Landscape Ecol (2011) 26:267–280
DOI 10.1007/s10980-010-9550-6

RESEARCH ARTICLE

Making molehills out of mountains: landscape genetics of the Mojave desert tortoise

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Received: 25 September 2009 / Accepted: 21 October 2010 / Published online: 13 November 2010

Abstract Heterogeneity in habitat often influences how organisms traverse the landscape matrix that connects populations. Understanding landscape connectivity is important to determine the ecological processes that influence those movements, which lead to evolutionary change due to gene flow. Here, we used landscape genetics and statistical models to evaluate hypotheses that could explain isolation among locations of the threatened Mojave desert tortoise (*Gopherus agassizii*). Within a causal modeling framework, we investigated three factors that can influence landscape connectivity: geographic distance, barriers to dispersal, and landscape friction. A statistical model of habitat suitability for the Mojave desert tortoise, based on topography, vegetation, and climate variables, was used as a proxy for landscape friction and barriers to dispersal. We quantified landscape friction with least-cost distances and with resistance distances among sampling locations. A set of diagnostic partial Mantel tests statistically separated the hypotheses of potential causes of genetic isolation. The best-supported model varied depending upon how landscape friction was quantified. Patterns of genetic structure were related to a combination of geographic distance and barriers as defined by least-cost distances, suggesting that mountain ranges and extremely low-elevation valleys influence connectivity at the regional scale beyond the tortoises' ability to disperse. However, geographic distance was the only influence detected using resistance distances, which we attributed to fundamental differences between the two ways of quantifying friction. Landscape friction, as we measured it, did not influence the observed patterns of genetic distances using either quantification. Barriers and distance may be more valuable predictors of observed population structure for species like the desert tortoise, which has high dispersal capability and a long generation time.

Keywords Landscape genetics · Desert tortoise · *Gopherus agassizii* · Mojave desert · Least-cost-path · Isolation-by-resistance · Habitat suitability model

Introduction

Habitat fragmentation can increase isolation among populations, and isolation can increase extinction risk for many species (Crooks and Sanjayan 2006; Fischer

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Electronic supplementary material The online version of this article (doi:10.1007/s10980-010-9550-6) contains supplementary material, which is available to authorized users.

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and Lindenmayer 2007) due to demographic stochasticity, increased numbers of deterministic threats, and loss of genetic variation (Lande 1988; Saunders et al. 2001; Fahrig 2003; Henle et al. 2004; Reed 2004; Fischer and Lindenmayer 2007). Although landscape connectivity alone is usually not sufficient to ensure population persistence (Taylor et al. 2006), it does provide several clearly important means of reducing some extinction risks (Crooks and Sanjayan 2006). Among other benefits, connectivity in the landscape allows dispersal from the natal range, aids in rescue effects to prevent local extinctions, facilitates gene flow that prevents inbreeding, and fosters adequate responses to environmental change through the potential for long-term adaptation, the ability to adjust the natural distribution, and potential for recolonization after disturbance (Crooks and Sanjayan 2006).

The degree to which a landscape facilitates or impedes an organism's movement within a population depends both upon structural and functional components (Taylor et al. 1993; Brooks 2003; Taylor et al. 2006). The structural components include landscape heterogeneity that influences the habitat available to the organism, and the functional component describes the organism's response to the available habitat (Brooks 2003; Taylor et al. 2006). Quantifying both components helps us to understand how organisms move through the landscape and to identify where important habitat connections exist within the landscape. Dispersal (or some measure of movement) is one common metric to evaluate the factors that facilitate connectivity and the consequences of the amount of connectivity (Wiens 2001; Uezu et al. 2005). Inferences from genetic data have been recognized as a viable alternative to direct measurements of dispersal (Koenig et al. 1996; Waples 1998; Bohonak 1999; Brooks 2003), and a means to quantify functional connectivity (Brooks 2003; Stevens et al. 2006; Holderegger and Wagner 2008). However, gene flow only represents a subset of dispersal movements because it requires effective reproduction (Brooks 2003; Cushman et al. 2006).

Spatially explicit models and genetic data analyzed using a landscape genetics approach can be used to test specific hypotheses regarding natural levels of habitat connectivity, the influence of particular landscape features on individual movement, and the effects of habitat fragmentation (Manel et al. 2003; Keyghobadi 2007; Storfer et al. 2007). The questions addressed are species-specific, and they are constrained to the temporal and spatial scale at which individuals of a species experience their surroundings (Wiens 2001; Brooks 2003; Holderegger and Wagner 2008). Natural populations often depart from strict isolation-by-distance (Wright 1943), which occurs when the only barrier to gene flow is geographic distance and results in an average increase in genetic differentiation as geographic distance increases (Wright 1943; Slatkin 1993; Epperson 2003). Departures from isolation-by-distance suggest that additional features govern the movement of individuals, and hence the spatial genetic structure (e.g., Coulon et al. 2004; Broquet et al. 2006; Cushman et al. 2006; Epps et al. 2007). Modifying a model of straight-line distance among habitat patches to include features representing the heterogeneity of the landscape that an organism experiences could improve our understanding of landscape connectivity (Adriaensen et al. 2003; Theobald 2006).

Here, we evaluated multiple hypotheses of isolation and quantified landscape connectivity for the Mojave population of the desert tortoise (*Gopherus agassizii*). The Mojave desert tortoise is listed as threatened under the U.S. Endangered Species Act of 1973 (USFWS 1994), and tortoise habitat in this region has become fragmented by transportation corridors, utility infrastructure, and urban development over the past century (Tracy et al. 2004). Although few data exist on dispersal of desert tortoises (Morafka 1994), a recent assessment of spatial genetic structure in this long-lived species suggests that historic movement among adjacent populations has been extensive (Hagerty and Tracy 2010). Genetic differentiation among populations is small, although spatial structure is present (Hagerty and Tracy 2010). Geographic distance explains approximately 68% of the variation in genetic distance (Murphy et al. 2007; Hagerty and Tracy 2010). Nevertheless, there are natural features of the landscape occupied by desert tortoises that likely facilitate or impede movement of individuals in the landscape, and identifying these key components is important for recovery of this threatened species.

