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Translocation as a Conservation Tool for Agassiz's Desert Tortoises: Survivorship, Reproduction, and Movements

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ABSTRACT We translocated 120 Agassiz's desert tortoises to 5 sites in Nevada and Utah to evaluate the effects of translocation on tortoise survivorship, reproduction, and habitat use. Translocation sites included several elevations, and extended to sites with vegetation assemblages not typically associated with desert tortoises in order to explore the possibility of moving animals to upper elevation areas. We measured survivorship, reproduction, and movements of translocated and resident animals at each site. Survivorship was not significantly different between translocated and resident animals within and among sites, and survivorship was greater overall during non-drought years. The number of eggs produced by tortoises was similar for translocated and resident females, but differed among sites. Animals translocated to atypical habitat generally moved until they reached vegetation communities more typical of desert tortoise habitat. Even within typical tortoise habitat, tortoises tended to move greater distances in the first year after translocation than did residents, but their movements in the second or third year after translocation were indistinguishable from those of resident tortoises. Our data show that tortoises translocated into typical Mojave desert scrub habitats perform well; however, the large first-year movements of translocated tortoises have important management implications. Projects that employ translocations must consider how much area will be needed to contain translocated tortoises and whether roads need fencing to prevent the loss of animals.

KEY WORDS animal movements, conservation strategies, *Gopherus agassizii*, reproduction, reptile, site fidelity, tortoise relocation, translocation.

Translocations and relocations are used as management tools for many purposes (Griffith et al. 1989), including re-colonization of formerly occupied habitat (Hambler 1994, Towns 1994, Armstrong and Seddon 2008), augmentation of depleted populations (Musil et al. 1993, Ostermann et al. 2001), reducing dangerous human-wildlife interactions (Fritts et al. 1984, Sullivan et al. 2004, Brown et al. 2009), and moving sensitive species from harm's way as human development encroaches on wildlife habitat (Burke 1989, Field et al. 2007, Osman 2010). Growing urban areas and alternative energy production in the Mojave desert are reducing the availability of Mojave desert scrub habitat and driving the extirpation of associated species such as the Agassiz's desert tortoise (*Gopherus agassizii*). One conservation measure to deal with this problem is the removal of tortoises from habitats that face development. In Clark County, Nevada, and Washington County, Utah, this practice has led to the accumulation of displaced tortoises in holding facilities. This has created an eminent need to reintroduce these tortoises into remaining, restored, or even alternate habitats. Translocation to alternative habitats may be necessary, as available sites become scarce, densely occupied, or are politically untenable, and may also be a benefit (e.g., to improve our understanding of species' adaptation to climate change). To date, few studies of translocation effects on desert tortoises have occurred, and the majority of those studies are gray literature or anecdotal (e.g., Crooker 1971, McCawley and Sheridan 1972, Berry 1976, Corn 1991, Science Applications International Corporation [SAIC] 1993). We know of only 2 published studies in peer-reviewed literature (Field et al. 2007, Esque et al. 2010). Thus, the potential for success of translocation in this species have not been subjected to thorough scientific peer review. As a result, translocations remain a controversial tool in desert tortoise conservation (Berry 1986, Dodd and Seigel 1991, U.S. Fish and Wildlife Service 1994).

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Contributing to the controversy over translocations is the variety of near and long-term metrics for evaluating translocation success. Ideally, successful translocation is indicated by the ability of the translocated, or augmented, population to become self-sustaining in the long term (Griffith et al. 1989, Dodd and Seigel 1991, Hambler 1994, Fisher and Lindenmayer 2000, Tuberville et al. 2008). In the near term, other metrics have been used as indicators of the potential for long-term failure or success (Tasse 1989, Dickinson and Fa 2000, Fisher and Lindenmayer 2000, Esque et al. 2005, Bertolero and Oro 2009). For example, if near term mortality among translocated animals is elevated, this might be interpreted as an indication that translocation will be unsuccessful (Platenberg and Griffiths 1999). Additional metrics for judging the success of translocation include the body condition of released individuals (Bertolero and Oro 2009, Pinter-Wollman et al. 2009), release site fidelity (Lohoefener and Lohmeier 1986, Sullivan et al. 2004, Riedl et al. 2008, Bertolero and Oro 2009), habitat use (Rittenhouse et al. 2008), social integration of translocated animals into an existing population (Berry 1986, Reinert 1991), and the ability of translocated animals to find mates and reproduce (Berry 1986, Pedrono and Sarovy 2000, Esque et al. 2005). Although individual translocation efforts clearly have their own criteria for success, an integrated research-based approach has been repeatedly called for to increase our understanding of reintroduction and translocation (Griffith et al. 1989, Burke 1991, Dodd and Seigel 1991, Armstrong and Seddon 2008, Germano and Bishop 2009).

We assessed the effects of translocation on survival, fecundity, and behavior of desert tortoises, and how desert tortoises would perform if translocated into habitats not characteristic of the species' current distribution (Armstrong and Seddon 2008). We wanted to determine whether the translocated tortoises would find food and shelter, integrate into existing tortoise populations (e.g., colonize sites and interact with and contribute to resident populations) without undue influence on resident populations, and produce offspring that could ultimately contribute to population growth. We quantified survivorship, reproduction, and movements (an index of behavior that could affect management decisions) of translocated tortoises and compared these measures to those of resident animals at the recipient sites so that the effect of translocation could be statistically separated from variations normally expected for resident animals in particular areas (Riedl et al. 2008).

STUDY AREA

We selected 5 study sites to represent the known elevational range (500–1,500 m) of extant desert tortoise populations in the northeastern portion of their geographical range (Germano et al. 1994), and to extend beyond those known limits to adjacent but unoccupied habitat. Two sites were located in Clark County, Nevada, and 3 sites were located in Washington County, Utah, near the city of St. George.

Bird Spring Valley (35.97°N, 115.33°W) was located on Bureau of Land Management (BLM) lands approximately 21 km southwest of Las Vegas, Nevada where tortoises were relatively common (approx. 30/km^2; Burge and Bradley 1976) and was well within the geographic and elevation range known for this species (Germano et al. 1994). The habitat was characterized by Mojave desert scrub (Turner 1994) with 18% perennial cover, where the most abundant shrubs (as measured by frequency) were *Ambrosia dumosa* (40%), and *Larrea tridentata* (13%), with *Ephedra nevadensis*, *Ceratoides lanata*, and *Lycium andersonii* each comprising roughly 5% of the perennial species. *Yucca schidigera* and *Y. brevifolia* occurred sparsely at the site. The valley was an extensive bajada, which ranged in elevation from 900 m to 1,300 m and was of relatively even terrain. Mountainous peaks bordered Bird Spring Valley to both the east and west.

