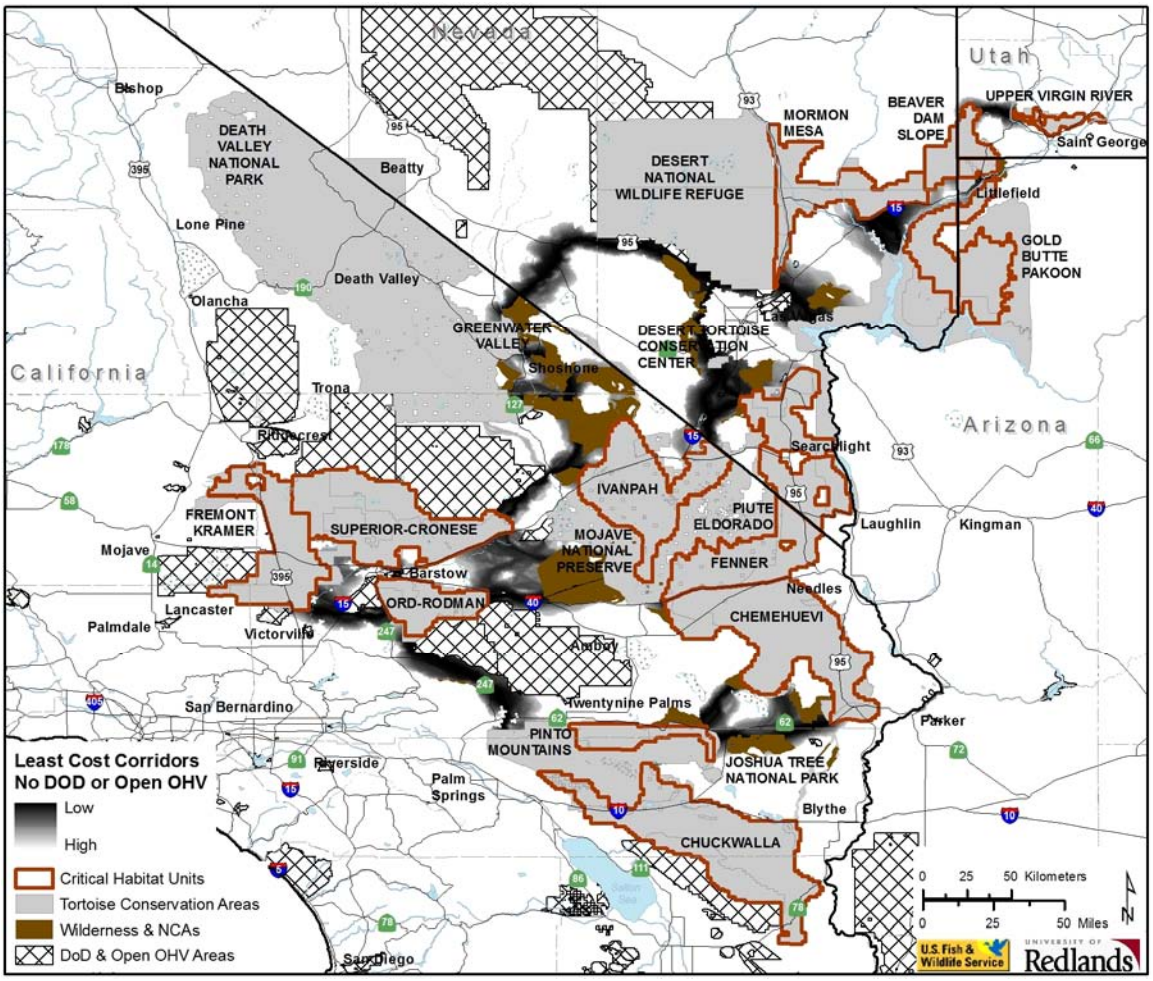

FIGURE 5. Base2 model: least-cost corridors between tortoise conservation areas (TCAs), overlaid with Department of Defense (DoD) lands and open off-highway vehicle (OHV) areas, and showing designated wilderness areas and National Conservation Areas (NCAs) clipped to the linkages. Each corridor includes the lowest 1% cost-distance paths between TCAs, where the relative cost to tortoises increases from black to white. White patterns within TCAs are private inholdings within federal lands.

linkages in the Binned model totals 43,597 km^2 (65% current, 52% historic). Military training operations or high-intensity OHV recreation affect 19% of habitat within the linkages in the Binned model (Table 2). Current wilderness or NCA designations protect 16% of linkages in the Binned model (Table 2).