We tested hypotheses about putative causes of isolation in a causal modeling framework (Legendre 1993; Cushman et al. 2006) to assess which potential drivers of genetic structure best correlate with patterns of gene flow. Our a priori models were chosen to test specific hypotheses regarding factors that seem to be the most relevant in determining connectivity among tortoise habitat. We assessed three possible causes of isolation: (1) geographic distance, (2) dispersal barriers, and (3) landscape friction or a measure of the habitat's resistance to flow of individuals through it. Seven potential models incorporated all combinations of isolation by barriers, isolation by landscape friction, and isolation by geographic distance. The causal modeling framework allowed us to identify a single supported model among this set of competing hypotheses. Additionally, we tested each of these models with two quantifications of landscape friction that require different algorithms and assumptions: least-cost path (Adriaensen et al. 2003; Theobald 2006) and isolation-by-resistance (McRae 2006; McRae and Beier 2007; McRae et al. 2008).

Materials and methods

Study system

The Mojave desert tortoise inhabits portions of the Mojave and Colorado Deserts, spanning four states in the southwestern United States (Utah, Arizona, Nevada, and California; Germano et al. 1994). The Mojave and Colorado deserts (>160,000 km^2) are heterogeneous in climate, geology, and topography (Rowlands et al. 1982); however, habitat is relatively continuous at low-elevations (300–900 m) where the vegetation is dominated by creosote scrub (*Larrea tridentata*; Luckenbach 1982). Mojave desert tortoises most commonly occur in areas with gentle slopes, sufficient shade resources, and friable soils to allow burrow construction (Bury et al. 1994; USFWS 1994; Andersen et al. 2000).

Sampling and genotyping

Between 2004 and 2006, blood was collected from 744 desert tortoises throughout the range where the species is federally listed, which includes areas north and west of the Colorado River (Hagerty and Tracy 2010). Sampling sites included areas sampled during annual population monitoring (USFWS 2006) along randomly placed transects within critical habitat, which are the areas that are actively managed for recovery by the U.S. Fish and Wildlife Service, and systematically-placed transects outside of critical habitat areas (Hagerty and Tracy 2010). Universal Transverse Mercator (UTM) coordinates of individual locations were recorded when DNA samples were collected. Individuals were pooled into 25 sampling locations (N = 12–80), which were identified based upon geographic features such as large valleys or combinations of small, connected valleys (Fig. 1). Each of these locations can be assigned to one of seven genotype groups that were identified previously using Bayesian assignment tests (Hagerty and Tracy 2010). The geographic centroid of each sampling location was calculated by finding the central point in polygons defined for the 25 defined sampling regions in ArcGIS (ver. 9.2, ESRI, Redlands, CA, USA) and used to represent populations for further analyses (Fig. 1). The average area of the polygons was 1000 km^2 with a 50 km diameter. We determined that this size polygon was reasonable for this study because desert tortoises have been observed moving greater than 30 km in a single foray (Edwards et al. 2004).

The 20 microsatellites used in this study were loci originally developed for *G. polyphemus* (GP15, GP30, GP61; Schwartz et al. 2003), the Sonoran population of *G. agassizii* (GOAG3, GOAG4, GOAG7; Edwards et al. 2003), and the Mojave population of *G. agassizii* (14 markers; Hagerty et al. 2008). Specific conditions for amplification and fragment analysis are described in detail elsewhere (Hagerty et al. 2008; Hagerty and Tracy 2010). We amplified the microsatellites and completed fragment analysis in collaboration with the Nevada Genomics Center (http://www.ag.unr.edu/Genomics/). All alleles were scored with GeneMapper 5.0 (Applied Biosystems, Inc., Foster City, CA, USA).

The microsatellite loci did not deviate from Hardy–Weinberg proportions and did not exhibit significant linkage disequilibrium (Hagerty and Tracy 2010). Loci exhibited high gene diversity and allelic richness (Hagerty and Tracy 2010). We calculated pair-wise genetic distance measures for the 25 sampling locations: $F_{ST}/(1 - F_{ST})$ (as recommended by Rousset (1997)) using pair-wise F_{ST} values from FSTAT (Goudet 1996), the genotype likelihood ratio (D_{LR}; Paetkau et al. 1997) in DOH (Paetkau et al. 1997), and Nei's standard genetic distance D_S (Nei