The Lake Mead site (36.48°N, 114.34°W) was located on National Park Service lands. It was a peninsula extending into Lake Mead at the northern end (Overton arm) of the Lake Mead National Recreation Area, near the town of Overton, Nevada. This site was located 105.8 km northeast of the Bird Spring Valley site. It was approximately 200–600 m in elevation, and was characterized by hotter air temperatures the other sites (Nussear et al. 2007). Tortoises were present at the site, but in very low densities (approx. 5/km^2 as encountered in this study). Vegetation was Mojave desert scrub (Turner 1994) with 20% perennial cover where the most abundant shrubs at the site were *A. dumosa* (47%), *L. tridentata* (12%), and *E. californica* (11%), with *Krameria parvifolia*, *Hilaria rigida*, and *Tetradymia spinosa* in heterogeneous patches. *Yucca* spp. were absent from this site.

The Shivwits site (37.21°N, 113.80°W) was located on BLM lands west of St. George, Utah and within the elevation range inhabited by tortoises (approx. 900–1,300 m; Germano et al. 1994). The dominant vegetation differed from that typically associated with desert tortoises; although, we found 1 resident animal at the site. The site was within the ecotone between Mojave desert scrub and Great Basin conifer woodland (Brown 1994) with 42% perennial cover. The perennial vegetation was dominated by *Coleogyne ramosissima* (35%), *Artemisia filifolia* (18%), *Gutierrezia sarothrae* (17%), and *Prunus fasciculata* (10%).

The Pahcoon Flat site (37.22°N, 113.84°W) was located on BLM lands west of St. George, Utah, and ranged in elevation from 1,350 m to 2,000 m, which was above the elevation typically associated with desert tortoises at similar latitude, and tortoises were not know to occur at the site. This site was characterized as Great Basin conifer woodland (Brown 1994) with 41% perennial cover, dominated by *A. tridentata* (44%), *G. sarothrae* (27%), and *C. ramosissima* (20%). *Cowania mexicana* (4%) and *Juniperus scopulorum* (2%) were also present at the Pahcoon site. A fire resulting from a prescribed burn by the BLM that escaped containment burned a large proportion of the Pahcoon release site in 1998. This resulted in loss of vegetation and killed 3 animals remaining on the release site.

The Sandstone Mountain site (37.21°N, 113.34°W) was located within an experimental section of the Red Cliffs Reserve, managed by Washington County, Utah. It was east of St. George, Utah, had an elevation range of

840–1,220 m, and vegetation characterized as Mojave desert scrub (Turner 1994) with 27% perennial cover. The most frequent perennials were *C. ramosissima* (26%), *G. sarothrae* (25%), *A. dumosa* (9%), *Ephedra* species (7%), and *A. filifolia* (7%). *L. tridentata* was present at Sandstone Mountain, but at a low frequency (3%). The Mojave desert scrub vegetation of this site existed as large (multi-hectare) patches adjoining patches of vegetation dominated by sage brush (*A. tridentata*). Few resident tortoises were located at this site (approx. 5), although tortoises existed in dense populations across the Virgin River in larger patches of Mojave desert scrub, a few kilometers away.

The Area 31 site (37.17°N, 113.57°W) was also located on the Red Cliffs Reserve, in Washington County, Utah. The vegetation was characterized as Mojave desert scrub, and was similar in elevation and composition to the Sandstone Mountain site. This site was un-manipulated and was monitored by a separate research group for assessing reproduction in residents at the site. The animals in Area 31 were monitored only during the reproductive season; therefore, we had too few observations to calculate movement indices or survivorship comparisons with our translocation sites.

METHODS

Vegetation Sampling

We estimated primary production of annual plants from vegetation samples on 20 transects, 200 m in length during the peak production of spring annuals in each year (1997–2000) in late April to early May. We determined sample sizes using bootstrap analysis of pilot data, by evaluating the stabilization of the mean and reduction of standard error with increasing sample size (Manly 1997, Nussear and Tracy 2007). Each transect began at a random point and extended in a random direction. We sampled 20 quadrats (1 m^2) at random distances along each transect. We ranked the amount of annual vegetation (biomass) in each quadrat on a scale of 1–10 separately for standing green and standing dry annuals (Reese et al. 1980, Andariese and Covington 1986, Tausch 1989). We clipped 10% of the vegetation for calibration of the ranks, and dried the clipped plants at 45° C to a constant mass. We generated calibration curves of subjective rank in relation to measured biomass, which we constructed separately for each vegetation type (dry or green), each site, each year, and for each person sampling annual vegetation. We calculated biomass estimates as the average biomass of all transects at each site. We sampled perennial plants once at each site along the same transects used for measuring annual vegetation because perennial composition and cover changed little over the study period. We calculated cover and frequency for each species using the line-intercept method (Canfield 1941).

Precipitation data were taken from the nearest National Weather Service weather station for each site as follows: Bird Spring Valley—Las Vegas, Nevada Airport (COOP ID 264436), 16 km to the northeast; Lake Mead—Overton, Nevada (COOP ID 265846), 11 km to the northwest; Shivwits—St. George, Utah (COOP ID 427516), 22 km to the southeast; Pahcoon Flat—Gunlock, Utah (COOP ID 423506), 10 km to the northeast; Sandstone Mountain—La Verkin, Utah (COOP ID 424968), 6.3 km to the east (Table 1).

Resident Animals

We used data from resident animals for comparison with translocated animals. We included nearly all resident animals encountered at the Bird Spring Valley and Lake Mead sites as we encountered them (Table 2). We only encountered 1 resident tortoise at the Shivwits, and potentially 5 at the Sandstone mountain site, and did not encounter any at the Pahcoon site. Because of low sample sizes, we were unable to monitor resident tortoises at these 3 sites. However, we were able to acquire data on egg production from collaborators monitoring resident animals at a nearby site (Area 31) in St. George adjacent to the Sandstone Mountain site. Animal locations and status were collected too infrequently to derive movement metrics and survivorship estimates for Area 31.

Translocation

We acquired the tortoises that we released in Nevada from the Desert Tortoise Conservation Center in southwestern Las Vegas, Nevada, and the tortoises released in Utah from the Washington County Temporary Care Facility, in Saint George, Utah. Both of these facilities are used to house tortoises displaced by urban development in the surrounding

Table 1. Estimates of the plant biomass of annuals (mean ± SD g/m^2) at each desert tortoise translocation site in Nevada and Utah, and for each year. We calculated cumulative precipitation (mm) for the summer (May–Sep) and winter (Oct–Apr) preceding the time the biomass was sampled. Abbreviations for site names are: Bird Spring Valley (BSV); Lake Mead (LM); Pahcoon (PAH); Shivwits (SHIV); and Sandstone Mountain (SSM).

