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Contributed Paper

Multiyear monitoring of survival following mitigation-driven translocation of a long-lived threatened reptile

Brett G. Dickson,[1,2]* Rick D. Scherer,[1] Amanda M. Kissel,[1] Bryan P. Wallace,[1] Kathryn M. Langin,[1] Miranda E. Gray,[1] Amanda F. Scheib,[3] and Bruce Weise[4]

[1]Conservation Science Partners, Inc. 11050 Pioneer Trail, Suite 202, Truckee, CA 96161, U.S.A.
[2]Landscape Conservation Initiative, School of Earth and Sustainability, Northern Arizona University, P.O. Box 5694, Flagstaff, AZ 86011-5694, U.S.A.
[3]Scheib Biological LLC, 2625 Chateau Clermont Street, Henderson, NV 89044, U.S.A.
[4]Southwestern Ecological Research Company, 215 E. 18th Street, Tucson, AZ 85701, U.S.A.

Abstract: Translocation is used by managers to mitigate the negative impacts of development on species. Moving individuals to a new location is challenging, and many translocation attempts have failed. Robust, post-translocation monitoring is therefore important for evaluating effects of translocation on target species. We evaluated the efficacy of a translocation designed to mitigate the effects of a utility-scale solar energy project on the U.S. federally listed Mojave desert tortoise (*Gopherus agassizii*). The species is a long-lived reptile threatened by a variety of factors, including habitat loss due to renewable energy development in the Mojave Desert and portions of the Colorado Desert in southern California (southwestern United States). We translocated 58 individual tortoises away from the project's construction site and intensively monitored them over 5 years (2012–2017). We monitored these individuals and tortoises located in the translocation release area (resident tortoises; $n = 112$) and control tortoises ($n = 149$) in a nearby location. We used our tortoise encounter data and known-fate survival models to estimate annual and cumulative survival. Translocated tortoises in each of 2 size classes (120–160 mm, >160 mm) did not survive at lower rates than resident and control tortoises over the study period. For models with different sets of biotic and abiotic covariates, annual and cumulative estimates of survival were always >0.87 and >0.56, respectively. Larger tortoises tended to have higher survival, but translocated tortoises were not differentially affected by the covariates used to model variation in survival. Based on these findings, our translocation design and study protocols could inform other translocation projects for desert species. Our case study highlights the benefits of combining rigorous scientific monitoring with well-designed, mitigation-driven management actions to reduce the negative effects of development on species of conservation concern.

Keywords: climate, conservation, desert ecosystems, habitat, renewable energy development

Monitoreo Multianual de la Supervivencia de un Reptil Longevo en Peligro después de una Reubicación por Mitigación

Resumen: Los administradores utilizan la reubicación para mitigar los impactos negativos que el desarrollo tiene sobre las especies. El traslado de individuos hacia una nueva ubicación es todo un reto y muchos intentos de reubicación han fallado. Por esto el monitoreo robusto post-reubicación es importante para la evaluación de los efectos de la reubicación sobre las especies. Evaluamos la eficiencia de una reubicación diseñada para mitigar los efectos de un proyecto de energía solar fotovoltaica sobre la tortuga terrestre del desierto de Mojave (*Gopherus agassizii*), una especie en la lista federal estadunidense de especies en peligro. Los reptiles de esta especie

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*email: brett.dickson@nau.edu

