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Habitat drives dispersal and survival of translocated juvenile desert tortoises

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Running Title: Habitat selection studies inform translocations

SUMMARY

1. In spite of growing reliance on translocations in wildlife conservation, translocation efficacy remains inconsistent. One factor that can contribute to failed translocations is releasing animals into poor quality or otherwise inadequate habitat.

2. Here we used a targeted approach to test the relationship of habitat features to post-translocation dispersal and survival of juvenile Mojave desert tortoises *Gopherus agassizii*.

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3. We selected three habitat characteristics—rodent burrows, substrate texture (prevalence and size of rocks), and washes (ephemeral river beds)–that are tied to desert tortoise ecology. At the point of release, we documented rodent burrow abundance, substrate texture, and wash presence and analysed their relationship to maximum dispersal. We also documented relative use by each individual for each habitat characteristic and analysed their relationships with survival and fatal encounters with a predator in the first year after release.

4. In general, the presence of refugia or other areas that enabled animals to avoid detection, such as burrows and substrate, decreased overall mortality as well as predator-mediated mortality. The presence of washes and substrate that enhanced the tortoises' ability to avoid detection also associated with reduced dispersal away from the release site. These results indicate an important role for all three measured habitat characteristics in driving dispersal, survival, or fatal encounters with a predator in the first year after translocation.

5. *Synthesis and applications*. Resource managers using translocations as a conservation tool should prioritize acquiring data linking habitat to fitness. In particular, for species that depend on avoiding detection, refuges such as burrows and habitat that improved concealment had notable ability to improve survival and dispersal. Our study on juvenile Mojave desert tortoises showed that refuge availability or the distributions of habitat appropriate for concealment are important considerations for identifying translocation sites for species highly dependent on crypsis, camouflage, or other forms of habitat matching.

Key-words: burrow, camouflage, concealment, desert tortoise, dispersal, *Gopherus agassizii*, refugia, reinforcement, substrate, translocation

INTRODUCTION

Translocation, or assisted movement of wildlife, is a widely used management tool (IUCN/SSC 2013). "Conservation" translocations are applied towards species recovery through population reintroduction and reinforcement (Seddon, Armstrong & Maloney 2007; Ewen *et al.* 2012; Seddon *et al*. 2014). Translocations are also applied as a form of mitigation against development impacts (Germano *et al.* 2015; Sullivan, Nowak & Kwiatkowski 2015). In spite of greater reliance on translocations for wildlife management (Seddon *et al*. 2014), success is inconsistent (Dodd & Seigel 1991; Germano & Bishop 2009; Miskelly & Powlesland 2013). Numerous factors such as life history, release strategy, and habitat can affect management outcomes (Griffith *et al.* 1989; Wolf, Garland & Griffith 1998; Seddon, Armstrong & Maloney 2007; Ewen *et al.* 2012). Design and implementation of conservation translocations can, however, be improved by applying a growing toolbox built from literature addressing these considerations (Batson *et al.* 2015).

Habitat suitability at the recipient site can influence translocation outcomes via effects on post-release dispersal, mortality, or other causes preventing establishment of viable populations (Griffith *et al.* 1989; Stamps & Swaisgood 2007; Germano & Bishop 2009; Le Gouar, Mihoub & Sarrazin 2012; Seddon *et al*. 2014; Attum & Cutshall 2015). Forage availability, an often-considered habitat feature, can affect site fidelity and survival after release (Bright & Morris 1994; Cabezas & Moreno 2007). The need for security areas—habitat that affords protection against predators or inclement weather—is, however, more poorly represented in the literature. Refugia, such as denning or nesting sites, are critical drivers of behaviours, survival, and reproduction and have known conservation value (Germano *et al*. 2012; Walters 1991; Zhang *et* *al.* 2007). Establishing artificial shelters prior to translocating European wild rabbits (*Oryctolagus cuniculus*), for instance, enhances translocation success (Cabezas & Moreno 2007). Rapid establishment in refugia after release can also increase survival rates (Shier & Swaisgood 2012). The availability of substrates that increase camouflage opportunity also have important conservation ramifications (Reed and Shine 2002; Forsman & Aberg 2008). However, with some notable exceptions (Gerber *et al.* 2003), availability and spatial distribution of suitable security areas within recipient habitats have received minimal attention during translocations.