		Green biomass (g/m^2)		Dry biomass (g/m^2)			
Year	Site	Mean	SD	Mean	SD	Winter rain (mm)	Summer rain (mm)
1997	BSV	2.9	1.6	5.2	2.8	36	33
1998	BSV	5.7	2.5	0.2	0.1	115	76
1999	BSV	4.6	4.9	8.3	4.3	45	54
1998	LM	3.3	3.7	0.6	0.9	117	34
1999	LM	1.5	1.2	0.4	0.4	44	95
1998	PAH	43.3	13.8	1.8	2.5	335	193
1999	PAH	Burned		Burned			
1998	SHIV	7.3	4.5	1.1	0.5	335	193
1999	SHIV	3.0	2.2	0.8	0.7	180	145
2000	SHIV	1.0	0.7	3.4	1.4	175	108
1999	SSM	3.1	2.6	8.6	9.2	136	150
2000	SSM	8.0	6.0	3.0	1.9	155	129

Table 2. Number of adult male (M) and female (F) and juvenile (J) desert tortoises tracked for each treatment group, site, and year. We report days in captivity for translocated tortoises (grouped by release year) Abbreviations for site names are: Bird Spring Valley (BSV); Lake Mead (LM); Pahcoon (PAH); Shivwits (SHIV); and Sandstone Mountain (SSM).

				Translocated 1997				Translocated 1998				Translocated 1999				Residents		
Site	Vegetation	Elevation (m)	Year tracked	M	F	J	Days in captivity	M	F	J	Days in captivity	M	F	J	Days in captivity	M	F	J
BSV	Mojave desert scrub	900–1,300	1997	20	30	10	181–1,246									20	29	
			1998	16	24	4		4	9		123–293					21	30	5
			1999	14	22	3		4	7							19	30	5
LM	Mojave desert scrub	200–600	1998					11	14	5	136–2,292					9	7	
			1999					10	14	4						9	7	
SHIV	Mojave desert scrub and Great Basin conifer woodland	900–1,300	1998					12	5	5	203–705							
			1999					7	5	4								
			2000					7	5	5								
PAH	Great Basin conifer woodland	1,350–2,000	1998					10	4	3	219–708							
			1999					8	2	3								
			2000					7	1	3								
SSM	Mojave desert scrub	820–1,220	1999									6	5	6	15–588			
			2000									5	4	6				

areas, although the ultimate source of animals in these facilities is not known. We tested all tortoises translocated during this experiment for an immune response to the pathogen implicated in an upper respiratory tract disease (*Mycoplasma agassizii*) using an Enzyme-linked immunosorbent assay (ELISA) test conducted at the University of Florida (Brown et al. 1994). In accordance with our permits, only animals that tested negative were translocated. All experiments using animals were conducted according to Institutional Animal Care and Use Committee guidelines (University of Nevada IACUC Protocols #A95/96-19, A98/99-19, A98/99-29, and A95/96-28) and under the appropriate state (Nevada Division of Wildlife Permit # S12355, Utah DWR Cooperative Agreement No. 14-48-0006-94-919) and federal permits (FWS PRT—704930 [sub permit 93-01], FWS Permit # 801045).

Translocations occurred in the early morning hours when temperatures were coolest. We carried animals to a designated release point and provided tortoises drinking water for 15–20 minutes immediately prior to release. We released tortoises in to an unoccupied burrow, in a burrow excavated with a power auger, or in the shade of a shrub, depending on the availability of natural burrows, and the severity of the daily ambient temperature at that time (Lohoefener and Lohmeier 1986, Corn 1991). During releases at Bird Spring Valley in 1997, we observed tortoises for the entire day of release to ensure that animals showed no immediate signs of heat stress (Cook 1983). In later releases, we observed tortoises for only 30 minutes after their release, because we saw no evidence of risks during the earlier observations.

We began translocations at the Bird Spring Valley site in late April of 1997, with the release of 60 tortoises in groups of 5–10 animals per week between April and June (Table 2). We released an additional 13 animals at Bird Spring Valley, and 30 animals at Lake Mead in early January of 1998. During winter releases, we transported the tortoises from the Desert Tortoise Conservation Center (while still in hibernation) and placed them into burrows that were covered with a board to encourage the animals to continue hibernating. The majority (84%) of the tortoises released in winter remained in their release burrows until early March of 1998 when we removed their cover boards. A minority exited the burrows and found or constructed burrows nearby. Translocations also occurred in 1998 at the Shivwits and Pahcoon sites with releases of 22 and 17 tortoises in late April, respectively. The final round of translocation was in late April of 1999 with the release of 17 tortoises at the Sandstone Mountain site.

Radio Telemetry

We monitored movements of all tortoises by radio telemetry using transmitters with a mass of 65 g (models G3, SB2, or SB2-RL; AVM, Colfax, CA) for adults. We used a smaller 25 g transmitter for juveniles (AVM model SM1-H). We numbered all tortoises on the carapace with a paper tag covered with clear epoxy, and additionally marked them with notches on the marginal scutes by creating a small groove using a triangular file (Cagle 1939). We located tortoises weekly using hand-held radio receivers (e.g., Telonics TR-2, Mesa, AZ) and recorded their positions using Global Positioning System (GPS) receivers. We altered the weekly telemetry schedule for some animals because of equipment failure and logistical constraints.

Survivorship

We compared survivorship among resident and translocated tortoises using a logistic exposure model (Shaffer 2004) coded in R (package nestsurvival 0.5 by M. Herzog USGS, R version 2.12; R Development Core Team, Vienna, Austria) for each site and year. However, with the exception of Bird Spring Valley in 1997, we observed too few mortalities in any given site and year to use this method with either daily or weekly observations. For this reason, we also calculated the Mayfield estimate of survivorship for each site, year, and treatment group (Johnson 1979; Table 3). We estimated a seasonal survival rate for each group by taking the daily survival rate to the power of the span of days that we monitored tortoises in each year. For the logistic exposure analysis, we conducted model selection using AIC_c for models including the treatment group, sex,

Table 3. Survival rate estimates for each year of study using the Mayfield estimate for each site and year for desert tortoises in Nevada and Utah within each treatment group (RES = residents, T = translocated tortoises and is followed by year translocated). Abbreviations for site names are: Bird Spring Valley (BSV); Lake Mead (LM); Pahcoon (PAH); Shivwits (SHIV); and Sandstone Mountain (SSM).