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son longevos y se encuentran en peligro por una variedad de factores, incluyendo la pérdida del hábitat por el desarrollo de energías renovables en el desierto de Mojave y en porciones del desierto del Colorado en el sur de California (suroeste de los Estados Unidos). Reubicamos a 58 individuos de esta especie para alejarlos del sitio de construcción del proyecto y los monitoreamos intensivamente durante cinco años (2012 – 2017). Monitoreamos a estos individuos y a las tortugas que ya se encontraban en el sitio de liberación (tortugas residentes; $n = 112$), así como a un grupo control de tortugas ($n = 149$) en una ubicación cercana. Usamos nuestros datos de encuentro con tortugas y modelos de supervivencia con destino conocido para estimar la supervivencia anual y acumulativa. Las tortugas reubicadas en cada una de las dos clases de tamaño (120–160 mm, >160 mm) no sobrevivieron a tasas más bajas que las residentes y las del grupo control durante el periodo de estudio. Para los modelos con conjuntos diferentes de co-variados bióticos y abióticos los estimados anuales y acumulativos de supervivencia fueron siempre >0.87 y >0.56, respectivamente. Las tortugas más grandes tendieron a tener una mayor supervivencia, aunque las tortugas reubicadas no se vieron afectadas diferencialmente por los co-variados que se usaron para modelar la variación de la supervivencia. Con base en estos hallazgos, nuestro diseño de reubicación y nuestros protocolos de estudio podrían informar a otros proyectos de reubicación para especies de desierto. Nuestro estudio de caso resalta los beneficios de la combinación del monitoreo científico riguroso con acciones de manejo bien diseñadas y llevadas por la mitigación para reducir los efectos negativos del desarrollo sobre las especies de importancia para la conservación.

Palabras Clave: clima, conservación, desarrollo de energía renovable, ecosistemas desérticos, hábitat

摘要: 管理者常常用迁地保护的策略来减缓发展对生物的负面影响。然而, 将生物转移到新环境也是一种挑战, 许多迁地保护的尝试都以失败告终。因此, 转移后需要通过稳健的监测来评估迁地行动对目标物种的影响。本研究评估了一项旨在减缓太阳能公共设施建设对莫哈韦沙漠龟 *(Gopherus agassizii)* 影响的迁地保护项目成果, 这种乌龟已被美国联邦政府列为濒危物种。该物种是一种寿命较长的爬行动物, 正面临许多因素的威胁, 包括因莫哈韦沙漠和科罗拉沙漠在南加州部分地区 (美国西南部) 的可再生能源开发导致的生境丧失。我们将五十八只龟从开发施工地迁出, 并在五年时间内 (2012–2017‘~‘¥) 对它们进行了严密监测。除了这些个体外, 我们还监测了分布在迁地保护释放区域的莫哈韦沙漠龟 (本地种群, $n = 112$) 和生活在附近区域的对照种群 ($n = 149$) 。我们利用这些乌龟的遇见数据和已知的生存模型估计了年存活率和累计存活率。在研究期间, 两组不同大小 (120–160 mm 或大于 160 mm) 迁地个体的存活率都不低于本地种群或对照种群。在考虑了不同生物及非生物协变量的模型中, 年存活率和累计存活率的估计值均分别高于 0.87 和 0.56 。较大的乌龟存活率更高, 而模型中影响存活率的因素对迁地保护个体的影响与其它个体相比没有很大差异。基于以上发现, 我们认为本研究的迁地保护设计及研究方案可以为其它荒漠物种的迁地保护计划提供参考。我们的案例研究还表明, 严格的科学监测与精心设计的减缓影响管理行动相结合, 有利于减缓发展对受保护物种的负面影响。**【翻译: 胡怡思; 审校: 聂永刚】**

关键词: 气候, 保护, 荒漠生态系统, 生境, 可再生能源发展

Introduction

Habitat loss and degradation are primary causes of species endangerment and extinction (Pimm et al. 2014), so strategies that help mitigate the negative effects of human activities that alter natural areas are important for long-term conservation of populations. In cases where habitat loss is unavoidable (e.g., due to expanding human needs for natural resources), translocation—the assisted movement of individual organisms from one location to another—can be a useful management tool for establishing new populations, augmenting existing populations, and maintaining connectivity across the landscape (Seddon et al. 2007; Germano et al. 2015). When used to move individuals away from areas slated for habitat alterations, mitigation-driven translocation of herpetofauna can reduce or otherwise minimize the negative impacts of anthropogenic activities on those individuals (Sullivan et al. 2015). Despite their increasing use as conservation tools, mitigation-driven translocations often are inadequately executed; for example, monitoring and documentation are insufficient and implemented without broader conservation goals in mind (Griffith et al. 1989; Germano et al. 2015). The variable outcomes of previous translocation attempts underscore the importance of testing designs and thoroughly documenting conditions that lead to successful translocations (Seddon et al. 2007; Batson et al. 2015).