Translocations are likely to figure prominently in the recovery of many chelonians (Turtle Conservation Fund 2002). Members of the Testudinidae family native to the United States have experienced sharp increases in mitigation-motivated translocations (Tuberville *et al.* 2005; Germano *et al.* 2015). Likewise, ‘head-starting’—captive rearing to reduce vulnerability to predation (Burke 2015)— has also been applied as a conservation tool for gopher tortoises *Gopherus polyphemus* (Tuberville *et al.* 2015) and Mojave desert tortoises *G. agassizii* (USFWS 2011). There is, however, limited understanding of the long-term efficacy of translocations and head-starting (for short-term efficacy in *Gopherus* spp., see Tuberville *et al.* 2005; Field *et al.* 2007; Nussear *et al.* 2012; Nagy *et al.* 2015; Tuberville *et al.* 2015). Because conservation translocations can contribute to species recovery (Miller, Bell & Germano 2014; Germano *et al.* 2015; Sullivan, Nowak & Kwiatkowski 2015), refinement of translocation protocols is needed to support successful translocations, especially for juvenile tortoises. For chelonians, the structure of the recipient habitat can exert important effects on translocation outcomes (Rittenhouse *et al.* 2008; Nussear *et al.* 2012; Attum & Cutshall 2015), where refuge availability especially can improve survival (DeGregorio, Buhlmann & Tuberville 2012).

The goal of this study was to investigate relationships between habitat characteristics and translocation outcomes, in particular dispersal and survival, for juvenile Mojave desert tortoises. Each is vital for establishment of viable populations at recipient sites (Le Gouar *et al.* 2008). Understanding factors that affect them is thus critical for improving the efficacy of translocation programs. We investigated their relationship with three habitat characteristics implicated to affect tortoise fitness: ephemeral riverbeds (washes), substrate texture, and rodent burrow abundance. Washes provide important food resources for desert tortoises (Jennings & Berry 2015), contain natural caves used as refuges (Woodbury & Hardy 1948), and are selected for by juveniles (Todd *et al*. 2016). Substrate is an important source of camouflage that can reduce juvenile detectability (Nafus *et al.* 2015). Burrows are strongly tied to the ecology of desert tortoises (Zimmerman *et al.* 1994; Bulova 2002). Because early life stages can suffer high predation rates (Bjurlin & Bissonette 2004), we also investigated the ability of each of these habitat characteristics to reduce predator-mediated mortality. In sum, we selected three habitat characteristics thought to be important as a source of refuge or forage to test against dispersal and first-year survivorship.

MATERIALS AND METHODS

Study areas

We selected four recipient sites. Boulder City Conservation Easement (BC), Eldorado Valley (EV), Hidden Valley (HV), and Trout Canyon (TC) are located in the eastern to north-eastern Mojave Desert within 100 km of Las Vegas, NV, USA (Fig.1). The release sites were primarily Mojave Desert scrub vegetation dominated by creosote, bush-white bursage *Larrea tridenta-Ambrosia dumosa* plant associations with Joshua trees *Yucca brevifolia* and Mojave yuccas *Y. schidigera* periodically intermixed. Soils were loamy or sandy compositions intermixed with pebbles and cobble. Releases occurred between 600 – 780 m in elevation at BC, 850 – 900 m at HV, 900 – 1100 m at EV, and 1100 – 1250 m at TC. Differences in elevation among recipient sites were an artefact of the translocation program designs rather than experimental treatments. Three of the recipient sites were publically managed land and one occurred on a conservation easement; the translocations were intended to reinforce locally declining populations and in all cases natural populations were already present at varying densities (BLM 2013).