Site	Year	Treatment group	Deaths	Daily survival rate	95% CI	Days monitored	Seasonal survival rate
BSV	1997	RES	8	0.9993	0.0001	313	0.81
	1997	T97	7	0.9994	0.0001	239	0.86
	1998	RES	0	1.0000		306	1
	1998	T97	2	0.9998	0.0001	305	0.95
	1998	T98	0	1.0000		294	1
	1999	RES	2	0.9999	0.0001	308	0.96
	1999	T97	0	1.0000		308	1
	1999	T98	0	1.0000		308	1
LM	1998	RES	1	0.9996	0.0007	244	0.92
	1998	T98	1	0.9998	0.0001	317	0.93
	1999	RES	0	1.0000		267	1
	1999	T98	0	1.0000		267	1
SHIV	1998	T98	0	1.0000		111	1
	1999	T98	0	1.0000		315	1
	2000	T98	0	1.0000		197	1
PAH	1998	T98	4	0.9985	0.0004	224	0.72
	1999	T98	1	0.9997	0.0006	301	0.92
	2000	T98	0	1.0000		171	1
SSM	1999	T99	2	0.9994	0.0004	227	0.88
	2000	T99	1	0.9996	0.0007	167	0.94

day of year, month, and likely interactions. We also used a logistic exposure model to analyze whether the time that translocated tortoises spent in captivity (in days) influenced survivorship of animals released in their first year for all study sites combined. Models using a daily scale of observations failed to converge due to daily survivorship at or near 1, so we estimated models using a weekly time scale by aggregating observation data to 1 observation per week by taking the first observation of each animal in each week. We typically released tortoises on the same day at each site, but since we released Bird Spring Valley tortoises over a 45-day period in 1997, for that site and year, we also analyzed whether the day of the year that we released tortoises influenced survivorship.

Reproduction

We assessed egg production from X-radiographs of female tortoises taken biweekly between April and August of each year (Turner et al. 1986, Henen 1997). We transported female tortoises to a portable X-ray station (MinXray Model P300, MinXray, Inc., Northbrook, IL), and X-rayed them using Kodak X-Omatic film cassettes (Eastman Kodak Company, Rochester, NY) at 75 KVP for 0.08 seconds (Hinton et al. 1997). We also weighed, measured, and returned them to their original location within 2 hours of capture.

To get an overall indication of the influence of translocation on reproduction, we compared translocation status (resident or translocated, irrespective of year) relative to total annual egg production for all sites combined using a linear mixed effects model (Package nlme ver 3.1-90 in R 2.9), with tortoise number as a random factor, precipitation and maximum carapace length (MCL) as covariates, and site as a fixed factor. We also used similar models to analyze the total number of eggs produced by females with respect to time since translocation. We grouped animals by year and resident status (resident or translocated animal).

Movement

We quantified tortoise movements from successive telemetry locations within each year. We calculated the start-to-end-distance as the straight-line distance from the point of release (or in non-release years, from the hibernation burrow) to the hibernation burrow for the next winter. We also calculated the maximum distance from the site of release as the straight-line distance from the point of release (or hibernation) to the farthest point recorded for that year. We used these distances in lieu of home ranges as animals were dispersing, and they did not exhibit typical home ranges (Burt 1943).

We conducted 2 analyses to explore movement distances of translocated animals, while controlling for differences associated with the study sites. We conducted a mixed model analysis of covariance using the log maximum movement distances and log start-to-end distances for translocated and resident animals as the response variables and time since translocation (in years; rather than the calendar year) as a covariate; time since translocation started with years = 0 for the initial year of translocation. We entered site, treatment group (resident or translocated), and sex as fixed factors in the analysis. We also included the interaction of treatment group by time since translocation interaction, as this was of primary interest to our study. We treated individual tortoises as a random factor in the analyses to account for repeated measurements. We did not use animals with fewer than 6 observations for the year in the analyses as these animals typically had telemetry failure or the animals were lost before the end of the year.

Site Fidelity

We conducted site fidelity tests (Hooge and Eichenlaub 2001) using both the initial location and the harmonic mean of spatial coordinates using all locations for each tortoise. This test computes the sum of all distances from a test location to all other locations for that tortoise. Random walks (1,000) are then created for each tortoise using the distances between the observed locations for that animal, but randomizing direction to each location. The collective distance moved by the animal is then compared to the distances generated from the random simulations. The tests are categorized using the site fidelity test in the Animal Movement Extension 2.04b (Hooge and Eichenlaub 2001) for Arcview 3.2 (ESRI, Redlands, CA) as constrained (i.e., had a home range) when the distance moved is less than that of 95% of the random walks, random when the animal's movement distance is within 5–95% of the random walks, and dispersal when the animal moved further than 95% of the random walks.

We conducted contingency table analyses on the counts of animals in each of the site fidelity categories (JMP V 5.0.1.2; SAS Institute, Inc., Cary, NC). The simulations starting from the initial animal location for the year, and the harmonic mean of the location coordinates for the year resulted in the same categorization in each case and thus we present only 1 categorization here. We conducted the analyses for Bird Spring Valley and Lake Mead comparing the site-fidelity category of residents to those of translocated animals of both translocation groups (1997 and 1998) for each year. The random-walk movements for tortoises at the Lake Mead site were restricted to locations on land as desert tortoises are not known to swim. For the Utah sites, we conducted analyses for each site over time to examine changes in site fidelity patterns in the years after translocation.

RESULTS

Survivorship

Survivorship was generally high for both translocated and resident tortoises among all sites and years, with seasonal survival rates averaging 0.94 (Table 3). We found no statistical differences in survivorship between resident and translocated tortoises. The most common source of mortality was predation (16 of the 30 observed). Other sources of mortality included exposure to temperature extremes (3), wildfire (3), falling in mineshafts (2), burrow collapse by livestock (1) or flooding (1), and disease (1).

Bird Spring Valley had 1 year in which we observed sufficient mortality to analyze survivorship among tortoises in different treatment groups (1997), and with other potential contributing factors and covariates using logistic exposure modeling. The best model as ranked by AIC_c and associated model weights included only the intercept (i.e., mean), indicating no significant effect of any of the factors (translocation group, sex, and month) or covariates (day of year). The date of the year that animals were released was not a significant predictor of mortality ($Z = -1.15$, $P = 0.25$) for tortoises translocated in 1997 to Bird Spring Valley.

