

## Translocation Relative to Spatial Genetic Structure of the Mojave Desert Tortoise, *Gopherus agassizii*

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**ABSTRACT.** – Mojave desert tortoises (*Gopherus agassizii*) have been translocated for decades, and research-oriented translocations recently have been recommended as a tool to help recover this threatened species. However, avoiding negative genetic impacts from wildlife translocations has been widely cautioned. Populations of the Mojave desert tortoise within a 200–276-km straight-line radius of each other (249–308 km measured around topographic barriers) tend to be genetically correlated and may be considered single genetic units for management purposes. When planning translocations among wild populations, releasing tortoises at recipient sites within a straight-line distance of 200 km from the source population would most conservatively maintain historic genetic population structure. However, the risk of causing outbreeding depression by inadvertently translocating Mojave desert tortoises between more distant populations or those of unknown provenance is low.

**KEY WORDS.** – Reptilia; Testudines; population structure; genetic provenance; outbreeding depression

Wildlife translocations have been increasingly used for conservation (Fischer and Lindenmayer 2000; Germano and Bishop 2009). In the face of loss of biodiversity, inadequate resources, and a lack of will to make difficult socio-economic decisions necessary to protect existing biodiversity from effects of human population growth and development, translocation has become an important conservation tool that can be used to conserve evolutionary processes in addition to conserving individual taxa (Moritz 1999). The rate at which wildlife translocations have been implemented has increased to the point that an entire book is now dedicated to improving the practice (Ewen et al. 2012). A complicated myriad of factors influence the success of translocations, including presence of threats that may have caused the original decline of the target population; habitat, demographic, and biophysical constraints; disease transmission; social structure; and movement and settlement rates (Berry 1986; Dodd and Seigel 1991). Additionally, minimizing genetic mixing to prevent outbreeding depression has been recommended when conducting a translocation (Burke 1991; Reinert 1991; Edmands 2007; Murphy et al. 2007). However, although translocation could potentially cause harm by reversing positive impacts of local adaptation via outbreeding depression (Edmands 2007), consideration of population genetics may have positive impacts on the success of translocations by preventing inbreeding and increasing genetic diversity within target populations (Bouzat et al. 2009). Overall, the genetic risks from translocation may have been overstated, thereby constraining management options (Frankham et al. 2011; Weeks et al. 2011).

Translocation of Mojave desert tortoises (*Gopherus agassizii*) has occurred for decades, often with little planning or monitoring (Murphy et al. 2007). It has been increasingly applied as a “rescue” measure to minimize population impacts caused by development projects occurring within desert tortoise habitat (e.g., Mullen and Ross 1997; Field et al. 2007). Although the survival and integration of translocated tortoises, particularly in early, long-distance cases, into resident populations have been questioned, these translocations provide one of multiple hypotheses to explain observed deviations in some populations from Hardy-Weinberg equilibrium, increased heterozygosity, or other genetic anomalies that could compromise the genetic integrity of the population (Murphy et al. 2007; Edwards and Berry 2013).

Recent translocations of the Mojave desert tortoise have resulted in short-term success as measured by movements, home range, reproduction, physiological stress, and survival relative to that of resident or control tortoises (Field et al. 2007; Esque et al. 2010; Drake et al. 2012; Nussear et al. 2012). However, long-term success remains to be measured by metrics such as recruitment into the adult population at the translocation site as a result of successful reproduction (Germano and Bishop 2009). While long-term success remains to be determined, managers continue to be faced with decisions to move tortoises from the path of development and must make decisions in light of both recent successes and documented risks (e.g., US Fish and Wildlife Service 2011a). More recently, translocation within a research-oriented framework has been recommended as a tool to augment depleted populations (US Fish and Wildlife Service 2011b).

Current applications of translocation of desert tortoises fall within the categories of augmentation or reinforcement (movement of individuals into a population of conspecifics) or reintroduction (movement into a part of the historical range from which the species has disappeared), rather than introduction (movements outside the historical range; Weeks et al. 2011; International Union for Conservation of Nature/Species Survival Commission [IUCN/SSC] 2013). In this article, we do not consider introductions of desert tortoises outside their historical range, but focus on augmentations or reintroductions, which are used to increase population sizes to avoid or recover from stochastic loss of small populations. From a genetic perspective, augmentations or reintroductions of desert tortoises may be classified as genetic rescues or genetic restorations (Weeks et al. 2011). These translocations can counter the expression of deleterious genes in small populations through the introduction of new genes (genetic rescue), or they can increase levels of genetic variation and adaptive potential (genetic restoration) (Hedrick 2005; Bouzat et al. 2009; Hedrick and Fredrickson 2010).