Study animals

The Mojave desert tortoise is an herbivorous reptile that occupies a broad range of habitats. They are typically found in areas with intermediate cover of woody perennial shrubs, loamy soils, and gentle slopes (Nussear and Tuberville 2014). At hatching, juvenile tortoises have a midline carapace length (MCL) of approximately 50 mm and typically don't reach sexually maturity until at least 180 mm MCL or approximately 15-20 years of age (Turner *et al.* 1986; Medica *et al*. 2012). Growth is annually variable, however, rates of 7 mm/yr are estimated for immature tortoises (Medica *et al*. 2012). Following translocations, average dispersal by adults is just over 1500 m, but can range upwards of 6000 m (Field *et al*. 2007; Nussear *et al*. 2012), which is generally much greater than typical movements displayed by resident tortoises (Nussear *et al*. 2012). Translocated juveniles under 100 mm MCL tend not to disperse more than 100 m, although they can sustain dispersal movements over 1600 m (Hazard, Morafka & Hillard 2015).

Juvenile tortoises used in this study originated from eggs produced by females housed at the Desert Tortoise Conservation Center in Las Vegas, NV, USA. Ages ranged from 6 months through 4 years. Sizes ranged from 50 to 85 mm MCL, which is similar to expected sizes in the wild based on their ages. Captive juveniles were fed a diet of ZooMed Grassland Diet and a range of plants available in their natural environment. Beginning in June 2014 each individual underwent three health assessments spread across 90 days. The health assessments documented clinical signs of disease, body condition, weight, activity, and carapace hardness following specified guidelines (USFWS 2013). We selected 80 animals for translocation that were asymptomatic for disease, in good body condition, possessed "firm" carapaces, and expressed normal activity. We fitted tortoises with VHF radio-transmitters (PD-2 [2.4 – 3.6 g], Holohil Systems Ltd, Carp, Ontario, Canada) on their fifth vertebral scute using 5-min. gel epoxy following descriptions outlined in Boarman *et al*. (1998) for immature tortoises. We replaced transmitters each 4 – 8 months.

Translocation and Monitoring

We released 21 juveniles at EV on 16 September 2014, 19 at HV on 22 September 2014, and 20 at TC on 11 September 2014. We released an additional 20 animals to BC on 01 April 2015 with the difference in time due to logistical constraints. For each recipient site, we selected two release zones separated by at least 3 km and divided animals evenly between them. Within each release zone we generated a random coordinate for each animal and released animals at least 20 m from each other to enact a solitary release structure. Each animal was released with its head placed inside the first encountered rodent burrow. We tracked tortoises weekly during their active season – March to October – and bi-weekly during hibernation – November to February –

using hand-held radio receivers (Telonics Model R-1000, Orange, CA, USA). At each encounter we recorded animal number, date, and geographic location using global positioning systems (±3 m).

Dispersal – We estimated dispersal by calculating the straight-line distance (m) between the coordinates at release and each tracking event until September 2015. We selected the maximum distance from release achieved at any point by animals that had "settled" as our measure of dispersal. We classified an animal as settled when it moved around a centralized point in a manner reminiscent of a home range for the remainder of the study. In order to measure the effect of habitat on dispersal, we documented wash presence, rodent burrow abundance, and substrate texture within 2-m of the point of release (see Table S1 in Supporting Information for sample sizes). Two meters was considered a manageable distance for a juvenile tortoise to achieve a refuge source after detecting a threat. The microhabitat scale, as is used here, is also frequently used to address behavioural decision-making that serves to avoid predation (Longland & Price 1991). We categorized wash as a binomial categorical variable of present (1) or absent (0). Rodent burrow abundance represented the total number of rodent burrows that the entire tortoise's body could fit inside. We categorized substrate texture by integrating two metrics acquired through ocular estimation: size of the exposed rock face on the surface layer and percent soil surface comprised of rock. We divided size into three categories: absent, small (pebbles less than 10 mm the size of the tortoise), and large (pebbles within 10 mm of the tortoise size or cobble; Table 1). Soil cover by rocks was also subdivided into three categories: 1) absent or low cover, 2) medium cover, and 3) high cover of the soil layer (Table 1). We then combined rock size and cover into a singular categorical measure of substrate that ranged from 0

– 5 (Table 1) following methods described by Nafus *et al*. (2015). Because the release point was largely random, sample sizes for each variable measured were not equal and not all have adequate sample size, e.g. no animals were released on substrate category 3 and only one animal on category 1 (Table S1).