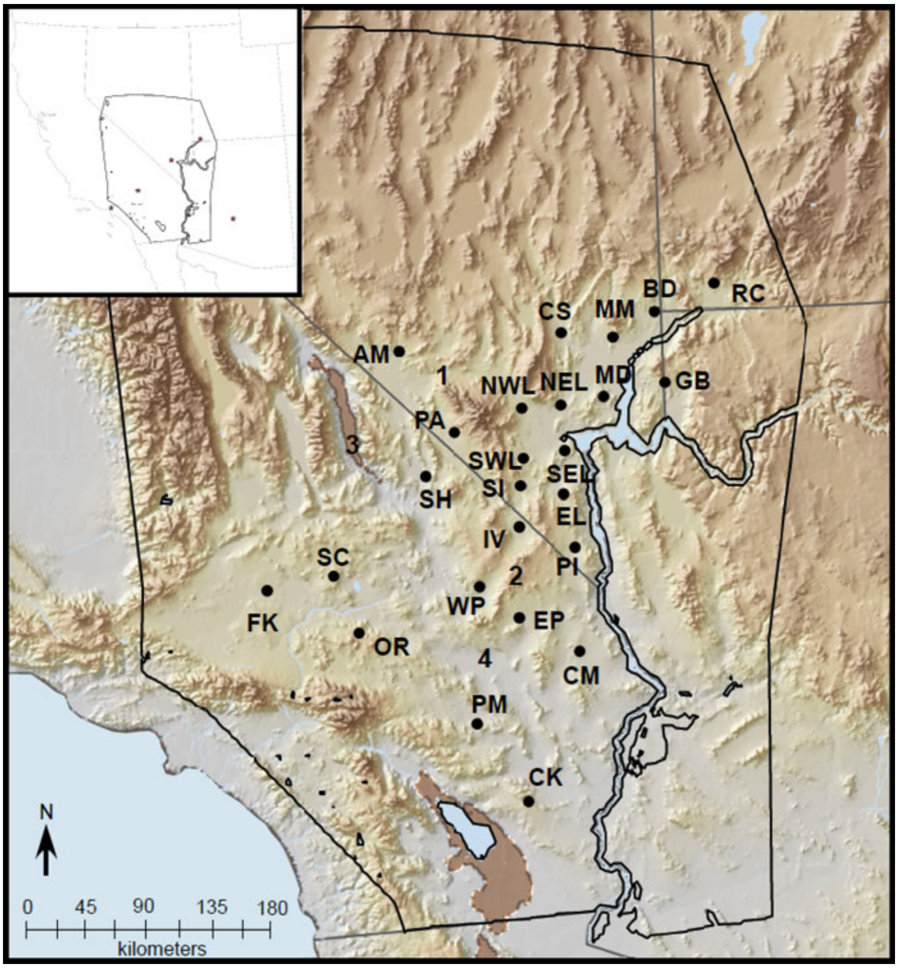

Fig. 1 Map of the sampled locations for landscape genetics of the Mojave desert tortoise. The *thick black line* designates the outline of the coverage of the habitat model. State outlines are designated as *grey lines*. The center for each of the 25 sampling locations are shown as *black dots* and are identified as follows: RC (Red Cliffs Desert Reserve, UT), Beaver Dam Slope (NV, UT), MM (Mormon Mesa, NV), GB (Gold Butte, NV), MD (Muddy Mountains, NV), CS (Coyote Springs, NV), NEL (Northeast Las Vegas, NV), NWL (Northwest Las Vegas, NV), AM (Amargosa Desert, NV), PA (Pahrump, NV), SH (Shadow Valley, CA), IV (Ivanpah, CA), WP (West Providence Mountains, CA), SI (South I-15 corridor—Sloan, Jean, Roach, NV), SWL (Southwest Las Vegas Valley, NV), SEL (Southeast Las Vegas, NV), EL (Eldorado Valley, NV), PI (Piute Valley, NV), CM (Chemehuevi Valley, NV), EP (East Providence Mountains, CA), CK (Chuckwalla Bench, CA), PM (Pinto Mountains, CA), OR (Ord-Rodman Valleys, CA), SC (Superior-Cronese Valleys, CA), FK (Fremont-Kramer Valleys, CA). Major topographic features include: (1) Spring Mountains, (2) New York and Providence Mountains, (3) Death Valley, and (4) Cadiz Valley. The Baker Sink begins near “3” and ends near “4”

1972) in Tools for Population Genetic Analysis (TFPGA; Miller 1997). Results were similar among all genetic distance measures, so we only report analyses using D_{LR} (Supplementary material). We also calculated pair-wise Euclidean distances (m) as a measure of straight-line geographic distance between pairs of the centroids of our sampling locations in ArcGIS (ver. 9.2, ESRI, Redlands, CA, USA).

Statistical model of suitable habitat

We identified levels of landscape friction with a model of the distribution of potential habitat in space (Wang et al. 2008) instead of the approach that uses expert opinion or ad hoc measures using environmental variables (Adriaensen et al. 2003; Verbeylen et al. 2003; Broquet et al. 2006; Theobald 2006; McRae and

Beier 2007). The implicit assumption is that a model of habitat suitability is a valid approximation for landscape permeability to dispersal (Broquet et al. 2006; Epps et al. 2007; Wang et al. 2008). We developed a model of habitat suitability using the presence data (15,311 observations) and environmental layers described in Nussear et al. (2009). We used 12 environmental variables to predict the presence of the Mojave desert tortoise throughout their geographic range. The environmental data consisted of various GIS layers of vegetation, topography, soils and precipitation (Table 1). Tortoise presence points were aggregated into a 1 km^2 grid where one or multiple locations per km^2 indicated presence of tortoises. The total number of number of presence points was reduced to 6,350 grid cells containing tortoises. Environmental layers were calculated at a 1 km^2 scale either directly (e.g., precipitation) or using an area-weighted average for each 1 km^2 cell (e.g., elevation). The number of environmental layers was reduced from an initial set of 16 GIS layers (Nussear et al. 2009) using AIC ranking (Burnham and Anderson 2002) in a bi-directional, stepwise model-ranking process (Lehmann et al. 2002). A Generalized Regression Analysis and Spatial Prediction (GRASP) modeling algorithm (Lehmann et al. 2002) was used to build the model using 80% of the points (5,080), and the remaining 20% of the points (1,270) were used for model evaluation. Model performance was evaluated using receiver-operating characteristics (ROC) that were calculated using the ROCR package (Sing et al. 2005) in R (R Development Core Team 2009). The 12-variable model had a high AUC (area under the ROC curve) test score (0.92) and had a significant Pearson's correlation coefficient of 0.75 ($P < 0.001$), indicating a substantial agreement between the predicted habitat and the observed presence of desert tortoises in the testing set. The resulting predictive model of Mojave desert tortoise occurrence was represented by a floating-point value ranging from 0 to 1, which we defined as suitability of tortoise habitat in each cell. We used this model of tortoise occurrence to create a cost surface for the isolation by landscape friction model. Thus, cells of lower potential habitat would reduce the ability to traverse the landscape. The cost surface was calculated by subtracting each cell value from 1.