Excluding DOD and OHV designations from the cost surface reduced total habitat areas by 8.7% and 18.3% in the Base2 and Binned2 models, respectively (Table 3), although a greater proportion of the linkages is protected by existing wilderness or NCA designations (Table 2). Excluding these areas resulted in expansion of remaining linkages between TCAs, especially in California in the Base2 model (Figs. 5,,6). Overall, linkages in the Base model overlapped 81% of Suitable Habitat in the Base2 model, while the Binned model included 97% of Suitable Habitat in the Binned2 model (Table 3). Differences from 100% in proportion of habitat in the Base and Binned models that overlap the smaller Base2 and Binned2 models reflect shifts in the 1% cost surfaces. For example, in the Base2 model more of the area east of the Ord-Rodman and Superior-Cronese critical habitat units was important for connectivity, and new linkage strands were identified between the Chemehuevi and Chuckwalla critical habitat units (Fig. 5).

DISCUSSION

Successfully conserving the Mojave Desert Tortoise will entail managing not just conservation areas alone, but also the connections between these areas (i.e., managing the matrix between reserves: Fahrig 2001; Prevedello and Vieira 2010). Some TCAs are contiguous with others and together may contain viable

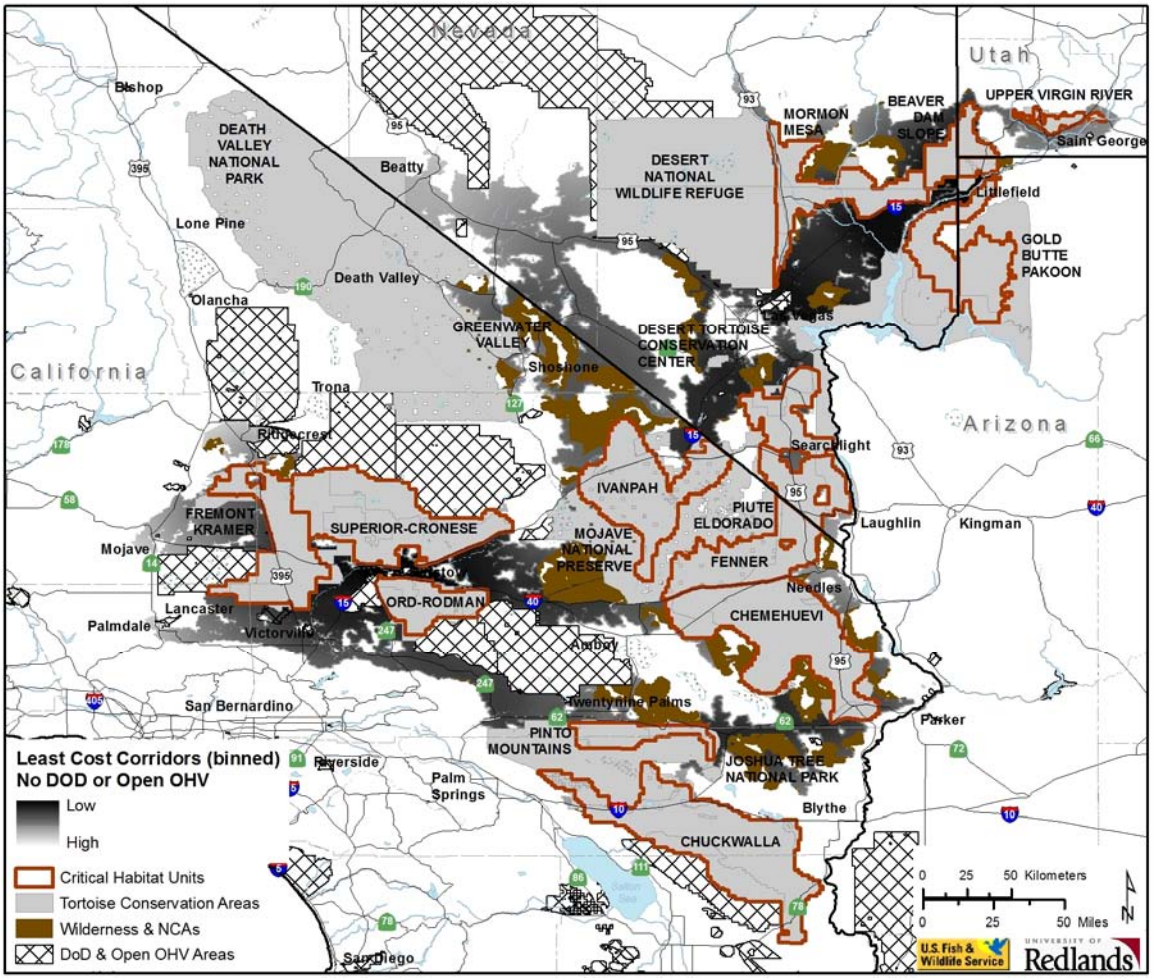

FIGURE 6. Binned2 model: least-cost corridors between tortoise conservation areas (TCAs), overlaid with Department of Defense (DoD) lands and open off-highway vehicle (OHV) areas, and showing designated wilderness areas and National Conservation Areas (NCAs) clipped to the linkages. Each corridor includes the lowest 1% cost-distance paths between TCAs, where the relative cost to tortoises increases from black to white. White patterns within TCAs are private inholdings within federal lands.

numbers of desert tortoises, but even these contiguous blocks are adjacent to smaller, more isolated TCAs. Therefore, the function of the collective TCA network could be solidified by ensuring that all remain connected. In cases where much of the matrix between reserves remains undeveloped, managing the matrix to increase permeability and occupancy will be easier than restoring corridors after development has occurred (Prugh et al. 2008; Prededello and Vieira 2010).

In addition, most wildlife, including the Mojave Desert Tortoise, does not occur at uniform densities across landscapes (Krzysik 2002). The extent to which populations may fluctuate asynchronously, such as localized declines attributed to drought or predation events (Peterson 1994; Longshore et al. 2003; see also the model of recruitment in chaotic environments in Morafka 1994) even within designated conservation areas, increases risks to population viability and places increased emphasis on preserving population connectivity through the surrounding habitat matrix. Even under an assumption that TCAs are source habitats surrounded by sinks, maintaining or improving conditions within