We examined the efficacy of a mitigation-driven translocation involving the Mojave desert tortoise (*Gopherus agassizii*). This species is listed as threatened under the U.S. Endangered Species Act due to several threats, including loss and degradation of habitat from human activities, increased predation by animals subsidized by the presence of human infrastructure (e.g., waste receptacles), and disease (USFWS 2011*a*). In recent years, translocation of tortoises has been implemented in several locations in the Mojave Desert to mitigate for military training and renewable energy development (Drake et al. 2012; Farnsworth et al. 2015). Desert tortoise translocations have had mixed results, and published studies of translocation events only include up to 3 years of monitoring (e.g., Field et al. 2007; Esque et al. 2010; Drake et al. 2012; Nussear et al. 2012). Mojave desert tortoises live to ∼50 years in the wild (Medica et al. 2012), and long-term studies of *Gopherus* spp. in the southwestern United States have detected substantial annual variation in survival (Zylstra et al. 2013; Lovich et al. 2014), mostly driven by drought severity. Thus, long-term monitoring is essential for understanding the efficacy of translocation, particularly for long-lived species such as desert tortoises (Tuberville et al. 2008; Germano et al. 2015).

Previous studies documented short-term effects on space-use patterns and thermal conditions of tortoises translocated as part of our study in the Ivanpah Valley, southern California (U.S.A.) (Farnsworth et al. 2015; Brand et al. 2016). Similar to other studies (Nussear et al. 2012; Hinderle et al. 2015), translocated tortoises in the Ivanpah Valley had larger home ranges and were subjected to higher ambient temperatures in the initial 2 months of the first active (i.e., nonhibernation) season after translocation than did resident and control tortoises. However, space-use patterns and thermal conditions of translocated tortoises were indistinguishable from control and resident tortoises thereafter (Farnsworth et al. 2015; Brand et al. 2016). Based on these findings, we hypothesized that long-term space-use patterns and thermal conditions could still influence survival of translocated tortoises.

We used a monitoring and modeling approach designed to estimate posttranslocation survival and identify potential drivers of variation in tortoise survival over 5 years (2012–2017). Five broad sets of biological and physical factors were hypothesized to influence survival (USFWS 2011*b*): weather (e.g., precipitation, temperature), disease, vegetation, physical features (e.g., soil, topography), and anthropogenic factors (e.g., barriers to movement). Our principal objectives were to evaluate, first, whether translocated tortoises had lower survival than control and resident study groups and, second, whether sets of biotic and abiotic covariates hypothesized to influence tortoise survival had a differential effect on tortoises in the 3 study groups.

Methods

Study Area

We conducted our study in an area adjacent to the Ivanpah Solar Electric Generating System (ISEGS), a ∼400-megawatt solar energy facility in the Ivanpah Valley of California, approximately 75 km southwest of Las Vegas, Nevada (U.S.A.) (Fig. 1). This area contains high-quality tortoise habitat and important for maintaining linkages between Mojave desert tortoise conservation areas in California and Nevada (USFWS 2011*a*, 2011*b*). The principal vegetation community is Mojave Desert scrub, a community dominated by creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*), though areas with alkali sink scrub vegetation (family Chenopodiaceae) also are present. Annual rainfall is low (∼20 cm), and most precipitation occurs in winter (December through February) and in the summer monsoon season (peak in July and August) (Global Historical Climatology Network station USC00267369, Searchlight, Nevada). Six on-site weather stations recorded annual rainfall of 17 cm in 2013, 18 cm in 2014, 9 cm in 2015, and 10 cm in 2016. Construction of the ISEGS facility was initiated in 2010 and completed in May 2014; infrastructure consisted of a solar thermal power plant and fences that surround the project.

Tortoise Translocation and Monitoring

Starting in October 2010, tortoises were collected in the area affected by ISEGS. Captured animals were placed in quarantine to test for signs of disease and bacterial infection (*Mycoplasma* spp.) (Fig. 1). Tortoises captured within the project boundary were held in quarantine until April 2012, at which point tortoises with a midline carapace length (MCL) of at least 120 mm were released into the area just outside (<500 m) the ISEGS project boundary ($n = 73$). Tortoises slated for translocation were soaked in water for 1 hour the day prior to release and were given access to drinking water immediately prior to release. All tortoise handling and translocation followed U.S. Fish and Wildlife Service protocols and handling guidelines (USFWS 2011*b*) and are detailed in Farnsworth et al. (2015).