We also created a binary representation of habitat suitability by classifying habitat suitability as a binary distribution where 1 equaled habitat and 0 equaled non-habitat by using a threshold that included 99% of all known presence cells (using a model value >0.125). Cells that were non-habitat were coded as "no data" in the binary cost surface, which caused those cells to be complete barriers to movement. This binary model was used as our isolation by barriers model because it designated places that would not be considered tortoise habitat, but explicitly allowed tortoises to move across all other cells without friction.

Table 1 Variables used to model potential habitat for the Mojave desert tortoise (Nussear et al. 2009)

Category	Variable	Data layer description	Source
Topography	Elevation	30 m DEM	Wallace and Gass (2008)
	Slope	Derived from 30 m DEM	Wallace and Gass (2008)
	Northness (aspect)	Derived from 30 m DEM	Wallace and Gass (2008)
	Average surface roughness	Derived from 30 m DEM	Wallace and Gass (2008)
	Percent smoothness	Derived from 30 m DEM	Wallace and Gass (2008)
Soils	Average bulk density		STATSGO database; Bliss (1998)
	Depth to bedrock		STATSGO database; Bliss (1998)
	Average percentage of rocks	>254 mm B-axis diameter	STATSGO database; Bliss (1998)
Vegetation	Perennial plant cover		Wallace et al. (2008)
	Annual plant proxy		Wallace and Thomas (2008)
Climate	Mean dry season precipitation	30 year normal period (1961–1990) May–October	Blainey et al. (2007)
	Mean wet season precipitation	30 year normal period (1961–1990) November–April	Blainey et al. (2007)

We analyzed the resulting cost surfaces with the centroids of the 25 tortoise sampling locations using least-cost-path and isolation-by-resistance as quantifications of landscape friction. The area covered by the GRASP model included the entire area sampled for population genetics, and the Colorado River was included as an absolute barrier in all models (Fig. 1; Nussear et al. 2009).

Quantifying landscape friction: least-cost path

Least-cost-path analyses are used to estimate a least-cost distance between habitat patches (Adriaensen et al. 2003; Theobald 2006). The least-cost distance is a modified Euclidean distance that uses landscape friction to determine a more ecologically-relevant path between patches (Verbeylen et al. 2003; Theobald 2006). Typically, least-cost distance is calculated using a cost-weighted function (cost associated with moving across a cell). The least-cost path for each pair of locations was quantified with the cumulative cost across all cells while moving from location A to B in GRASS GIS (ver. 6.3; GRASS Development Team 2008). We plotted the least-cost path between each of the 25 sampling locations in ArcGIS (ver. 9.2, ESRI, Redlands, CA, USA).

Quantifying landscape friction: isolation-by-resistance

Isolation-by-resistance is based in circuit theory, and uses a graph theoretic approach to predict movement patterns and quantify the effects of certain landscape features (McRae 2006; McRae et al. 2008). The edges between nodes (or locations) in the graph network are represented as analogs to resistors in an electrical circuit and the same basic concepts apply (i.e., Ohm's Law; McRae et al. 2008). Resistance distance is a measure of isolation that is similar to the least-cost distance; however, the resistance distance decreases as the number of available pathways between locations increases (McRae et al. 2008). In addition to integrating connectivity across all possible paths, the resistance distance assumes that the disperser does a random walk between points, basing each movement on the relative quality of the habitat in all directions. When the movement corresponds to gene flow, which operates on a different spatio-temporal scale, the surrogate is migration rate per generation (McRae 2006).

We calculated resistance distance between all pairs of desert tortoise locations in Circuitscape (ver. 3.4; McRae and Shah 2009). For our models, the habitat suitability in each grid cell was treated as a conductance value (the inverse is resistance). Circuitscape provided a pair-wise resistance distance matrix as well as a cumulative (additive among pairs) current map, representing the expected probability of movement for random walkers, which we viewed in ArcGIS (ver. 9.2, ESRI, Redlands, CA, USA).

Causal modeling framework and Mantel tests

To evaluate geographic distance, barriers, and landscape friction in a causal modeling framework (Legendre 1993; Cushman et al. 2006), we identified the diagnostic expectations for each of the seven possible hypotheses of causal relationships (Table 2). Diagnostic expectations for each model included a specific set of partial correlations to be statistically significant or not (Table 2). For example, under the distance only model, geographic distance would have a significant positive correlation with genetic distance after parsing out the barrier or landscape-friction matrix (Table 2). Under the same model, the barrier and landscape-friction matrices would not be significantly correlated to genetic distance after parsing out geographic distance (Table 2). Then, we compared the statistical relationship between genetic distance and each model (Legendre 1993; Cushman et al. 2006). We determined a single supported model by testing each factor against the competing factors and then evaluating the combined results. The hypothesis with the most support should meet all of the diagnostic expectations associated with that hypothesis, providing a rigorous evaluation of the potential factors that impede gene flow (Table 2).