Although dispersal ecology of desert tortoises is not well understood (Morafka 1994), adult individuals have been known to move long distances (e.g., > 30 km for the closely related Sonoran desert tortoise, *Gopherus morafkai*; Edwards et al. 2004). Historically, habitat of the Mojave desert tortoise was well connected, and gene flow among adjacent populations within the Mojave and Colorado deserts was relatively high (Murphy et al. 2007; Hagerty and Tracy 2010; Hagerty et al. 2011). For example, the Las Vegas Valley has been hypothesized to be a transitional corridor between the northern and southern reaches of the geographic range (Britten et al. 1997; Hagerty and Tracy 2010). Habitat in the southwestern portion of the range is more continuous than in the northeastern Mojave Desert and has few “pinch points” or restricted habitat corridors (Hagerty et al. 2011).

Even though advances in molecular techniques have improved the ability to describe genetic structure of wildlife populations, defining discrete units for conservation purposes has been problematic for species with continuous distributions (Diniz-Filho and Telles 2002). Guidance on translocation issued by the IUCN specifies that translocated individuals should show “genetic provenance” relative to the recipient, wild population and that captive individuals should have “appropriate” genetics (IUCN/SSC 2013), but specific guidelines for determining genetic appropriateness are lacking. Such is the case for the Mojave desert tortoise. Even though various genetic groups have been identified (Murphy et al. 2007; Hagerty and Tracy 2010), these groups vary depending on sampling designs and locations, markers used, and resolution of analysis. In addition, high gene flow historically occurred between identified genetic

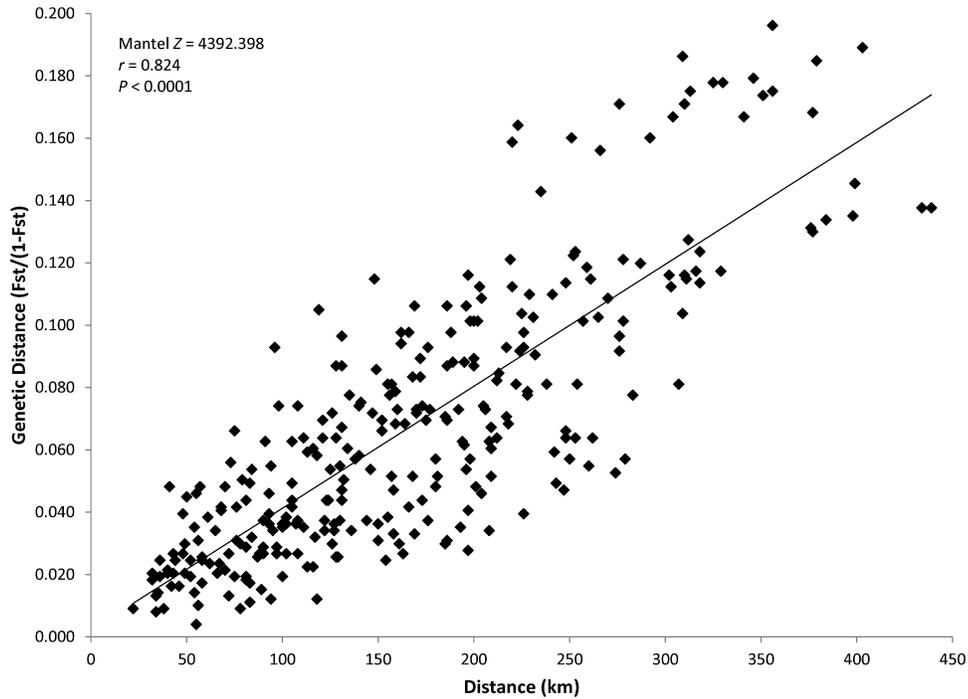
groups, which are not defined by discrete boundaries (Hagerty 2008).