In 2011 surveys were conducted in the area surrounding the ISEGS project boundary to locate, measure, and track tortoises, with the goal of monitoring individuals that had not been subject to translocation. A portion ($n = 112$) of those individuals were located in the vicinity of the ISEGS boundary in the area where translocated tortoises were moved. These tortoises were referred to as the resident group. An additional study group ($n = 149$) occupied 2 areas on the east side of Interstate Highway 15, opposite the ISEGS site, and were separated by a dry lake bed and a railroad line (Fig. 1). Tortoises in these 2 areas, which together encompassed the range of habitat conditions found in each of the other areas, were pooled for the survival analyses and are referred to as the control group.

Tortoises in all 3 study groups were equipped with radio transmitters (Holohil Systems, Ontario, Canada) with the method described in Boarman et al. (1998). A subset of radio-tagged tortoises ($n = 236$; 87 control, 75 resident, and 58 translocated) was also fitted with temperature data loggers (Thermochron DS1922L, iButtonLink, Whitewater, WI, U.S.A.) on their carapaces to record ambient temperatures (Brand et al. 2016) and

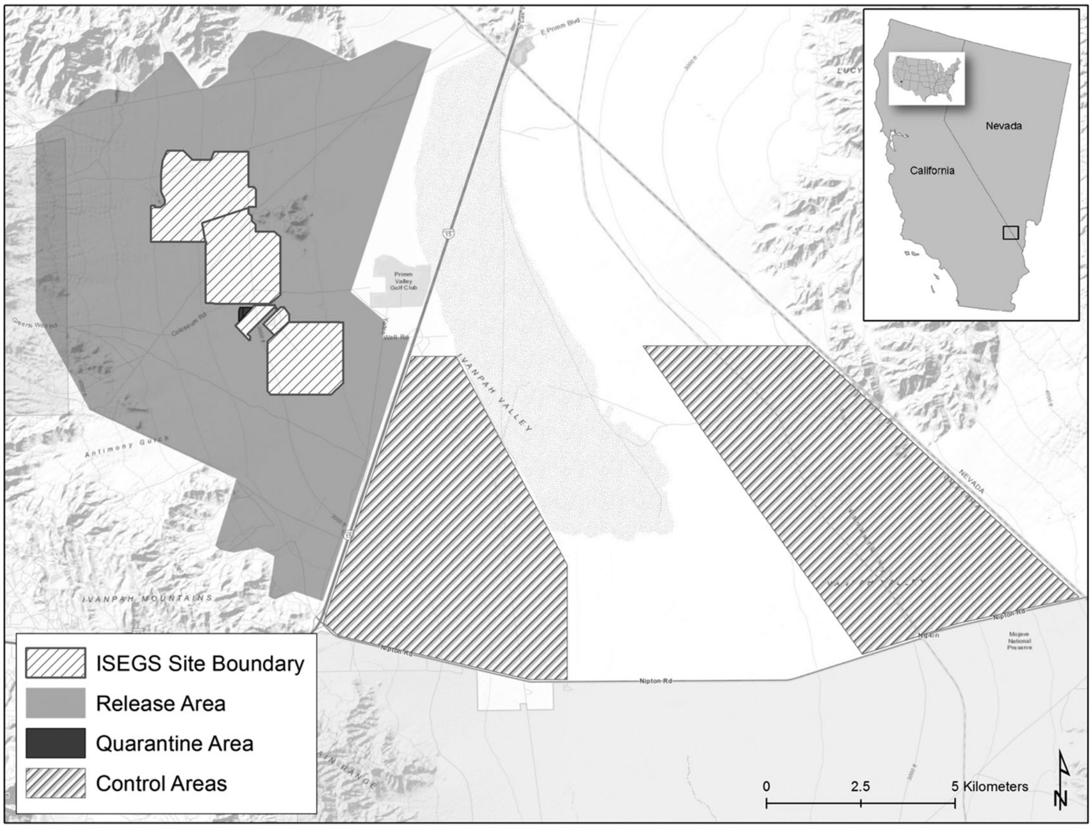

Figure 1. Ivanpah Valley, California, study area, including area affected by Ivanpah Solar Electric Generating System (ISEGS) facility, tortoise translocation release area, quarantine area, and control areas.