We completed Mantel tests (Mantel 1967) and partial Mantel tests (Smouse et al. 1986) in Program R using the "vegan package" (Oksanen et al. 2007). A Pearson product-moment correlation was calculated, and we determined significant correlations by using a permutation test with 10,000 replicates. We used the Monte Carlo *P*-value to determine significant simple and partial Mantel correlations, but only used them to determine which diagnostic expectations were met for each model. These actions reduced the chance of bias in our interpretations, and they address some of the criticisms of partial Mantel tests

Table 2 Evaluation of the isolation hypotheses using two quantifications of landscape friction: least-cost path (LCP) and isolation-by-resistance (IBR)

Partial Mantel	Diagnostic expectations and model support													
	Distance only		Barrier only		Landscape only		Distance and barrier		Distance and landscape		Landscape and barrier		Distance, landscape, barrier	
	LCP	IBR*	LCP	IBR	LCP	IBR	LCP*	IBR	LCP	IBR	LCP	IBR	LCP	IBR
DG.B	**>0**	**>0**	NS	NS	NA	NA	**>0**	**>0**	**>0**	**>0**	NS	NS	**>0**	**>0**
DG.L	**>0**	**>0**	NA	NA	NS	NS	**>0**	**>0**	**>0**	**>0**	NS	NS	**>0**	**>0**
BG.D	NS	**NS**	**>0**	>0	NA	NA	**>0**	>0	NS	**NS**	**>0**	>0	**>0**	>0
BG.L	NA	NA	**>0**	**>0**	NS	NS	**>0**	**>0**	NS	NS	**>0**	**>0**	**>0**	**>0**
LG.B	NA	NA	**NS**	**NS**	>0	>0	**NS**	**NS**	>0	>0	>0	>0	>0	>0
LG.D	**NS**	**NS**	NA	NA	>0	>0	**NS**	**NS**	>0	>0	>0	>0	>0	>0

The diagnostic expectations (partial Mantel test and the expected significance value) for each hypothesis are listed. *D* distance, *B* barrier (binary habitat model), *L* landscape (continuous habitat model), *G* genetic distance (D_{LR}), *NS* not significant, >0 = *P*-value below 0.05, *NA* not applicable. A period separates the main matrices on the left from the covariate matrix on the right that is partialed out in the partial Mantel test. For example, DG.B is a partial Mantel test between the distance, and the genetic distance matrices with the barrier matrix partialed out. Model support is indicated with bold type based upon the *P*-value for each partial Mantel test compared to the diagnostic expectations. Refer to Table 3 for the exact *P*-values for each partial Mantel test

* The hypothesis with the most support

(Raufaste and Rousset 2001; Rousset 2002, but see Castellano and Balletto 2002; Balkenhol et al. 2009).

Results

Mantel correlations

Euclidean distance correlated significantly with pairwise genetic distance, as evidenced by a significant Mantel correlation (Table 3). Additionally, least-cost distances and resistance distances for the landscape-friction and barrier models were correlated significantly with genetic distances between pairs of sampling locations (Table 3). However, the simple Mantel correlations were lower for the resistance-distance matrices (Table 3).

Causal modeling and partial Mantel tests

The hypothesis of isolation with the most support varied depending on the quantification of landscape friction (Table 2). Using least-cost distances, the barrier and distance model was fully supported by all the statistical expectations. Using resistance

Table 3 Mantel and partial Mantel correlations (*r*) between spatial and genetic pairwise distances among 25 sampling locations

Mantel or partial Mantel test	Least-cost distance		Resistance distance	
	r	*P*-value	*r*	*P*-value
DG	0.821	**0.0001**		
BG	0.820	**0.0001**	0.467	**0.0001**
LG	0.738	**0.0001**	0.351	**0.0001**
DG.B	0.194	**0.0300**	0.766	**0.0001**
DG.L	0.537	**0.0001**	0.806	**0.0001**
BG.D	0.188	**0.0250**	−0.094	0.7900
BG.L	0.339	**0.0004**	0.580	**0.0001**
LG.B	−0.256	0.9930	−0.507	0.9900
LG.D	−0.077	0.7740	−0.241	0.1940

Spatial distances are resistance distance or least-cost distance using the cost surface from the habitat model. The Mantel test statistic *r* is based on a one-sided Pearson's product-moment correlation and significance values are based on 10,000 permutations. *D* distance, *B* barrier (binary habitat model), *L* landscape (continuous habitat model), *G* genetic distance (D_{LR}). A period separates the main matrices on the left from the covariate matrix on the right that is partialed out in the partial Mantel test. For example, DG.B is a partial Mantel test between the Euclidean distance and the genetic distance matrices with the barrier distance matrix partialed out. Bold values indicate *P*-values < 0.05

distances, the distance model was fully supported (Table 2). The outcome of the BG.D partial Mantel test was the main difference between the two landscape friction quantifications, causing the barrier and distance model to not be fully supported using resistance distances (Tables 2, 3). The landscape-friction component of all hypotheses had no support based on the diagnostic expectations (Tables 2, 3).

The cumulative, least-cost paths across the 25 locations were similar in the landscape-friction and barrier models (Fig. 2). The paths for both models did not include large areas of unsuitable habitat such as the northwest corner of the range and major mountain ranges such as the Spring Mountains (Fig. 2). The barriers were apparent in both models, however, the lack of a gradient across other habitat in the barrier model made individual paths between locations more direct, making them more similar to the Euclidean distance (not shown). Similar barriers and habitat corridors were visible in the isolation-by-resistance maps (Fig. 3) when compared to the least-cost-path maps (Fig. 2). Mountain ranges (e.g., Spring, New York, Providence, and Sheep Ranges) and low elevation areas (Death and Cadiz Valley) had no current flow (Fig. 3). The northeastern portion of the desert tortoise's range in Nevada and into California,