We investigated proactively the scale at which translocations would have the least impact on the genetic composition of Mojave desert tortoise populations. Spatial autocorrelation analysis provides a useful technique to establish geographic distances within which continuously distributed populations may be considered a single genetic unit (Diniz-Filho and Telles 2002). We applied such an analysis to population genetic data from the Mojave desert tortoise to provide managers with guidance on the distance within which individual tortoises can be moved between populations for population augmentation or reintroduction purposes. We also specifically discuss the risks of outbreeding depression relative to the potential of releasing tortoises of distant origin to new populations.

## METHODS

We reanalyzed data from Hagerty and Tracy (2010) regarding variation of 20 microsatellite loci among 25 sampling locations distributed across the range of the Mojave desert tortoise. Genetic and geographic distances among sampling locations were correlated strongly (Fig. 1; Hagerty and Tracy 2010). We performed a Mantel spatial autocorrelation analysis of the pairwise genetic distances ( $F_{ST}/[1 - F_{ST}]$ ; Rousset 1997) and Euclidian geographic distances using the computer program PASSaGE 2 (Rosenberg and Anderson 2011). Spatial autocorrelation is an analysis tool used to identify patterns of genetic similarity, and the intercept is particularly valuable for distinguishing groups of individuals that can be considered demographically independent (Peakall et al. 2003; Double et al. 2005). Samples at geographic distances lower than the intercept in spatial autocorrelograms, particularly in stabilizing correlograms (those that show a sharp drop across the intercept before leveling), can be considered a single genetic unit for conservation (Diniz-Filho and Telles 2002). Genetic units at scales within the intercept distance are too small to be considered genetically independent (Diniz-Filho and Telles 2002).

The capacity to detect spatial structure is dependent on the true extent of genetic structure, the distance classes chosen for the analyses, and the sample size per distance class (i.e., number of pairwise comparisons within the distance class; Peakall et al. 2003). We performed analyses using 6, 10, and 15 distance classes with approximately equal numbers of pairs of sampling locations per distance class to ensure that choice of distance class size had no effect on analysis results (cf. Miller et al. 2006; Table 1). We used a randomization procedure of 10,000 replicates to identify distance classes where average genetic distances were significantly different than expected. We repeated the analysis using pairwise least-cost path distances with data from a



**Figure 1.** Relationship between genetic distance [ $F_{ST}/(1 - F_{ST})$ ] and Euclidean geographic distance (km) for pairwise comparisons of sampling sites ( $n = 25$ ) across the range of *Gopherus agassizii*.

landscape genetics study by Hagerty et al. (2011), which take into account habitat probability and barriers to gene flow (Nussear et al. 2009), given the role topographic features have played in genetic structuring of Mojave desert tortoise populations (Hagerty et al. 2011).

**RESULTS**

We detected significant spatial genetic autocorrelation when we tested all the individuals in our data set as a single population (Fig. 2). In both single-population tests, the strongest correlation between geographic and genetic distance occurred at the smallest distance classes. The autocorrelation coefficient gradually decreased as the distance class increased and changed from positive to negative autocorrelation. The 6-class multivariate correlogram using Euclidian distances indicated a clinal profile for the genetic variation (Fig. 2A). The shape and intercept (conservatively reported as the minimum end of the nonsignificant distance class) were similar to the 10- and 15-class correlograms, with intercepts ranging