derive survival model covariates (Table 1). From April 2012 to May 2017, tortoises were located on an approximately weekly basis during the active period (i.e., typically mid-February through mid-October) to confirm survival and to quantify space-use patterns and movement behavior (Farnsworth et al. 2015; Sadoti et al. 2017).

Tortoises were also located and recaptured on a biannual basis (May and September) to conduct health assessments, which included the collection of data on sex (when possible, based on physical characteristics), size (MCL, measured to 1.0 mm with metal calipers), and body condition scores (Lamberski 2013). As stipulated by USFWS guidelines (USFWS 2011*c*), health assessments also facilitated enzyme-linked immunosorbent assay (ELISA) testing for presence of *Mycoplasma* spp. infections, as well as analyses of heavy metal concentrations in tortoise blood (USFWS 2011*b*). However, disease prevalence was extremely low (32 of 4,158 samples; <1%) and metal concentrations (e.g., mercury) rarely exceeded detection thresholds, or were extremely low when they did (e.g., lead) (Dickson et al. 2017). Thus, neither disease nor toxicology data were included in our survival analyses.

Upon finding a dead tortoise, we recorded the suspected circumstances of its death (Supporting Information). This included notes of trauma on the tortoise (e.g., tooth or chew marks, missing limbs, etc.), other evidence of predators or scavengers (e.g., scat, hair, tracks), and other indicators that may have provided insight into the suspected cause of death. Because of substantial uncertainty associated with the specific cause and timing of death, as well as small sample sizes, these records were not included in our survival analyses.

Environmental Variables

To quantify environmental variables hypothesized to influence tortoise survival, we derived multiple data layers (Table 1), including shrub density, wash density, and the normalized difference vegetation index (a proxy for vegetation cover or forage availability [Pettorelli et al. 2011]) developed from remotely sensed data (high-resolution aerial photography and satellite imagery). Daily gridded 4-km weather data (gridMET) (Abatzoglou 2011) were used to derive temperature and precipitation variables. We cross-checked these data with ground data on vegetation attributes (namely, shrub species, cover, and height), temperature, and precipitation collected at our study area and found that our field data were strongly correlated with the corresponding remote-sensing and gridded weather data (Dickson et al. 2017; Supporting Information). We also obtained or derived data layers describing elevation, slope, aspect, topographic

Table 1. Covariates used in 4 analyses of tortoise survival in the Ivanpah Valley, California. individual (analysis 1), body condition (analysis 2), ambient temperature (analysis 3), and environmental covariates (analysis 4).

Analysis	*Covariates*	*Description*
Individual	group	translocated, resident, and control
	size	midline carapace length (MCL) during spring health assessment preceding survival interval
	sex	adult male, adult female, and immature (i.e., unknown sex)
Body condition[a]	body condition score	numeric score (1–7) indicating the relative degree of emaciation (lowest body condition = 1)
Ambient temperature[a]	maximum temperature (maximum)	average daily maximum temperature a tortoise experienced during an active season, based on iButton data loggers
	duration ≥ 35 °C (duration)	average daily duration a tortoise experienced temperatures ≥ 35 °C during an active season, based on iButton data loggers
Environmental covariates[a]	area	area (ha) of the active season home range (i.e., under the utilization distribution)
	burrow density (burrow)	estimate of burrow density within each individual's home range based on a map derived from tortoise encounters within burrows
	shrub density (shrub)	estimate of shrub cover within each individual's home range based on 1-m aerial photography and estimates of normalized difference vegetation index (NDVI)
	wash density (wash)	estimate of wash density within each individual's home range based on 1-m aerial photography and estimates of NDVI
	topographic roughness	standard deviation of elevation within a home range
	soil bulk density (soil)	weight of soil in a given volume
	mean NDVI (NDVI.Mean)	Landsat-derived proxy for forage availability and vegetation cover across a home range
	coefficient of variation of NDVI (NDVI.CV)	Landsat-derived proxy for of the variability in forage availability and vegetation cover across a home range
	road density (road)	estimate of the density of roads within a home range
	fence density (fence)	estimate of the density of fences within a home range
	precipitation	total precipitation at a home range over each active season, derived using gridded weather data
	maximum temperature (Tmax)	mean daily maximum temperature within a home range over each active season, derived using gridded weather data