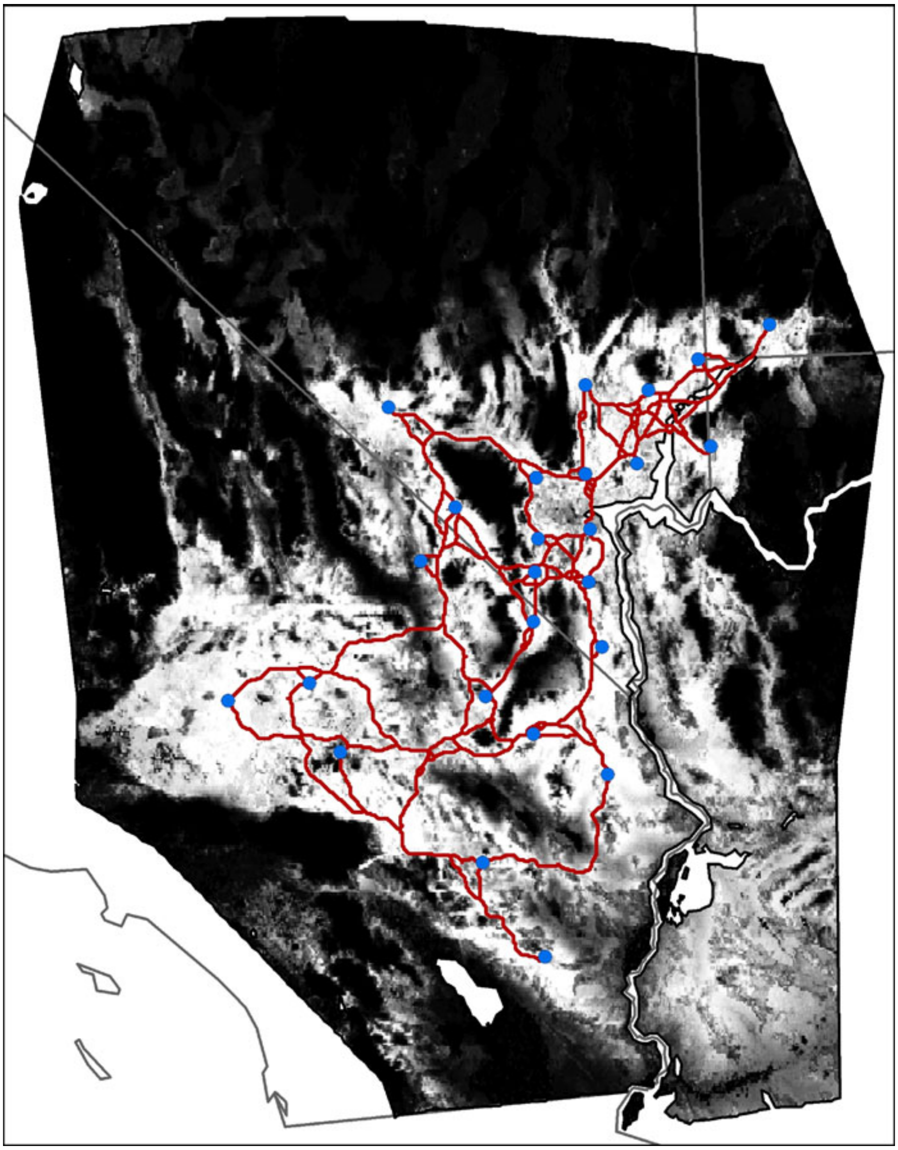

Fig. 2 Distribution of desert tortoise habitat in the Mojave Desert predicted using the 12-variable GRASP model in Program R and the cumulative least-cost path using the 25 pair-wise population comparisons. Gradient of *grey* (floating values) indicate probability of desert tortoise occurrence. *Black* indicates lowest probability (0) while *white* indicates highest probability (1). *Red lines* indicate least-cost paths between pairs of sampling locations. *Blue dots* represent the 25 population centroids