We natural log transformed dispersal distances to meet statistical assumptions. We used wash presence, burrow abundance, and substrate category at release to test for a relationship between each variable and dispersal distance using a linear model in R version 3.1 (R Core Team 2013, Vienna, Austria). We also tested for an interactive effect between wash and substrate, as washes often have substrates that vary from the surrounding landscape. We included release zone blocked by recipient site as a covariate. After confirming that dispersal distance was independent of survival and MCL, we excluded MCL and any animals that died prior to settling from the final model and accepted significance at $\alpha = 0.05$.

Survival – In order to measure the effect of habitat on survival in the first year following translocation, once per week we recorded the same habitat characteristics as described above within a 2-m radius: wash presence, rock size, percent surface composition that was rocks, and burrow abundance. Burrows abundance counts included rodent burrows and those constructed by the juvenile tortoises themselves. We calculated the proportion of tracking events each animal was encountered in a wash. We combined rock size and cover into substrate categories using the methods described above. We calculated mean substrate category and mean burrow number within 2-m of each individual. We used a binomial logistic regression in R version 3.1 (R Core Team 2013, Vienna, Austria) to measure the correlation between proportion of tracking events in a wash, mean substrate category, mean burrow abundance and the tortoises' status at the close of the study. Survival status was considered living (1) or dead (0) at 30 September 2015. We excluded two missing animals from the analysis. Additionally, MCL was not found to significantly affect survival and omitted from the final model.

When a carcass was found, we attempted to assign cause of death from physical characteristics of the carcass, as well as sign (scat, tracks, etc.) present. We subsequently broke mortalities into two probable causes: predation or other (starvation, desiccation, or exposure). We completed an additional logistic regression to test the relationship of the aforementioned variables and depredation (carcasses with signs of predator detection [0]) or avoidance of fatal or post-mortem predator encounters (living or dead with no evidence of predator consumption [1]). For each survival model, release zone was blocked within recipient site and included as a covariate. Data used in the analysis are published at Dryad Digital Repository (Nafus *et al.* 2016).

RESULTS

Dispersal

Nine individuals died before settling into a movement pattern reminiscent of a home range. Of the remaining 71 individuals, 46 (65%) settled within two weeks and 100% had settled by two months. Mean maximum dispersal distance for all individuals was 103 ± 10 m ($\mu \pm$ SE; range: 11-487 m) from release. For the model describing maximum dispersal distance ($F_{6,65}$ = 1.94, $P = 0.08$) release substrate ($t = 2.4$, $P = 0.01$) and wash presence ($t = 2.1$, $P = 0.03$) correlated with dispersal. Rodent burrow abundance ($t = 0.01$, $P = 0.99$) and recipient site did not

(t = 0.65, P = 0.51) correlate with dispersal, nor was there evidence for an interactive effect between substrate category and wash presence on dispersal (t = 1.6, P = 0.10). Juvenile tortoises released greater than 2-m from a wash dispersed approximately 30 m farther on average than tortoises released in washes (118 ± 16 m versus 87 ± 12 m, respectively). Tortoises released amongst larger pebbles and cobble also showed greater site fidelity following their release than those placed amongst smaller pebbles (Fig. 2). Consequently, of the habitat characteristics measured, wash presence and rock size were most predictive of dispersal of juvenile desert tortoises following translocation.

Survivorship

Across all four recipient sites, 53 of 78 (68%) juveniles survived through September 2015, and two (2.5%) were lost due to radio malfunctions. The most common cause of death in the first year was desiccation, starvation or exposure, which explained 14 of the 25 (56%) mortalities (Table S2). The remaining 11 (44%) carcasses showed evidence of predation or scavenging primarily from canids, rodents, and ravens *Corvus corvax* (Table S2).