[a] *Effects of MCL and group included in all analyses, as defined under individual analysis.*

roughness, soil properties, road and fence density, and burrow density. Data and methods used to derive our environmental variables also followed Farnsworth et al. (2015) and Sadoti et al. (2017).

All environmental variables were summarized within the areas of individual tortoise home ranges and used as covariates in the models described below. For each individual tortoise in each group and in each active season, home range area was derived using a 95% fixed-kernel density estimation approach and a resultant utilization distribution (UD) (Farnsworth et al. 2015). A UD was calculated for all individuals with ≥25 encounters during an active season, which was meant to balance the selection of an appropriate minimum number of encounters with removal of individuals from the data set.

Survival Analyses

We used the tortoise tracking data and a known-fate model (White & Garrott 1990) implemented in program R (R Core Team 2017) using the package RMark (Laake 2013) to estimate annual and cumulative (duration of the study) survival probabilities and to evaluate the influence of individual and environmental covariates from May 2012 to May 2017 for control, resident, and translocated tortoises. A known-fate model is often used to estimate survival probability when marked individuals can be located with certainty. This was the case in our study because animals were radio tagged and monitored consistently. We used encounter data collected during annual spring health assessments as the focal sampling period; thus, estimates of survival probability are for the interval from May in a given year to May the following year. Tortoises from the easternmost control area were not monitored after May 2016, so tortoises from this group were removed for the final interval (May 2016 to May 2017).

Based on the covariates described above, we developed a set of candidate models that represented competing hypotheses regarding causes of variation in survival probability. We used an information-theoretic approach (Burnham & Anderson 2002) to evaluate relative levels of support for competing models. We calculated Akaike's information criterion adjusted for small sample size (AIC_c) and, prior to modeling, centered and standardized values

Table 2. Sample sizes for the large (midline carapace length [MCL] > 160 mm) and small (MCL 120–160 mm) tortoise size classes and for each of 4 analyses of tortoise survival in the Ivanpah Valley, California.

Analysis	*Size class*	*Control*	*Resident*	*Translocated*	*Total*	*Encounters*[a]
Individual covariates	large	125	95	67	287	1263
	small	24	8	8	40	68
Body condition covariates	large	125	95	67	287	1247
	small	24	8	8	40	68
Ambient temperature covariates	large	84	73	53	210	925
	small	11	4	7	22	31
Environmental covariates	large	123	93	65	281	1232
	small	23	8	8	39	67

[a] *Number of encounters reflects the total number of times individuals were encountered with certainty from May 2012 to May 2017. A tortoise was removed from an analysis when it was not encountered or covariate data were not available for a particular interval.*

for all continuous covariates. We tested for correlations between covariates using a Pearson's correlation matrix, but no 2 covariates had a Pearson's correlation coefficient $> |0.70|$, so all combinations of covariates could be included in the same models. We ranked candidate survival models according to differences in their AIC_c values and considered models within 8.0 AIC_c of the lowest relative value to be those that best approximated the data (Anderson 2008), and we used a model with no covariates (i.e., a null model) to help evaluate how well candidate models with covariates approximated (and fit) the data (Anderson 2008). For each set of candidate models, we evaluated the relative strength of evidence in favor of a given covariate using the sum of AIC_c weights ($w_+[j]$; Burnham & Anderson 2002). We used model averaging of all possible subsets of covariates to produce estimates of annual and cumulative survival probability, drawing inference from more than 1 model when multiple models were supported by the data (Burnham & Anderson 2002).