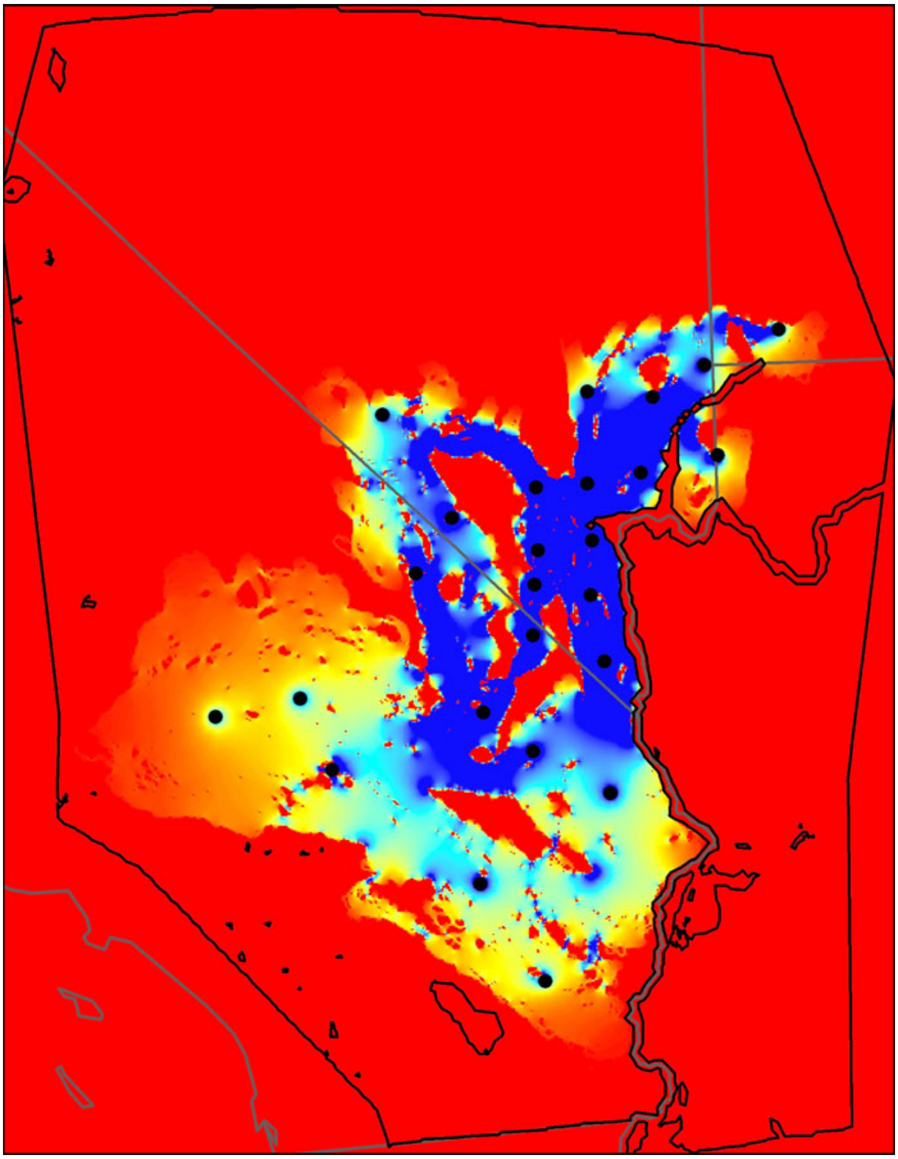

Fig. 3 Cumulative current maps between pairs of populations from the isolation-by-resistance models using the binary 12-variable habitat model (barrier). The gradients of colors indicate the probability of desert tortoise movement, with *red regions* indicating no current, *yellow* and *orange regions* representing low current, and *blue regions* representing high current. *Black dots* represent the 25 population centroids

mainly through Las Vegas valley, along the Colorado River, and regions between mountain ranges, contained areas of very high current density (Fig. 3). In contrast, natural barriers did not fragment habitat within California and had more diffuse current flow between sampling locations (Fig. 3).

Discussion

We evaluated hypotheses about isolation among populations of the Mojave desert tortoise in a causal modeling framework to determine which factors most likely limit gene flow. Hypotheses included combinations of three factors: geographic distance, dispersal barriers, and landscape friction. We identified geographic distance and dispersal barriers as dominant factors associated with genetic structure, while landscape friction, as we defined it, had little to no little influence.

Previously, the desert tortoise was identified as a model organism for studying isolation-by-distance (Edwards et al. 2004). Straight-line distances among locations of desert tortoises strongly correlates with genetic distances, suggesting that dispersal distance is a major factor shaping genetic structure among, and within, populations (Edwards et al. 2004; Murphy et al. 2007; Hagerty and Tracy 2010). Our data supported these previous assertions, which is an unusual circumstance for natural populations. For a majority of terrestrial species, straight-line distances are correlated only weakly with genetic distance (e.g., Vos et al. 2001; Coulon et al. 2004; Broquet et al. 2006; McRae and Beier 2007). However, genetic distance correlates well with geographic distance at a landscape scale for some terrestrial turtles and tortoises (e.g., Howeth et al. 2008).

Dispersal barriers also were correlated with genetic distance, and the distance and barriers hypothesis was the best-supported model with the least-cost distance quantification. Therefore, dispersal distance may not be the only factor impeding gene flow. Gene flow among desert tortoise populations is at least partially restricted by large topographic features such as high-elevation mountain ranges (e.g., Spring Mountains, New York Mountains, Providence Mountains) and very low elevation regions (e.g., Death Valley, Cadiz Valley; Fig. 1). These apparent elevation barriers are visible in the maps of landscape friction (Figs. 2, 3) and elevation explained a high proportion of the variance in tortoise presence in the habitat model (Nussear et al. 2009). Elevation appears to be an important determinant of these partial barriers, but it is an indirect measure of several variables, including thermal environment, soil type, and vegetation assemblages (e.g., Nagy and Medica 1986; Germano et al. 1994; Zimmerman et al. 1994; Andersen et al. 2000; Nussear 2004). Thus, areas with extremely high or low elevations likely impose thermal constraints that we were unable to model directly, provide suboptimal vegetative cover, and physically impair movements.

Due to one diagnostic expectation, barriers appeared not to affect genetic structure with the resistance-distance quantification. Differences between the quantifications of landscape friction could explain this result. Most importantly, when more than one pathway is available to traverse the landscape or the size of the path increases, the resistance distance effectively decreases, but the least-cost distance does not (McRae et al. 2008). The redundancy in habitat corridors may have reduced resistance (friction) enough that the barriers were no longer correlated with genetic distance between sampling locations of desert tortoises. The underlying assumptions of the algorithm are also different. The least-cost-path algorithm, which is an overall measure of landscape friction, assumes that a disperser has complete knowledge of the landscape as it chooses the "preferred" route (McRae et al. 2008), though the feasibility of the route is not considered (Adriaensen et al. 2003). The isolation-by-resistance algorithm assumes that the disperser is equivalent to a random walker that chooses a direction for each step based only on the relative quality of the habitat in the adjacent directions, allowing the potential for wandering (McRae et al. 2008). However, it is important to recall that we investigated how the landscape influences migration rates per generation across a large geographic area, not individual dispersers among habitat patches. In this case, we can interpret the optimal path (s) as proportionally increasing the amount of gene flow.

The differences between the two quantifications can be compared by regression of the residuals from linear regressions of the friction measures against Euclidean distance. Individual comparisons with higher least-cost distances compared to the Euclidean distance (higher residuals) are locations that are separated by large mountain ranges. For example, the South I-15 corridor (SI) and Pahrump (PA) are separated by approximately 66 km straight-line distance, but are also separated by the Spring Mountains. These locations have a pair-wise F_{ST} of 0.023 (Hagerty and Tracy 2010). In contrast, two locations with an equivalent straight-line distance that are not separated by a mountain range (Amargosa Desert and Pahrump) have a pair-wise F_{ST} value of 0.009 (Hagerty and Tracy 2010). This example illustrates why the barriers and distance hypothesis was supported by the diagnostic expectations with the least-cost distance. However, individual comparisons with higher resistance distances compared to the Euclidean distance (higher residuals) are locations that are separated by "pinch points," or areas with very narrow habitat corridors that increase the resistance distance. For example, high resistance distances are connected to locations such as Red Cliffs Desert Reserve (RC), which has a very narrow area of habitat that connects it to the rest of the range (Fig. 3). These narrow habitat corridors appear to drive the results for isolation-by-resistance. Multiple habitat corridors that circumvent the mountain barriers reduce the resistance, and could explain the reduction in support for the barriers and distance hypothesis.