sinks/linkages can be as important to regional viability as protecting source TCAs because of their effect on neighboring source habitat (Carroll et al. 2003). Consequently, the effectiveness of TCAs will be improved if they are connected with functional habitat to ensure desert tortoise population persistence (U.S. Fish and Wildlife Service 1994, 2011). Ideally, linkages between TCAs would also be wide enough to buffer against detrimental edge effects (Beier et al. 2008), a recommendation applicable also to the TCAs, themselves (U.S. Fish and Wildlife Service 1994).

While specific management is needed within TCAs, these areas provide only an initial framework upon which to focus recovery efforts, especially given uncertainties related to the effects of climate change on Mojave Desert Tortoise populations and distribution (Barrows et al. 2011; U.S. Fish and Wildlife Service 2011). Temperatures are projected to change relatively quickly within desert ecosystems. To keep pace with changes from current temperature regimes within the current century, desert wildlife populations or species would need to shift their distributions at approximately 0.7 km/year (Loarie et al. 2009). At this rate, the current climate would cross each critical habitat unit (ranging in latitudinal extent of approximately 33–267 km) within 23–187 years. Notwithstanding potential elevational shifts by tortoise populations in response to climate change, which may be constrained in many areas as a result of geologic limitations on burrow construction, preserving connectivity between TCAs may allow shifts in the species' distribution and allow for future flexibility in refocusing management to ensure long-term recovery (Crooks and Sanjayan 2006; Krosby et al. 2010).

Connectivity conservation also is integral to maintaining genetic variability and ecological heterogeneity within and among populations of widely distributed species. Genetic analyses suggest that, historically, levels of gene flow among subpopulations of the Mojave Desert Tortoise were high, corresponding to high levels of habitat connectivity (Murphy et al. 2007; Hagerty 2008). All recent genetic studies of the Mojave Desert Tortoise have suggested that its population structure is characterized by isolation-by-distance; populations at the farthest extremes of the distribution are most differentiated, but a gradient of genetic differentiation occurs between those populations across the range (Britten et al. 1997; Murphy et al. 2007; Hagerty and Tracy 2010). This isolation-by-distance genetic structure across the relatively continuous historic distribution of the Mojave Desert Tortoise (Germano et al. 1994; Nussear et al. 2009) indicates that gene flow generally occurs (or historically occurred) according to a continuous-distribution model (Allendorf and Luikart 2007), as opposed to a metapopulation or stepping-stone model where individual tortoises move from one patch of suitable habitat across less suitable or non-habitat to another patch of suitable habitat.