We also analyzed survivorship in the first year of release relative to the time spent in captivity for all sites combined. Model selection was conducted for models including site, sex, winter precipitation, and time in captivity. The best models describing weekly survival rates for first year translocatees included the intercept only, or site as a factor, whereas models including time in captivity performed poorly (the P-value for the model including days in captivity was 0.987). This indicated no apparent effect of the amount of time an animal spent in captivity (collectively ranging from 15 to 2,292 days; Table 2) on the likelihood of survival after translocation.

Reproduction

Tortoise reproduction depends on adequate precipitation and the production of annual plants that provide forage for tortoises. Taken across all sites and years, these 2 variables were correlated ($r = 0.8$), and typically produced nearly equivalent models when compared using AIC_c model selection at any given site. Thus when annual biomass data were unavailable, we used precipitation data for model comparisons. Model selection for all sites combined yielded a model with winter precipitation, body size (MCL), and site as the best performing model. Both precipitation and body size were positively correlated with the total number of eggs produced ($F_{1,124} = 4.04$, $P = 0.05$ and $F_{1,124} = 21.7$, $P \leq 0.001$, respectively). The addition of translocation as a factor in the model, comparing only residents and translocated animals, performed poorly, with a non-significant effect of translocation ($F_{1,123} = 0.29$, $P = 0.59$). When we examined total eggs produced by animals with respect to time since translocation, we found that in the first year since translocation mean reproductive effort for translocated tortoises was less than that of residents ($t = -2.54$, $P = 0.01$; an average of 1 egg less; Table 4); however, the mean number of eggs was not different between resident and translocated tortoises ($t = 0.99$, $P = 0.32$; and $t = -1.06$, $P = 0.29$ for 2 and 3 years after translocation, respectively). The best model to predict the number of eggs produced included both body size and precipitation.

Movement

Maximum movement and start-to-end movement distances generally showed a pattern of asymptotically decreasing distances over time for translocated animals (Figs. 1 and 2). Translocated tortoises exhibited similar movements to residents in the second and third years after translocation (Table 5).

In the analysis of maximum distance moved by tortoises relative to the time (yr) since translocation, we found males in general tended to move farther than females (1,567 m vs. 917 m, respectively; $F_{1,248} = 19.14$, $P \leq 0.001$), and translocated animals moved farther overall than did residents (1,578 m vs. 582 m; $F_{1,196} = 38.6$, $P \leq 0.001$). We found differences in the pattern over time of the translocated and resident animals ($F_{1,248} = 83.79$, $P \leq 0.001$); movements of residents were similar among the 3 years and the maximum distance moved by translocated animals decreased in each year following translocation (Fig. 2).

Analyses of the start-to-end distances for each year showed a similar pattern to that of the maximum distance analyses; males displaced farther than females ($F_{1,248} = 19.14$, $P \leq 0.001$), and translocated animals displaced farther annually than residents ($F_{1,196} = 83.79$, $P \leq 0.001$). We found a time by translocation interaction for this measure

Table 4. Average number of eggs produced by female desert tortoises at each study site for each year of the study in Nevada and Utah. We summarize animals (*n*) within sites by treatment groups (RES = residents, T = translocated tortoises and is followed by year translocated). Abbreviations for site names are: Bird Spring Valley (BSV); Lake Mead (LM); Pahcoon (PAH); Shivwits (SHIV); and Sandstone Mountain (SSM). There were no significant differences among translocation groups within sites.

Site	Year	Treatment group	No. eggs	95% CI	*n*
BSV	1997	Res	2.5	0.89	26
BSV	1998	Res	6.0	0.98	33
BSV	1999	Res	4.4	1.11	33
BSV	1997	T97	2.8	1.92	11
BSV	1998	T97	4.7	1.83	22
BSV	1999	T97	3.3	1.60	20
BSV	1998	T98	7.0	4.80	7
BSV	1999	T98	5.7	3.74	6
LM	1998	Res	2.8	1.90	5
LM	1999	Res	3.8	2.27	5
LM	1998	T98	3.2	2.11	14
LM	1999	T98	7.0	2.19	14
Area 31	1998	Res	7.5	2.39	10
Area 31	1999	Res	7.3	2.32	12
Area 31	2000	Res	5.0	1.03	10
SHIV/PAH	1998	T98	5.3	2.86	7
SHIV/PAH	1999	T98	5.6	7.46	5
SHIV/PAH	2000	T98	6.0	2.25	4
SSM	1999	T99	1.5	8.61	4
SSM	2000	T99	6.0	13.15	3

of movement as well; displacement distances of translocated animals decreased over time, and residents remained similar among years ($F_{1,248} = 83.79$, $P \leq 0.001$).

Site Fidelity

After translocation, we found a general progression of habitat use where the majority of animals transitioned from random or dispersal movement patterns to constrained movements in subsequent years, indicating increasing site fidelity. This pattern was evident at each of our sites, with the exception of Sandstone Mountain, where a greater proportion of animals had constrained habitat use patterns in their first year (Table 6). Resident animals had fairly consistent patterns among years, and translocated animals approached those levels over time. The proportion of translocated animals with constrained habitat use patterns 2–3 years after translocation tended to be approximately 0.60–0.65. The Pahcoon and Shivwits sites were unique in that they were the only sites with substantial numbers of animals that showed habitat use patterns categorized as dispersal after 3 years, and these were also the sites with atypical tortoise habitat (Table 6).

DISCUSSION

Survivorship

Reported survivorship in translocation studies of reptiles is mixed, with examples of both low and high survivorship reported for many species groups (e.g., snakes, Plummer and Mills 2000, King and Stanford 2006; lizards, Towns 1994, Platenberg and Griffiths 1999; and turtles, Hester et al. 2008, Tuberville et al. 2008). Reviews of translocation studies in the literature provide mixed interpretation of reported results among taxa (Burke 1991, Dodd and Seigel 1991), thus species-specific research is clearly needed. In this study, survivorship of translocated desert tortoises was not significantly different from that of resident tortoises, and estimated survival rates for the season were frequently greater than 0.9 across all sites (Table 3). Exceptions to this were during 1997 (a drought year); tortoises at Bird Spring Valley experienced the highest mortality (annualized percentage = 16%) for any of the sites in any year with an estimated seasonal survival rate approximately 0.8 (Table 3). Additionally, at the Pahcoon site in 1998, we observed a 23.5% annualized mortality (and seasonal estimate of 0.7) when several animals were consumed by a fire that elevated mortality unrelated to the treatments in this study. However, neither the release date (for Bird Spring Valley tortoises released in 1997), nor the length of time that tortoises spent in captivity prior to translocation (among all of our sites) were significant predictors of the survivorship of translocated tortoises. Animals released among all study sites spent an average of 1.25 years (455 days) in captivity, with many (approx. 20%) exceeding 2 years. Thus, animals subsidized with food and water while in captivity for long periods were equally able to survive as those that spent less time in captivity. This finding is corroborated by Field et al. (2007); they directly manipulated pre-release feeding and watering, and found similar survivorship.