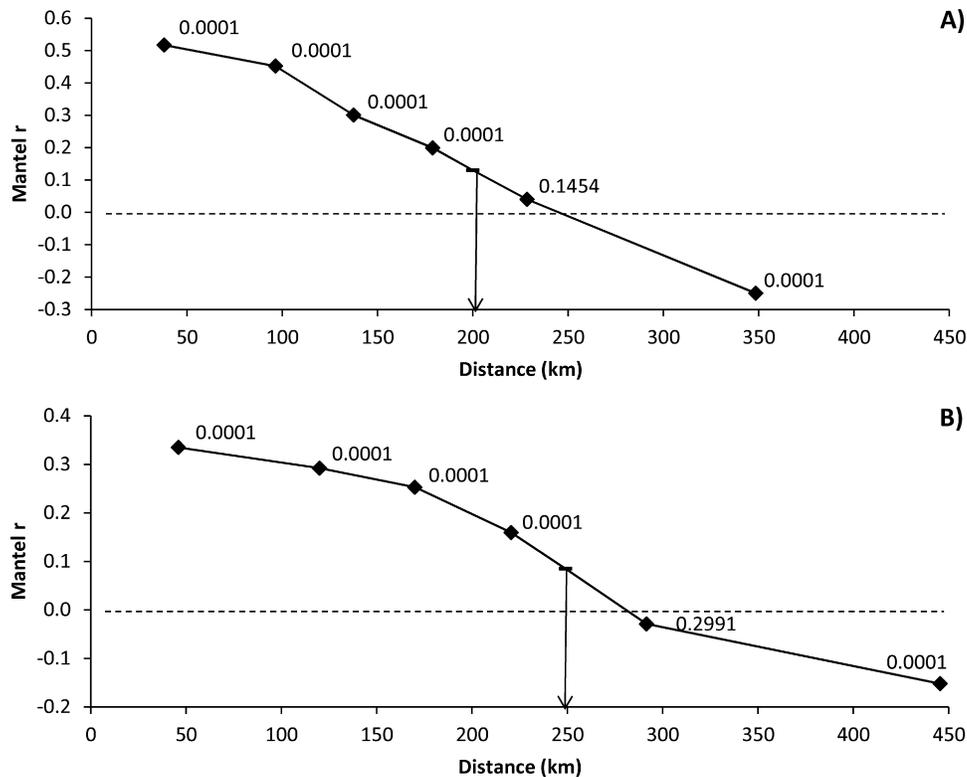
from 200 to 276 km. Correlograms based on least-cost path distances indicated a more “stabilizing” profile, with a sharper drop across the intercept before leveling (Diniz-Filho and Telles 2002); intercepts ranged from 249 to 308 km (6-class analysis; shown in Fig. 2B). These intercepts are consistent with the Euclidian distance-based analysis, with larger intercept distances reflecting obstacles of natural topographic barriers on the landscape.

**DISCUSSION**

For the Mojave desert tortoise, we may consider local populations within the most conservative intercept distance of 200 km to be genetically correlated (genetic distance < 0.12; Fig. 1) and compatible for translocation. Therefore, an appropriate management guideline relative to genetics is to limit translocations from wild populations to straight-line distances less than 200 km. Taking historical barriers such as large mountain ranges previously identified as barriers to gene flow into account (Hagerty et al. 2011), the 200-km guideline is consistent

**Table 1.** Range of distance class sizes and pairwise sample sizes used in spatial autocorrelation analyses of Mojave desert tortoise genetic data. The first and last distance classes typically were larger than the other classes in order to include similar sample sizes; these class sizes are shown separately from the rest of the range.

Distance classes	Euclidian distance		Least-cost path distance	
	Class size (km)	Sample size per class	Class size (km)	Sample size per class
6	76, 41–57, 183	48–51	92, 44–85, 223	49–51
10	56, 23–56, 137	28–31	69, 27–73, 176	29–31
15	49, 13–40, 124	18–22	56, 14–52, 147	18–21



**Figure 2.** Mantel correlograms obtained after partitioning geographic distances into 6 connectivity matrices with an approximately equal number of pairs. Each point is the midpoint of its distance class. Numbers above each point are probability values (standardized Mantel's  $Z$ ) established after 10,000 random permutations. Arrows represent intercepts as defined by the minimum end of the nonsignificant distance class. A) Euclidian distances between sample pairs ( $n = 48$ –51 pairs per distance category). B) Least-cost path distances ( $n = 49$ –51 pairs per distance category; data from Hagerty et al. 2011).

with a “historical approach,” in which translocation among populations that historically exchanged genes may be considered (Moritz 1999). Although mixing major phylogeographic units as defined by mtDNA has been discouraged (Morales et al. 1997; Clostio et al. 2012), such units that might confound this guidance do not exist for the Mojave desert tortoise. Haplotypes identified by restriction fragment length polymorphisms in what is now recognized as *Gopherus agassizii* differed by only 1–2 mutation steps (Lamb et al. 1989), and the 2 haplogroups identified from mtDNA sequences were only weakly supported (maximum parsimony bootstrap proportions  $\leq 65\%$  with decay values of 1–2 steps; Murphy et al. 2007).

Some level of caution is warranted when interpreting neutral genetic variation to make conservation decisions about translocation (Funk et al. 2012). Neutral variation and adaptive variation may not always be directly correlated because different forces are acting (gene flow and genetic drift vs. natural selection) (Holdregger et al. 2006; Funk et al. 2012). For example, Mojave desert tortoises occur along environmental gradients; precipitation regimes change from west to east, and latitudinal gradients result in northeastern tortoises experiencing more freezing days than those in the southwest (US Fish and Wildlife Service 2011b). The mean number of days

with below-freezing temperatures appears to influence the proportion of populations with an antibody response to *Mycoplasma* spp. (Sandmeier et al. 2013). Although this variability could reflect phenotypic plasticity, our best available genetic data using neutral microsatellites likely does not give us a complete picture of genetic variation in Mojave desert tortoise populations.