For the binomial model for survival (β = 3.1, SE = 2.2, z = 1.3, P = 0.16), mean burrow abundance was the only parameter that significantly correlated with survival (z = 2.2, P = 0.02; Fig 3a). Each additional burrow added to mean burrow abundance increased the odds of survival by 0.6. Similarly, association with one or fewer burrows on average resulted in a survival rate almost half that of tortoises that associated with ≥3 burrows (Table 2). Tortoises that associated with larger rocks (substrate categories ≥3) had marginally greater survival, but not significantly so (β = z = 1.7, P = 0.07; Table 2). Neither wash use (z = 0.6, P = 0.52) nor recipient site (z =

0.2, $P = 0.77$) significantly correlated with overall survivorship. In other words, cumulative mortality was approximately equal across all four sites in the time interval measured (Fig. 4), but highly related to burrow abundances.

The binomial model for the effects of habitat parameters on fatal or post-mortem encounters with predators ($\beta = 4.7$, SE = 3.1, z = 1.4, $P = 0.13$) identified mean burrow abundance (z = 2.4, $P = 0.01$) and mean substrate category (z = 2.0, $P = 0.04$) as significantly correlated to signs of predation being present. Juvenile tortoises were more likely to be found with signs of predation as mean burrow abundance decreased (Fig. 3b). For each burrow lost the odds of predation increased by 1.3. Tortoises with signs of predation were encountered on small rock sizes (primarily substrate category 2) more often, while those that were not detected by a predator or scavenger associated with large rocks (Fig. 5). For each decrease in substrate category the odds of predation on the tortoise or its carcass increased by 0.8. Frequency of encounters in a wash did not correlate significantly with fatal or post-mortem predator encounters (z = 1.3, $P = 0.16$). Rates of predation were equal across all four recipient sites (z = 1.2, $P = 0.20$), although the major predators varied by site (Table S2). In sum, fatal or post-mortem encounters with a predator were less likely if juvenile tortoises associated with areas containing abundant burrows and larger rock sizes.

DISCUSSION

We found that habitat characteristics with known ecological relevance to our study species tied directly to translocation-related dispersal until the majority of individuals had settled and first-year survival. A notable implication of our work is that choosing release habitat based on species ecology and behaviour can increase translocation success rates. The potential of habitat to affect translocations are well documented (Griffith *et al.* 1989; Dodd & Seigel 1991). Information gained by evaluating habitat effects on translocation outcomes can also guide preservation and management of habitat outside of a translocation context, serving as "probes" into habitat quality.

Post-release dispersal is a common phenomenon in translocation programs and can have detrimental effects on outcomes by increasing risk exposure and mortality rates (Stamps & Swaisgood 2007; Le Gouar, Mihoub & Sarrazin 2012; Shier & Swaisgood 2012). We did not find an effect of dispersal on survival, but notably the majority of our animals dispersed small distances from their release. Holding animals in acclimation pens can generally serve to reduce dispersal (Bright & Morris 1994), including for reptiles (Knox & Monks 2014; Attum & Cutshall 2015) and tortoises specifically (Tuberville *et al.* 2005). However, acclimation pens are sometimes ineffective (Nagy *et al.* 2015) and often financially unfeasible. Information provided by studies of desert tortoise behavioural ecology and habitat selection identified habitat characteristics that increased site fidelity following translocation in the absence of acclimation pens.

Selecting appropriate microhabitat at the release site can dampen dispersal outside of the translocation site. We found that washes and larger rocks were two ecological variables that reduced dispersal distance. Washes are used as foraging corridors by desert tortoises (Jennings & Berry 2015), can reduce adult dispersal away from translocation sites (Germano *et al*. 2012), and are selected for by juveniles (Todd *et al*. 2016). Provisioning supplemental food during translocation can improve translocation outcomes for other taxa (Cabezas & Moreno 2007; Jones & Merton 2012). Releasing animals into habitats associated with foraging activity may accomplish similar objectives, and may explain the greater site fidelity we found for tortoises released in washes. Perception of vulnerability to predators may also influence dispersal decisions following a translocation. Dispersal was reduced for juvenile tortoises in this study when they were released into areas that had similarly sized rocks present. Previous studies have shown juvenile preference for larger rocks, which is likely driven by their camouflage potential (Nafus *et al*. 2015). Our results indicate that releasing individuals adjacent to habitat features that they are known to selectively use can reduce dispersal.