Most mortality during our study appeared to be due to canid predation, and irrespective of whether the tortoises had been translocated. Neither disease nor stress due to translocation seemed to predict which tortoises would be killed (Woodbury and Hardy 1948, Peterson 1994), which is a similar result to that reported by Esque et al. (2010) in desert tortoises. Most of the dead tortoises were found eviscerated, but with their shells intact, and canid footprints typically surrounded the carcasses. Fresh digesta often remained near the carcasses, thus although forage was relatively scarce that year (Table 1), starvation seemed an unlikely cause of death. Similar research found that desert tortoises might be subject to elevated mortality following drought periods, especially in

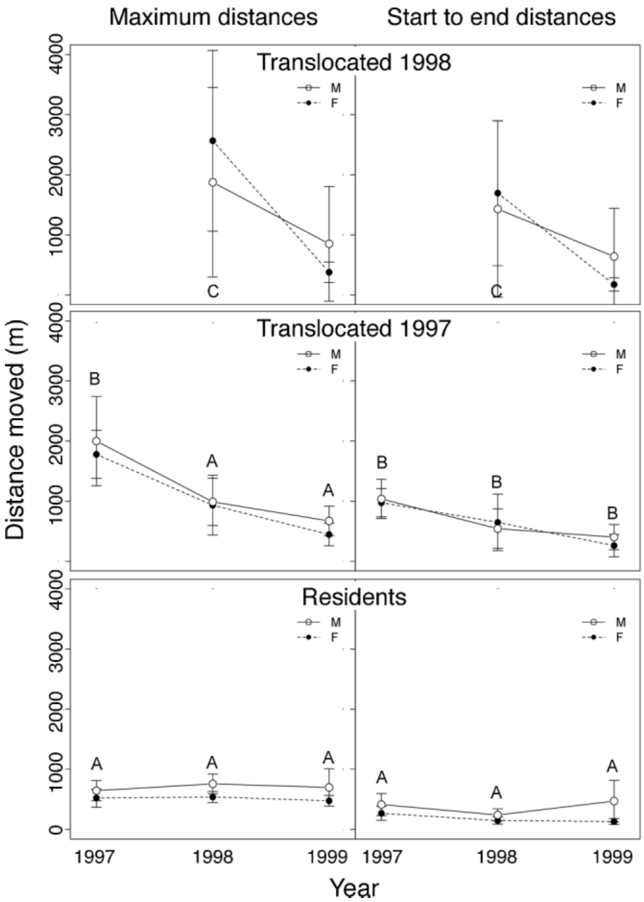

Figure 1. Means of maximum distances moved (left hand column) and start to end distances (right hand column) by desert tortoises at the Bird Spring Valley site. Residents are in the bottom panel, tortoises translocated in 1997 are in the center panel, and tortoises translocated in 1998 are in the top panel. Males are indicated by the open circles, and females are indicated by the black circles. Males moved significantly further than females for both maximum and start to end distances. Significant differences when comparing treatment groups for each movement are indicated by letters (A, B, or C) above the values for each year. Error bars are the 95% confidence interval of the mean.

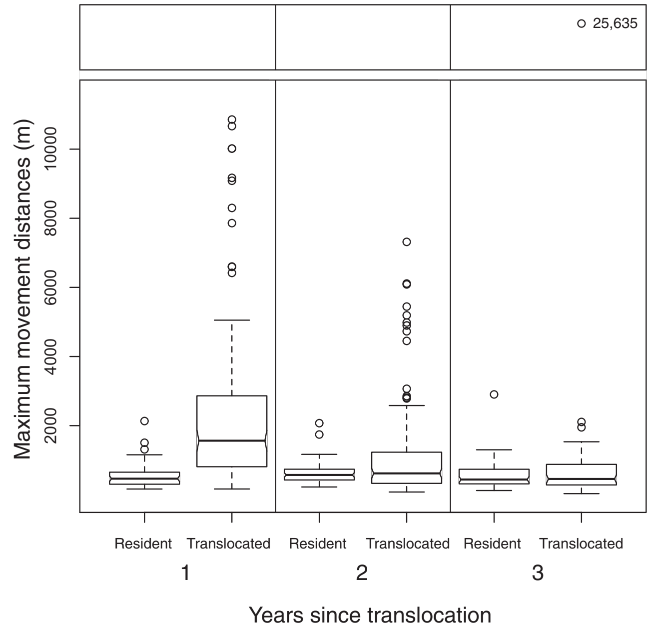

Figure 2. Maximum movement distances and years since translocation for resident (left) and translocated (right) desert tortoises at all sites combined in Nevada and Utah, 1997–2000. The median for each year and group is given as the bold horizontal line, with the notches indicating the confidence interval of the median. The upper and lower edges of the box indicate the 75th and 25th quartiles, respectively, and the whiskers indicate the range of the data that are non-outliers (open circles).

areas with elevated human populations nearby (Esque et al. 2010).

We translocated animals to Bird Spring Valley in 1997 over a 45-day period. During this time, environment temperatures increased greatly, which could have caused additional stress to animals released later in the season, as tortoises may have been unfamiliar with the shade resources and cover sites needed to protect them from temperature extremes (Cook et al. 1978). However, we did not find evidence that the

Table 5. Means of maximum displacement and start to end displacement distances of desert tortoises in Nevada and Utah for each site, year, and treatment group (RES = residents, T = translocated tortoises and is followed by year translocated). Comparisons of groups within each site are given in columns immediately following distances, with letters indicating significant differences at the $\alpha = 0.05$ (**), or $\alpha = 0.10$ (*) level. Abbreviations for site names are: Bird Spring Valley (BSV); Lake Mead (LM); Pahcoon (PAH); Shivwits (SHIV); and Sandstone Mountain (SSM).