Our modeling approach was similar to that of Hagerty et al. (2011), who modeled historic gene flow between populations across the range of the species across a cost surface based on the original (historic) USGS habitat model. Gene flow historically occurred in a diffuse pattern across the landscape unless otherwise constrained to more narrow, concentrated pathways created by topographic barriers (e.g., around the Spring Mountains in southern Nevada; Hagerty et al. 2011). Linkages between conservation areas are needed to conserve historic genetic gradation, thereby preventing habitat specialization and genetic divergence between populations (Frankham 2006). Where gene flow is constrained by topographic barriers, conservation of such concentrated pathways or linkages is especially important.

For gene flow to reliably occur across the range, and for populations within existing conservation areas to be buffered against detrimental effects of low numbers or density, populations need to be connected by areas of habitat occupied by tortoises. Low levels of genetic differentiation in Mojave Desert Tortoises have been detected across even relatively recent and narrow anthropogenic impacts on the landscape (Latch et al. 2011). Pairs of tortoises from opposite sides of a road exhibited significantly greater genetic differentiation than pairs from the same side of a road (Latch et al. 2011), raising even greater concerns for population fragmentation from larger scale habitat loss.

Assumptions and limitations.—Our assessment of important areas within which to preserve connectivity of Mojave Desert Tortoise populations is limited by shortcomings in our knowledge. We assumed that potential tortoise occupancy was accurately reflected by the USGS habitat model, as modified by our interpretation of the altered-habitat datasets, and that linkages of high-probability habitat between existing TCAs will help sustain viable populations across the range of the species. Implicit in this assumption is that various land uses or impacts occurring on the landscape (e.g., unpaved roads, exotic plant invasions) that were not explicitly included in the geospatial data we used do not impede connectivity of tortoise populations. We evaluated the effect of this assumption relative to large-scale potential impacts of high-intensity land uses (military training maneuvers and open OHV recreation), and additional areas emerged that may be important to connectivity.

Least-cost path analyses provide only a snapshot of current habitat conditions and are uninformative about demographic processes or how individuals actually move through a landscape (Noss and Daly 2006; Taylor et al. 2006). We assumed that a 1% cost surface would identify linkages wide enough to provide functional connectivity between TCAs. However, application of different resistance values from the underlying habitat model greatly influenced the total area and configuration of the 1% cost surface.

Indeed, limiting the cost surface to the lowest 1% is an arbitrary choice (Sawyer et al. 2011). The mean model score for all cells with known tortoise presence in the USGS habitat model was 0.84, and 95% of cells with known presence had scores greater than 0.7 (Nussear et al. 2009). Therefore, connectivity between tortoise

populations (TCAs) may occur more broadly than estimated in the Base model. The more permeable Binned model identified linkages 245% larger in area than those in the Base model, while the linkages in the Binned2 model were 219% larger than those in the Base2 model.

Limited guidance is available for determining precise linkage widths, but minimum widths for corridor dwellers such as the Mojave Desert Tortoise should be substantially larger than a home range diameter (Beier et al. 2008). Inevitably, however, questions will be asked about what is the minimum width for a particular desert tortoise linkage, what is the relevant home range size from which to estimate that minimum width, and what are the minimum sampling considerations in estimating home ranges (cf. Harless et al. 2010). We agree with Beier et al. (2008) that this is analogous to asking an engineer, "what are the fewest number of rivets that might keep this wing on the airplane?" A more appropriate question for conservation is "what is the narrowest width that is not likely to be regretted after the adjacent area is converted to human use?" Managers and policy-makers must realize that conservation is not primarily a set-aside issue that can be dealt with by reserving a minimal percentage or amount of the landscape; rather, it is a pervasive issue that must be considered across the entire landscape (Franklin and Lindenmayer 2009).