Data for development of covariates were not available for all tortoises in all years. For example, only a subset of radio-tagged tortoises were fitted with temperature data loggers. Similarly, MCL or body condition scores were missing at the start of an interval for <1% of tortoises. In those cases, we removed tortoises for the interval for which MCL or body condition data were missing. To leverage all existing data, we developed different data sets to evaluate the effects of covariates on survival (see below and Tables 1 & 2 for details), and ran 4 separate analyses based on individual (analysis 1), body condition (analysis 2), ambient temperature (analysis 3), and environmental covariates (analysis 4).

The first analysis (individual covariates, analysis 1) had the largest number of encounters and the least amount of censoring caused by missing covariate data (Table 2). Thus, this analysis was the most robust evaluation of the effects of translocation on the survival probability of tortoises. For analyses 2–4, we evaluated effects of other covariates and interactions between covariates and study group, while controlling for MCL. To determine whether survival probability differed between males, females, and individuals of unknown sex (i.e., immature tortoises), we conducted a preliminary analysis of the analysis 1 data set. Because we found no differences, we did not include effects of sex or life stage in subsequent analyses.

We performed separate survival analyses for large (MCL > 160 mm) and small (MCL = 120–160 mm) tortoises based on size classes defined in and required by the Revised Biological Opinion (USFWS 2011*b*). Tortoises were assigned to 1 of these size classes based on their MCL measurement at the beginning of a given survival interval. Due to small sample sizes in the small-tortoise data set (Table 2), we did not include sex and year as covariates in any analyses and we omitted interactions between group and covariates in analyses 3 and 4.

Results

Individual Covariates

For the large tortoises (>160 mm), there were no statistical differences among groups for the annual or cumulative survival estimates (Fig. 2). Model-averaged estimates of annual survival probability were >0.96 and cumulative survival was ≥0.80 or greater for all groups (Fig. 2 & Supporting Information). The MCL was a strong ($w_+[j] = 1.0$) predictor of survival probability for individual tortoises in the large size class and was included in each of the 5 highest ranked models (Table 3). For reference, estimates of annual survival probability from the highest ranked model for the large tortoise size class ranged from 0.89 (95% CI, 0.77–0.95) for a tortoise with an MCL of 161 mm (the smallest tortoise in the large-size-class data set) to 1.00 (95% CI, 0.98–1.00) for a tortoise with an MCL of 319 mm (largest tortoise in our large-size-class data set). The model that included only the effect of MCL had considerably more support than the model with no covariates ($\Delta\text{AIC}_\text{c} = 11.3$). The model that included only a group effect, in contrast, had less support than the model with no covariates ($\Delta\text{AIC}_\text{c} = 0.4$). For both size classes, we did not detect a group-level effect (i.e., a statistical difference among groups) in any of the survival analyses that follow.