Site	Year	Treatment group	Max. distance (m)	Start to end distance (m)
BSV	1997	RES	588a	149a
	1997	T97	1867b**	781b**
	1998	RES	613a	59a
	1998	T97	955a	244b**
	1998	T98	2,354b**	969c**
	1999	RES	561a	68a
	1999	T97	533a	157b*
	1999	T98	551a	214b*
LM	1998	RES	721a	463a
	1998	T98	1,295b*	1,052b**
	1999	RES	524a	252
	1999	T98	554a	307
SHIV	1998	T98	3,422a	2,644
	1999	T98	2,119b**	1,654
	2000	T98	2,873a	2,556
PAH	1998	T98	6,164a	5,835a
	1999	T98	2,452b**	1,545b**
	2000	T98	761c**	493c*
SSM	1999	T99	1,811a	1,185a
	2000	T99	491b**	198b*

Table 6. Site fidelity for resident and translocated desert tortoises in Nevada and Utah expressed as proportions of animals at each site. We provide sample sizes (*n*) for each site within treatment groups (RES = residents, T = translocated tortoises and is followed by year translocated). We report differences within site and years that differ in proportions of animals with movements that were categorized as constrained, random, and dispersal; different letters in the grouping column represent significant differences between groups and we report *P* values for each comparison. Abbreviations for site names are: Bird Spring Valley (BSV); Lake Mead (LM); Pahcoon (PAH); Shivwits (SHIV); and Sandstone Mountain (SSM). PAH, SHIV, and SSM analyses are within sites among years as there were no residents present for comparison.

Site	Year	Treatment group	Constrained	Random	Dispersal	*n*	Grouping	*P*
BSV	1997	RES	0.63	0.37	0	51	a	0
BSV	1997	T97	0.29	0.71	0	31	b	
BSV	1998	RES	0.89	0.11	0	53	a	<0.001
BSV	1998	T97	0.62	0.38	0	42	b	
BSV	1998	T98	0.23	0.77	0	13	c	
BSV	1999	RES	0.63	0.37	0	49	a	0.55
BSV	1999	T97	0.58	0.42	0	36	a	
BSV	1999	T98	0.45	0.55	0	11	a	
LM	1998	RES	0.54	0.15	0.31	13	a	0.17
LM	1988	T98	0.37	0.04	0.59	27	a	
LM	1999	RES	0.62	0.38	0	13	a	0.95
LM	1999	T98	0.63	0.38	0	24	a	
PAH	1998	T98	0	0.64	0.36	11	a	0.01
PAH	1999	T98	0.38	0.46	0.15	13	b	
PAH	2000	T98	0.6	0.2	0.2	10	c	
SHIV	1998	T98	0.06	0.61	0.33	18	a	0
SHIV	1999	T98	0.53	0.33	0.13	15	b	
SHIV	2000	T98	0.69	0.19	0.13	16	c	
SSM	1999	T99	0.65	0.29	0.06	17	a	0.4
SSM	2000	T99	0.8	0.2	0	15	a	

release date influenced survival over the range of days we released tortoises, and no mortality occurred in that year until late summer. However, summer releases have previously been reported to be potentially lethal to translocated tortoises (Cook et al. 1978), often with high mortality within days of release. In an earlier study carried out near Lancaster, California, translocation of desert tortoises was judged to be successful (Cook et al. 1978) with an overall survival of 79%, and animals increasing in body mass in the first year after translocation. The 6 reported deaths in that study were due to the animals' inability to avoid excessive thermal conditions at the time of release. This was largely because tortoises were released in June and July of 1977, which are among the hottest times of the year (Cook et al. 1978). In fact, 3 of the 6 deaths occurred on the day of release, whereas the other 3 died within 2 weeks of release. A second group of translocated animals released in May of 1978 had 100% survivorship (Cook et al. 1978). Another translocation study (SAIC 1993) reported high mortality, but had flaws in the experimental design that severely limited the conclusions that could be drawn from the data. For example, tortoises were assumed to have died if they were missing from a study plot for a given time period rather than when carcasses were actually found, which inflated the mortality rates reported. This assumption clearly biased estimates of mortality, elevating them to as high as 57%, when in fact a mortality rate of 14% among translocated animals was supported by definitive evidence (SAIC 1993).

Reproduction

Reproduction of translocated populations is a key determinant of success (Dodd and Seigel 1991, Germano and Bishop 2009), especially translocations establishing new populations (Platenberg and Griffiths 1999, Towns and Ferreira 2001), which do not benefit from the reproduction of the resident population. Reproduction in translocated amphibians and reptiles is frequently reported (Dodd and Seigel 1991, Cook 2004, Osman 2010), but few studies report quantitative reproductive comparisons of translocated animals with residents, perhaps because of the difficulty of measuring it directly (Cook 2004, King and Stanford 2006, Hester et al. 2008). In our study, we found a slight reduction overall (approx. 1 egg less) in the first year after translocation, but similar numbers of eggs were produced every year thereafter among all sites combined. Earlier studies (SAIC 1993) suggested that the physiological stress, increased movements, and energy expenditure associated with translocation might cause female tortoises to reduce reproductive investment after translocation (Henen 2002). This could be exacerbated by animals settling in, or moving through areas with lower quality resources (Rittenhouse et al. 2008). We found similar reproductive output between residents and translocated tortoises even with increased movements for the latter. The successful first-year reproduction by our translocated animals may have been influenced, in part, by the food supplied to the tortoises while in their pre-translocation holding facilities (Henen 1997, 2002). The number of eggs produced by tortoises differed among sites and years (Table 1), which could indicate the relative dearth of food at our different sites (Henen 1997, 2002). For example, tortoises at the Lake Mead site produced approximately half the number of eggs as animals at Bird Spring Valley in each year. In 1998, which was a year of high rainfall and elevated levels of primary production (Table 1), animals at Lake Mead and Bird Spring Valley produced double the number of eggs as in the previous year (Table 4). Nevertheless, tortoises at Bird

Spring Valley still produced more eggs than tortoises from Lake Mead by the same amount as in the previous year. The numbers of eggs produced by animals at the Utah sites in all years was as high as the best year at Bird Spring Valley (1998). In addition, even the animals that were translocated to the upland sagebrush-dominated sites produced large numbers of eggs per year, perhaps reflecting the greater primary productivity of these sites as annual production and rainfall were correlated with the total number of eggs produced (Table 4).