The primary genetic risk associated with releasing tortoises of distant origin to new populations is that of outbreeding depression, i.e., reduction in reproductive fitness following attempted crossing of populations (Storfer 1999; Frankham et al. 2011). Given that dispersal ability is a driving factor in desert tortoise movement, which can be seen as a pattern of isolation by distance (Britten et al. 1997; Murphy et al. 2007; Hagerty and Tracy 2010), the most likely mechanism of outbreeding depression is adaptive differentiation of populations from different parts of the desert tortoise's range. Edwards and Berry (2013) discouraged the use of captive desert tortoises in the recovery of wild populations based largely on perceived risks of outbreeding depression, despite finding that only a small proportion of their captive samples appeared to have originated from extremely disparate regions. However, in similar environments, thousands of generations of evolution in isolated populations of a species are required to initiate outbreeding

depression, and dozens of generations are still required for populations in different natural environments (Frankham et al. 2011). For Mojave desert tortoises, with a generation time on the order of 25 yrs (US Fish and Wildlife Service 1994), the time scale in which outbreeding depression might occur is 600 or more years. The historically continuous distribution of the species suggests that populations have not been isolated from gene flow for more than 20 generations (Hagerty and Tracy 2010), further reducing the probability of outbreeding depression (Frankham et al. 2011).

Based on both spatial autocorrelation and qualitative risk assessment (Frankham et al. 2011), the risk of initiating outbreeding depression by translocating tortoises appears to be low, particularly for movements between populations within 200 km. More distant populations, even across an environmental gradient, may contain adaptive differences, so translocations between near-neighbor populations would be conservative (Frankham et al. 2011; Edwards and Berry 2013). However, thousands of desert tortoises have been translocated by management agencies or the general public through release of unwanted pets (Murphy et al. 2007), creating at least some degree of uncertainty in populations of origin, even for tortoises captured in the wild. To most conservatively prevent undesired genetic mixing, obtaining genotypic data for all individuals would provide information that can be used in decision-making regarding translocation (Edwards and Berry 2013).

Nevertheless, genotyping every individual to be translocated may be cost-prohibitive and unnecessary, given the low risks involved in making a mistake. Consequences of mistakenly releasing a small number of tortoises of distant origin to a new population would often be temporary, because natural selection can act on the enhanced genetic diversity to eliminate outbreeding depression over time and in some cases can produce populations with similar or greater fitness than either parent population (Edmands et al. 2005; Erickson and Fenster 2006; Haanes et al. 2010). Individuals poorly adapted to unintended distant release sites also may not successfully integrate into the resident population (Edwards and Berry 2013; we note that despite the limited genetic impact, large numbers of mortalities unknowingly related to poor adaptation to the release site may compromise evaluation of overall translocation success).

Notwithstanding recommendations based on neutral genetic variation, new developments in next-generation sequencing are opening the door for managers to learn much more about the level of adaptive variation that exists among populations of species of concern (Funk et al. 2012). We recommend that future research include such techniques so that managers can evaluate neutral and adaptive divergence when making decisions. Within the framework outlined by Funk and colleagues (2012), quantifying adaptive differentiation would be the final step in identifying conservation units. In some cases,

adaptive divergence may be more valuable for prioritizing conservation actions and making translocation decisions (Moritz 1999; Funk et al. 2012). Using similarity across adaptive loci as a criterion for translocating individuals among conservation units would further minimize risks of outbreeding depression (Funk et al. 2012). However, such an approach will also need to consider the extent to which genetic adaptations for an existing or historical environment will be relevant under the rapid effects of climate change. For example, each critical habitat unit designated for the Mojave desert tortoise is expected to experience a new temperature regime within 23–187 yrs compared with the present (Averill-Murray et al. 2013), leaving tortoise populations in environments potentially very different from those in their recent past. Translocations for the purpose of increasing genetic variation and adaptive potential may become important to introduce new alleles for traits important for environmental change from different parts of the species' range (Weeks et al. 2011; IUCN/SSC 2013).

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