Management implications and recommendations.— In general, land and wildlife managers should think about "corridors" between conservation areas that are large enough for resident tortoises to persist and to continue to interact with their neighbors within and outside broad habitat linkages, rather than expect that a more narrow band of habitat will allow an individual tortoise to move through it to the other side, breed with a tortoise on that side, and produce viable offspring that contribute to the next generation. Linkage integrity with sufficient habitat to support sustainable populations is important for Mojave Desert Tortoises and other corridor dwellers to support connectivity between core reserves (cf. Barrows et al. 2011). Given the underlying geospatial data, linkages in the Base2 model illustrate a minimum connection of habitat for Mojave Desert Tortoises between TCA pairs and therefore represent priority areas for conservation of population connectivity. However, large areas within these linkages are at risk of permanent habitat loss as a result of solar energy development.

Utility-scale solar development will require 831 km^2 of land by 2030 to meet the reasonably foreseeable development scenario within the entire states of California and Nevada (U.S. Bureau of Land Management and U.S. Department of Energy 2012). To meet this need, BLM has identified 39,830 km^2 of potentially developable public lands throughout these states (not all within Mojave Desert Tortoise habitat), including 866 km^2 of proposed solar energy zones (SEZs) within which solar energy production would be prioritized and facilitated. Meanwhile, projects totaling 190 km^2 and 1,470 km^2 had already been approved or were pending, respectively, across BLM land within the range of the Mojave Desert Tortoise (U.S. Bureau of Land Management and U.S. Department of Energy 2012). Relatively little linkage area would be consumed by the proposed SEZs (40 km^2), but 37 km^2 of approved and 703 km^2 of pending projects overlap linkages in the Base2 model, with some linkages at particular risk (Fig. 7). Even though substantial uncertainty surrounds the ultimate development footprint of pending solar development projects (or other proposed projects, including wind energy development), a separate analysis found that between 2,000 km^2 and 7,400 km^2 of lower conservation value land could meet California's renewable energy goal by up to seven times over (Cameron et al. 2012). This suggests that renewable energy goals can be met without compromising the conservation of important Mojave Desert Tortoise habitat.

The Binned2 model includes blocks of contiguous habitat outside the Base2 linkage network, and many such areas likely contain substantial numbers of Mojave Desert Tortoises. Managers should consider additional conservation of occupied habitat adjacent to the Base2 linkages and existing TCAs to provide security against edge effects and population declines, especially given limitations previously identified in the existing reserve architecture. For example, even though use of DOD lands may be subject to change depending on national security needs, the value of military lands to conservation has long been recognized (Stein et al. 2008), and DOD-managed habitat that is unaffected by military training operations adds to the conservation base. Of additional note are blocks of habitat at the northern extent of the Mojave Desert Tortoise's range, which may be of particular relevance for additional evaluation to determine more precisely how the modeled linkages will accommodate climate change (Beier et al. 2008).

Application of models from this study will require refinement at the local level and at a higher-resolution scale than the available geospatial data (i.e., finer resolution than 1 km^2) to account for on-the-ground limitations to tortoise occupancy and movement either not reflected in the geospatial data used here or as a result of errors in the land cover data we used to identify Suitable Habitat (Beier et al. 2009). For example, habitat connections through the northern end and across the boundary of the Chuckwalla critical habitat unit may be more limited by rugged topography than suggested by Figure 1 (Jody Fraser and Pete Sorensen, pers. comm.),