Movement

Increased movements among translocated and reintroduced animals are among the most commonly reported responses across a broad range of taxa (e.g., black rhinoceros [*Diceros bicornis*], Linklater and Swaisgood 2008; white-tailed deer [*Odocoileus virginianus*], Jones and Witham 1990; gray wolves [*Canis lupus*], Fritts et al. 1984; sage-grouse [*Centrocercus urophasianus*], Musil et al. 1993; timber rattlesnakes [*Crotalus horridus*], Reinert and Rupert 1999; Whitaker's skinks [*Cyclodina whitakeri*], Towns 1994; Gila monsters [*Heloderma suspectum*], Sullivan et al. 2004; and three-toed box turtles [*Terrapene carolina triunguis*], Rittenhouse et al. 2007). This frequently leads to a determination of an unsuccessful translocation if site colonization is a goal of the project (Fritts et al. 1984, Dodd and Seigel 1991, Sullivan et al. 2004). Earlier translocation studies on desert tortoises indicated that animals may move away from the release site after translocation (Berry 1974, 1975, 1976, 1986; Cook 1983; Field et al. 2007), or return to the site from which they were taken (P. S. Corn, U. S. Geological Survey, unpublished data; Berry 1986). Although large movements, or site abandonment, by translocated tortoises have been recorded previously for desert tortoises (Berry 1986), and gopher tortoises (*Gopherus polyphemus*; Diemer 1984, Burke 1989, Tuberville et al. 2008), releases of other tortoise species reported different results. For example, released captive-bred ploughshare tortoises (*Geochelone yniphora*) had little movement, or homing tendency (Pedrono and Sarovy 2000), whereas gopher tortoises released into pens for a year or more showed increasing site fidelity (Tuberville et al. 2005). Two measures of movement, along with site fidelity metrics provided us with information on dispersal and habitat use of translocated and resident tortoises. In our study, translocated animals initially moved great distances (regardless of the measure of movement used) compared to residents (Fig. 3), decreasing over time for up to 2 or 3 years; site fidelity patterns transitioned from dispersal toward constrained indicating establishment of home ranges.

The patterns of movement of tortoises in atypical tortoise habitat at our 2 sites in Utah (Great Basin scrub) were qualitatively similar to movements at sites with typical habitat (Mojave desert scrub), but with important differences. The tortoises released at the Shivwits and Pahcoon sites had movement distances that were 3 to 4 times those observed at sites with typical tortoise habitat, and sustained numbers of animals with dispersal habitat use patterns. For example, tortoises at the Pahcoon site had average movement distances of 6 km during their first season in the field; 2 seasons elapsed before their movements were similar to those of Nevada residents. These longer movements generally took animals from the higher elevation site, dominated by Great Basin scrub, to a habitat more typical of higher elevation Mojave desert scrub (Brown 1994, Turner 1994). At the Shivwits site, there was no simple route to habitat containing characteristic Mojave vegetation. Tortoises at this site spent all 3 seasons in blackbrush- and sagebrush-dominated habitat, and their movement distances remained high relative to residents and other translocated animals at any of the sites for all 3 seasons. Collectively these results may indicate that tortoises at these sites continued moving in order to find areas with familiar habitat attributes and resources, as has been demonstrated in box turtles (Rittenhouse et al. 2008).

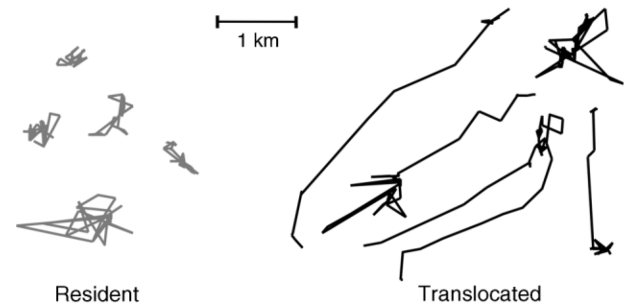

Figure 3. Movement segments between successive relocations for the first year of movement (1997) for 5 resident (gray lines) and 5 translocated (black lines) desert tortoises at Bird Spring Valley, Nevada illustrating typical first-year movements for each group.

Increased movements of translocated animals are hypothesized to have several detrimental effects, including increased exposure to predation (Sullivan et al. 2004), increased stress and excessive energy expenditure that can affect reproduction and health of individuals (Cook 2004, Sullivan et al. 2004, Kahn 2006), and preferences for different habitats or unfamiliarity with local resources (Rittenhouse et al. 2008, Pinter-Wollman et al. 2009). Counter to these hypotheses, translocated animals at each of our sites showed increased movement for 1 or more activity seasons, yet we found no evidence of elevated mortality, or reduced fecundity in these animals. Potential impacts to resident populations must also be considered when translocating animals to occupied habitats, as there may be deleterious effects to social structure, and limited resource availability (Berry 1986, Strum 2005, Linklater and Swaisgood 2008). Resident animals in our study showed no apparent change in habitat use or movements with the addition of translocated tortoises to their habitat. In addition, we saw no change in survivorship or reproductive rates during the study, which indirectly indicates that resident tortoises still had sufficient resources. Residents in other translocation studies on gopher tortoises have shown similar results (Riedl et al. 2008).

MANAGEMENT IMPLICATIONS

Using translocation for conservation is simultaneously a biological, economic, and political decision. The conservation of habitat should always take precedence for conservation planning (Reinert 1991), but when habitat is lost because of political or economical decisions, only 2 choices remain: 1) leave animals in harm's way to die (no conservation), or 2) collect the animals assuming that they may be useful for conservation in the future. Translocation can be especially valuable to deal with animals that have already been displaced from natural habitat (e.g., taken animals under the Endangered Species Act). Indeed, translocation really is the last and only biological and economic alternative under these circumstances. The protocol by which we have translocated desert tortoises has been successful by all reasonable short-term measures. Below are several issues that should be considered for future translocation efforts of this species.

1. Desert tortoises tend to move great distances in the first season after translocation. They do not adopt home ranges in their first season, but rather engage in more linear, dispersal, movement patterns. By the second season, translocated tortoises tend to establish home ranges. However, this settling process (Berry 1986) takes longer or may not be reached for tortoises translocated to atypical tortoise habitat (e.g., areas with vegetation not typically associated with desert tortoise). This may be important when selecting a translocation site, or when selecting where to release animals within a large site (Berry 1986). Mangers should consider increased movement distances of translocated tortoises when evaluating sites for potentially risky features within expected movement paths such roads with heavy traffic (von Seckendorff Hoff and Marlow 2002), unless the boundaries of the unsuitable features are fenced.
2. Tortoises should be released in spring or fall, to avoid inhospitably hot summer months as animals that are initially released in inhospitable abiotic conditions may fail to find adequate shelter from potentially lethal environments (Cook 1983). Although we found no detriment in our winter releases, further study may be needed to ensure the merits of winter translocations.
3. At each of our study sites, translocated tortoises produced the same number of eggs as resident animals. Thus, translocated animals may contribute to recruitment of hatchlings to the population. Adult female tortoises may be especially valuable members of the population (Doak et al. 1994) and would be a preferred demographic group when considering candidates for translocation (Berry 1986).

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