In contrast, we did not find that burrow abundance affected dispersal. Previous work suggests that juvenile desert tortoises select areas with greater availability of small mammal burrows (Todd *et al*. 2016) and that releasing adults near rock caves can reduce dispersal (Germano *et al.* 2012). Refugia, thus, can affect desert tortoise movement patterns. Availability, density, and structure of refugia can affect the value of local habitat patches. Habitat analyses for woodrats (*Neotoma*), for instance, indicate that deviation from optimal spatial distributions patterns for refugia can negatively affect individual fitness (Gerber *et al*. 2003). The apparent lack of effect of rodent burrow abundance on dispersal in our study may reflect an absence of a relationship. The presence of even one rodent burrow at release, however, may have been sufficient to enhance site fidelity. Alternatively, the 2-m sampling area may not have accurately measured refuge availability or the perception of availability. While we found little evidence for rodent burrow abundance driving post-release dispersal, we caution against interpreting our findings as indicating refugia are not important without additional studies.

The general patterns of dispersal observed in our study are similar to those found in previous releases of juvenile desert tortoises under 100 mm MCL. Movement away from the release site occurred in a short period after release, with most tortoises dispersing less than 100 m (Hazard & Morafka 2002; Hazard, Morafka & Hillard 2015). These results contrast with translocations of adult tortoises, in which animals readily move more than 5 km (Field *et al.* 2007; Nussear *et al.* 2012). Their comparatively high site fidelity makes juveniles appealing for conservation translocations, if rates of survival and recruitment into the adult population can be improved (see Reed, Fefferman & Averill-Murray 2009).

Understanding the drivers of mortality following a translocation may be improved by careful examination of habitat selection. Mortality due to predation of translocated juvenile desert tortoises has shown a poor correlation with individual activity levels (Hazard, Morafka & Hillard 2015). One possible mechanistic explanation as to why individual activity didn't affect predator susceptibility is the extent to which their surrounding habitat provided refuge from predators. Larger rocks can camouflage juvenile tortoises against visual detection (Nafus *et al.* 2015), which in our study coincided with reduced rates of predator consumption. Juveniles surrounded by camouflaging rocks may remain active and hidden from predators. Although the role of substrate in promoting camouflage has predominately been studied in the context of animal behaviour (Stevens & Merilaita 2009), there is increasing awareness that it may play a central role in conservation (Reed and Shine 2002; Forsman & Aberg 2008; Nafus *et al.* 2015). Camouflage-dependent species select for better-matched backgrounds that reduce their visual detectability (Dimitrova & Merilaita 2012; Skelhorn & Ruxton 2012; Nafus *et al.* 2015); such selection can reduce mortality post-translocation (King, Berg & Hay 2004).

Burrows represent critical components of desert tortoise ecology. Adult desert tortoises spend an estimated 95% of their lives underground (Nagy & Medica 1986). Burrows function as thermal refuges and improve water conservation (Zimmerman *et al.* 1994; Bulova 2002). Individual burrows, however, differ in their capacity to maintain ideal conditions and reduce evaporative water loss (Bulova 2002; Wilson *et al.* 2001). The relationship between burrow abundance and juvenile tortoise survival may thus have two origins. Greater refuge availability may have reduced the distance to any one burrow, which increased the likelihood of evading predators. Additionally, increased burrow abundance may increase the probability of individuals locating quality burrows. We cannot, however, ignore the possibility of broader behavioural differences between juveniles that associated with abundant burrows versus those that did not, differences that may also affect their susceptibility to mortality. Regardless, refuge availability in this study likely offered a two-fold protection for translocated animals: reduced susceptibility to predators and provisioning buffers against desiccation or heat exhaustion (Zimmerman *et al.* 1994; Nussear *et al.* 2007). Although a small number of tortoises were scavenged or depredated by rodents, the net effect of a large rodent population is expected to be positive through the beneficial effects provided by their burrows. Supporting healthy rodent populations in the Mojave Desert through habitat management may improve juvenile desert tortoise survival and recruitment.