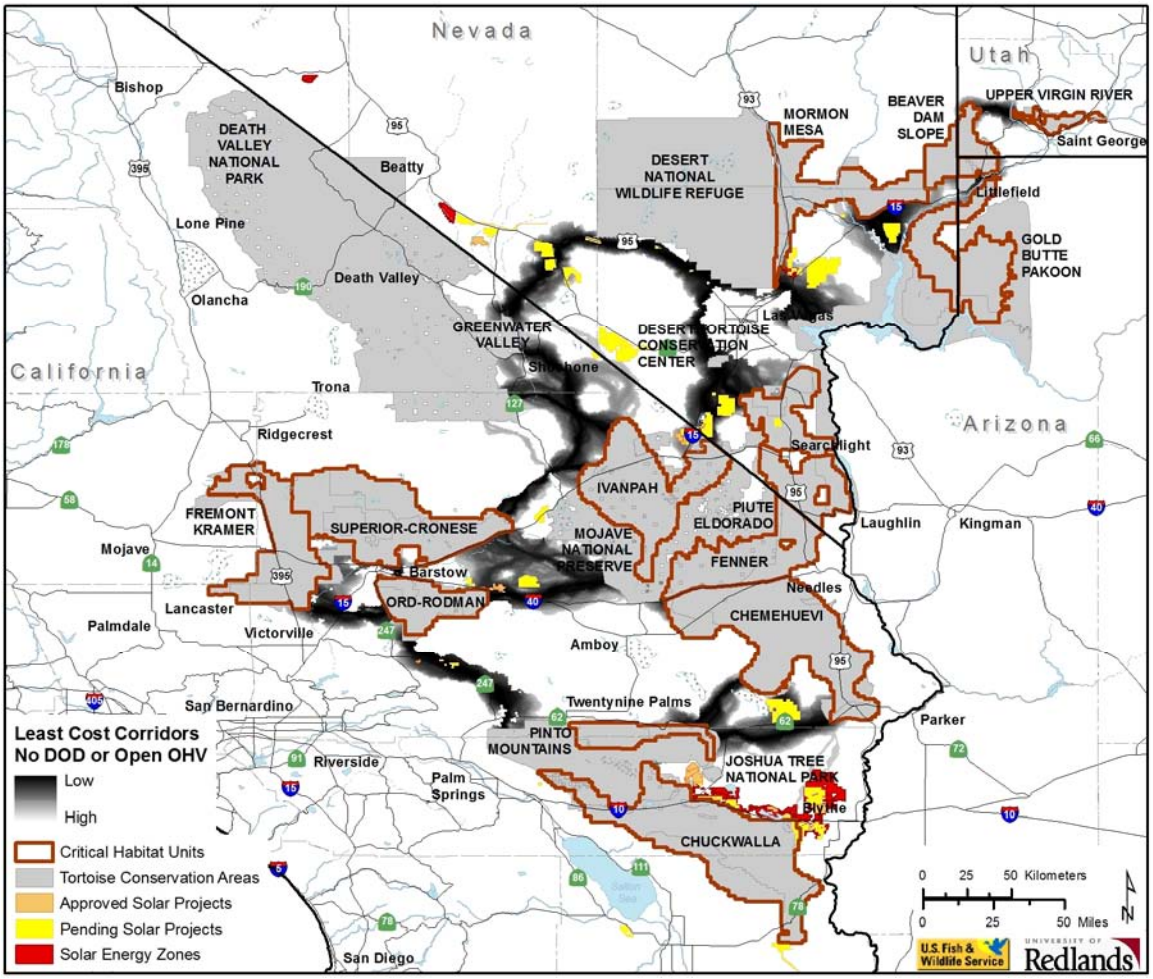

FIGURE 7. Least-cost corridors (Base2 model) between tortoise conservation areas (TCAs) relative to approved solar development projects, pending solar development projects, and solar energy zones. Each corridor includes the lowest 1% cost-distance paths between TCAs, where the relative cost to tortoises increases from black to white. White patterns within TCAs are private inholdings within federal lands.

thereby placing greater potential importance on the linkage identified on the north end of the critical habitat unit in the Binned2 model. In addition, more detailed or spatially explicit population viability analyses based on regional population and distribution patterns are needed to evaluate the ability of a conservation network such as that modeled here to ensure long-term persistence of Mojave Desert Tortoise populations (U.S. Fish and Wildlife Service 2011; e.g., Carroll et al. 2003).

While there is much still to be learned about the science and application of connectivity, land managers cannot wait for research to resolve all relevant questions before focusing effort on enhancing connectivity. Instead, science and management must proceed in parallel with the flexibility to modify future management in the light of new knowledge (Lovejoy 2006). In areas proposed for essentially permanent habitat conversion, such as by large-scale development, there is the risk that critical linkages will be severed before they are protected (Morrison and Reynolds 2006). For species with long generation times like the Mojave Desert Tortoise, this risk is compounded by the fact that we are not likely to detect a problem with a population until well after we have reduced the habitat below its extinction threshold (Fahrig 2001).

Acknowledgments.—Discussion with Linda Allison, Ashleigh Blackford, Brian Croft, Diane Elam, Kimberleigh Field, and the Desert Tortoise Science Advisory Committee (Peter Hudson, Earl McCoy, Katherine Ralls, Michael Reed, and Robert Steidl) contributed to the development of this manuscript. Additional review and comments by Todd Esque, Kimberleigh Field, Michael Reed, and Andrew Walde improved the manuscript. We thank Lisa Benvenuti at the Redlands Institute for her excellent map-making

skills. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

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