We did not find any support for the hypothesis that landscape friction per se causes isolation for Mojave desert tortoises and there are several potential reasons for this. First, friction accumulates with distance, so isolation-by-distance may dominate the explained variance, thus masking additional resistance. Second, our landscape variables may be insufficient to capture the factors influencing the movement of tortoises through the landscape, although they are good predictors of tortoise presence. Quantifying landscape friction relies on relevant landscape variables, which accurately reflect the cost of dispersal for the individual at the appropriate temporal and spatial scale (Balkenhol et al. 2009). Therefore, the effectiveness of the approach depends upon success in modeling landscape friction (Holderegger and Wagner 2008). Our chosen landscape variables, which describe desert tortoise habitat in the present, also may not capture the appropriate temporal scale to explain the genetic population structure (Balkenhol et al. 2009). Further, we used statistical habitat models (Austin 2002; Lehmann et al. 2002), where the chosen variables were predictors of tortoise habitat suitability, and used as a proxy for landscape friction. Thus, the cost surfaces from the habitat suitability model may only reflect habitat use and not the cost of dispersal (Epps et al. 2007).

Another potential explanation for the lack of support for landscape resistance is that the processes that influence movement at finer spatial and temporal scales may not impact observed, broad scale patterns of population structure (Lee-Yaw et al. 2009). Although heterogeneity in variables such as annual and perennial vegetation and precipitation likely influence daily, seasonal, and annual movements of tortoises, these variables provided little explanation for the patterns of genetic structure that we observed at the regional level. The effects of landscape variables may be limited at these broader spatial scales, especially for species with strong dispersal capabilities that have multiple avenues for gene flow (Lee-Yaw et al. 2009). At the regional scale, desert tortoise habitat had considerable redundancy in habitat corridors, which may reduce the impact of any high resistance areas at a local scale (Fig. 3). The most influential features in this system are likely absolute barriers to dispersal such as the Colorado River, which separates the Mojave and Sonoran populations of the desert tortoise (Murphy et al. 2007).

Our study reinforces the hypothesis that habitat within the Mojave population of the desert tortoise was well connected. We can deduce from the *F*-statistics and assignment tests that gene flow among adjacent populations within the Mojave and Colorado Deserts was relatively high, at least historically (Hagerty and Tracy 2010). Las Vegas Valley was hypothesized previously to be a transitional corridor between the northern and southern reaches of the geographic range (Britten et al. 1997; Hagerty and Tracy 2010). We detected habitat corridors in Las Vegas Valley, and along the foothills of the New York and Providence Mountains (Fig. 3). In comparison to the northeastern Mojave Desert, habitat in the southwestern portion of the range is more continuous and has few "pinch points" that indicate important, restricted habitat corridors (i.e., low habitat redundancy). The Baker Sink is a low-elevation barrier that begins in Death Valley and separates these topographically different areas (Fig. 1).

Despite inferring the existence of partial barriers, gene flow was most likely possible through local interactions over many generations. Therefore, most, if not all, dispersal barriers were permeable over the long temporal scale at which tortoise population dynamics likely occur. Genetic exchange and dispersal are population-level processes, which occur over long temporal scales from decades to centuries, especially for species with long generation times (Brooks 2003; Keyghobadi 2007). Thus, our models are best used for addressing large-scale patterns of gene flow that were present for generations, not the nuances of dispersal over short time scales (McRae 2006; Epps et al. 2007; Lee-Yaw et al. 2009).

Our modeling cannot address any present day barriers to gene flow for the Mojave desert tortoise. For species with long generations times (such as the desert tortoise), detecting the effects of recent habitat fragmentation may be difficult, even when using variable molecular markers (Keyghobadi 2007, though see Murphy et al. 2008). Indeed, any changes in gene flow that have occurred over the past century, such as the construction of major highways, are likely not yet visible with microsatellite markers because the generation time for a desert tortoise is estimated to be 25 years (USFWS 1994; Hagerty and Tracy 2010). However, evidence exists that roads can cause changes in genetic structure with sufficient time (e.g., Vos et al. 2001; Epps et al. 2005), and in some cases as few as five generations (Murphy et al. 2008). We can hypothesize that fragmentation of the Mojave Desert has altered the natural patterns of dispersal and gene flow for this species, which we began to uncover in this study. Future work should include tests of the effects of fragmentation and modeling to predict any resulting genetic effects.

Acknowledgments The Clark County Multi-Species Habitat Conservation Plan and the U.S. Fish and Wildlife Service supported this research. Sample collection was permitted by the USFWS (TE-076710), NDOW (S 24403), CADFG (SC-007374), UDWR (5BAND6646), and the UNR IACUC (A03/04-12, A05/06-23). We thank F. Sandmeier and technicians from the University of Nevada, Reno, the Student Conservation Association, and Kiva Biological for helping with sample collection. We thank V. Kirchoff and the Nevada Genomics Center (NIH Grant P20 RR016463) for helping to genotype individuals. BH McRae provided helpful technical support and advice on the connectivity modeling. Members of the FWS Desert Tortoise Recovery Office were helpful sounding boards for ideas, and facilitated research that provided data for this study. We thank G Hoelzer, MM Peacock, LC Zimmerman, H Wagner and two anonymous reviewers for helpful comments on previous drafts of this manuscript. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

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