Management implications and conclusions

On the whole, reinforcement of desert tortoise populations through conservation translocations shows promise as a recovery tool. Although translocated animals initially engage in heightened movement after translocation (Nussear *et al*. 2012), that does not appear to translate into greater mortality (Esque *et al.* 2010; Nussear *et al*. 2012). Annual survival of juvenile tortoises that associated with an average of ≥2 burrows in our study were within the range of estimates from life tables constructed for populations in southern California—64-85% for the size classes used in our study (Turner *et al*. 1987; Karl 1988). Therefore head-starting and translocation of juvenile tortoises warrants continued use as a management tool. In particular, careful selection of local microhabitat at the release point has the potential to increase survival above what is typical for the average wild juvenile. Of notable import to the survival of juvenile tortoises after translocation was the distribution and availability of refugia or security areas. One tactic for improving the conservation value of translocations for this species and other species that are reliant of crypsis or denning sites is mapping the spatial distributions of these resources at prospective release locations. Translocations can then be designed to ensure that each released individual has access to the refugia that are necessary for long-term survival.

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Data accessibility

Habitat data are stored at Dryad Digital Repository http://dx.doi.org/10.5061/dryad.ds8j3 (Nafus *et al*. 2016).

Coordinates for individual tortoises are not provided to prevent harvesting of a sensitive species. Contact M. Nafus if interested in more detail regarding the data.

Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1. Sample size of tortoises released by each habitat characteristic measured.

Table S2. Cause of mortality broken down by recipient site.

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Table 1: Rock size and soil cover were combined into a single categorical variable ranking from 0 – 5. Size was based on the largest rocks present and relative to tortoise sizes. Soil cover was divided into three general categories based on ocular surveys within a 2-m radius of the animal.

	Substrate Category	
Rank	Size	Soil Cover
0	Absent or small	Low (<10%)
1	Small	Med (10-49%)
2	Small	High (>50%)
3	Large	Low
4	Large	Med
5	Large	High

Table 2: Annual survival rates for animals released in September 2014 relative to mean burrow abundance or mean substrate category within 2-m. Multiple categories were combined if there

were fewer than 10 animals in a given category. Substrate category is a categorical ranking of rocks on the surface ranging from 0 – 5 where cover and size increase with ranking.

Burrow Abundance	≤1	2	3	≥4
n	10	15	15	17
Proportion alive	0.40	0.67	0.80	0.76
Substrate Category	-	≤2	3	≥4
n	-	12	10	34
Proportion alive	-	0.25	0.80	0.80

Figure 1

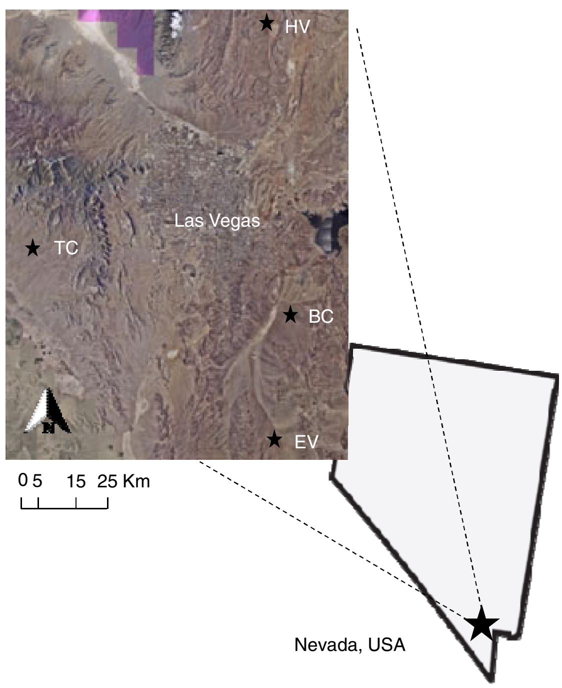

Figure 1 – Map of the recipient sites relative to Las Vegas, NV, USA (UTM: 3988210, 0664449), including Boulder City Conservation Easement (BC), Eldorado Valley (EV), Hidden Valley (HV), and Trout Canyon (TC).

Figure 2

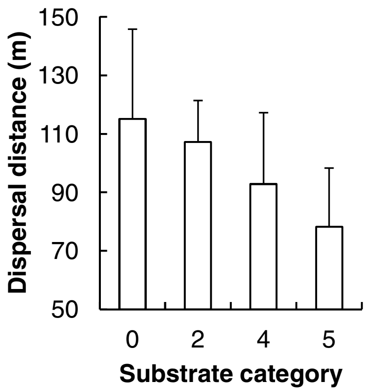

Figure 2 – Juveniles released amongst larger rock sizes had a smaller mean (+/- SE) dispersal distance. Insufficient juveniles were released amongst categories 1 (*n* = 0) and 3 (*n* = 1) to be included. Substrate category is a categorical ranking of rocks on the surface ranging from 0 – 5 where cover and size increase with ranking.

Figure 3

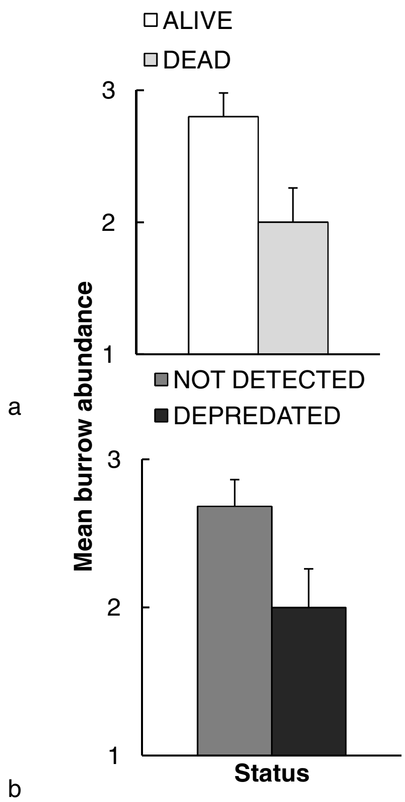

Figure 3 – On average (+/- SE), juvenile tortoises that survived through September 2015 associated with a greater mean abundance of rodent burrows than tortoises that died (a). Tortoise carcasses that showed signs of predation (depredated) associated with significantly fewer burrows on average than tortoises that were not detected – living or found as a complete carcass (b). Sixty tortoises were released in September 2014 and 20 in April 2015.

Figure 4

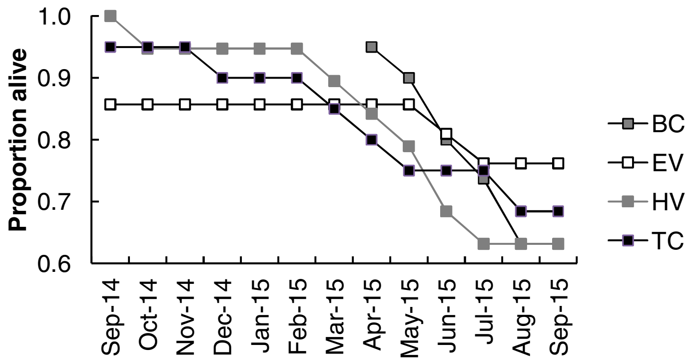

Figure 4 – Proportion of tortoises alive at the end of each month for each recipient site: Boulder City Conservation Easement (BC), Eldorado Valley (EV), Hidden Valley (HV), and Trout Canyon (TC). Releases at EV, HV, and TC occurred in September 2014 and in April 2015 at BC.

Figure 5

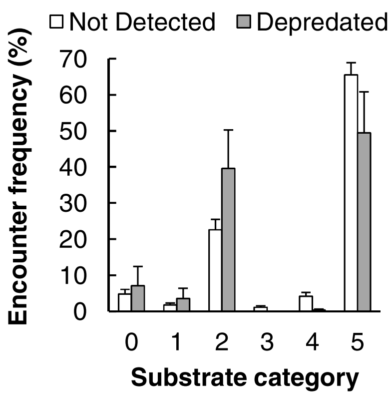

Figure 5 – The mean frequency (%) of encounters on each substrate category for animals that were depredated (signs of predation) or not detected (living or dead with no signs of predation). Substrate category is a categorical ranking of rocks on the surface ranging from 0 – 5 where cover and size increase with ranking.