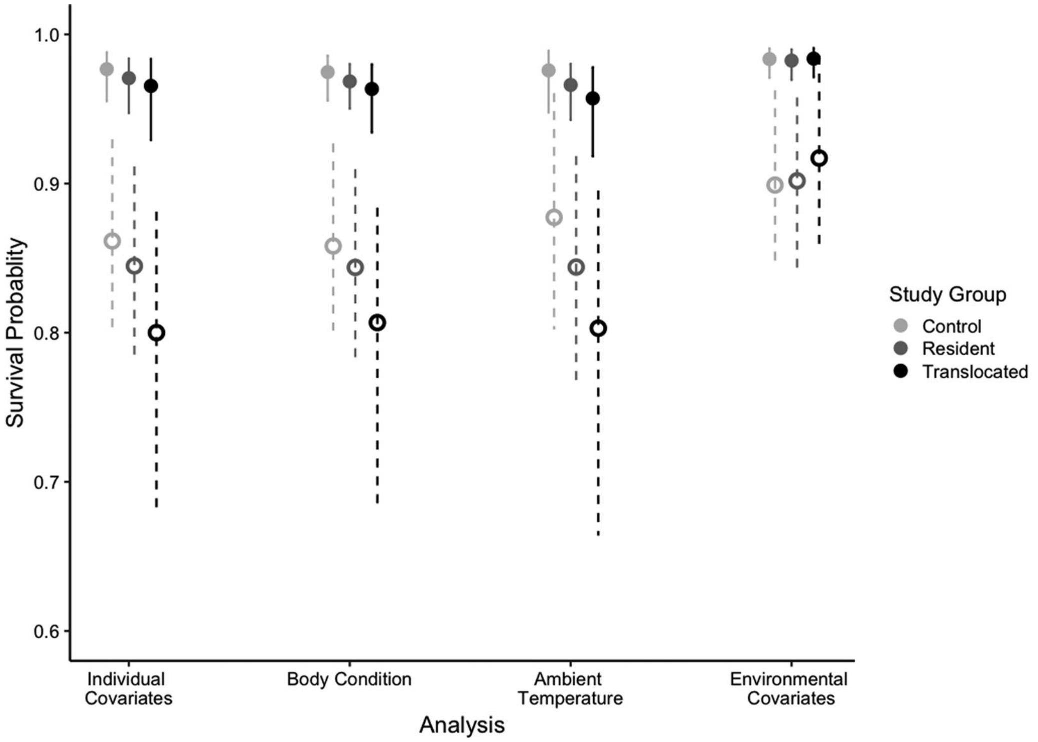

Figure 2. Average annual (filled circles) and cumulative (2012–2017) (open circles) survival estimates for Mojave desert tortoises with a midline carapace length >160 mm (large-tortoise data set) in 3 study groups (control, resident, translocated) and for 4 analyses with different sets of covariates (Table 1) (dashed lines, 95% CI).

Table 3. Candidate model-selection results for the evaluation of effects of group, midline carapace length (MCL), and year for the large (MCL > 160 mm) and small (MCL 120–160 mm) tortoise size classes monitored in the Ivanpah Valley, California.

Model	k^a	$-2LL^b$	AIC_c^c	ΔAIC_c^d	w_i^e
Large tortoises					
group + MCL	4	357.8	365.8	0.0	0.43
MCL	2	361.9	365.9	0.1	0.41
year + MCL	6	357.1	369.2	3.4	0.08
group * MCL	6	357.5	369.6	3.7	0.07
year * MCL	10	354.0	374.1	8.3	0.01
no covariates	1	375.2	377.2	11.4	0.00
group	3	371.6	377.6	11.8	0.00
group + year	7	367.4	381.5	15.7	0.00
group * year	15	360.3	390.7	24.9	0.00
Small tortoises[f]					
no covariates	1	45.1	47.1	0.0	0.49
MCL	2	43.5	47.7	0.6	0.37
group	3	44.2	50.6	3.5	0.09
group + MCL	4	43.0	51.6	4.5	0.05
group * MCL	6	42.5	55.9	8.8	0.00

[a] *Number of parameters in model.*
[b] *At its maximum, −2 times the log of the likelihood function.*
[c] *Akaike's information criterion value adjusted for small sample size.*
[d] *Difference between AIC_c of a given model and AIC_c of highest ranked model.*
[e] *Akaike's information criterion weight.*
[f] *Models did not include effects of sex and year due to insufficient data.*

For the small tortoises (120–160 mm), model-averaged estimates of annual survival probability were nearly identical for control, resident, and translocated tortoises (~0.90), and cumulative survival was >0.56 for all groups (Fig. 3 & Supporting Information). We did not detect variation in survival by study group or MCL (year was not included due to lower sample sizes [Table 3]). The highest ranked model had no covariates.

Body Condition Covariates

For the large tortoises, estimates of model-averaged annual survival probability with body condition as a covariate were >0.95 for all groups, and model-averaged cumulative survival probability estimates were >0.80 (Fig. 2 & Supporting Information). Similarly, for tortoises in the smaller size class, model-averaged annual survival probability estimates ranged from 0.92 to 0.93, and cumulative survival probability ranged from 0.68 to 0.71 for all groups (Fig. 3 & Supporting Information).

For both size classes, the body condition of tortoises during spring health assessments was not a strong predictor of survival probability over the following year (Supporting Information). As with analysis 1, we did detect strong evidence ($w_+[j] = 0.83$) for the positive effect of MCL on survival in the large-tortoise data set. The model

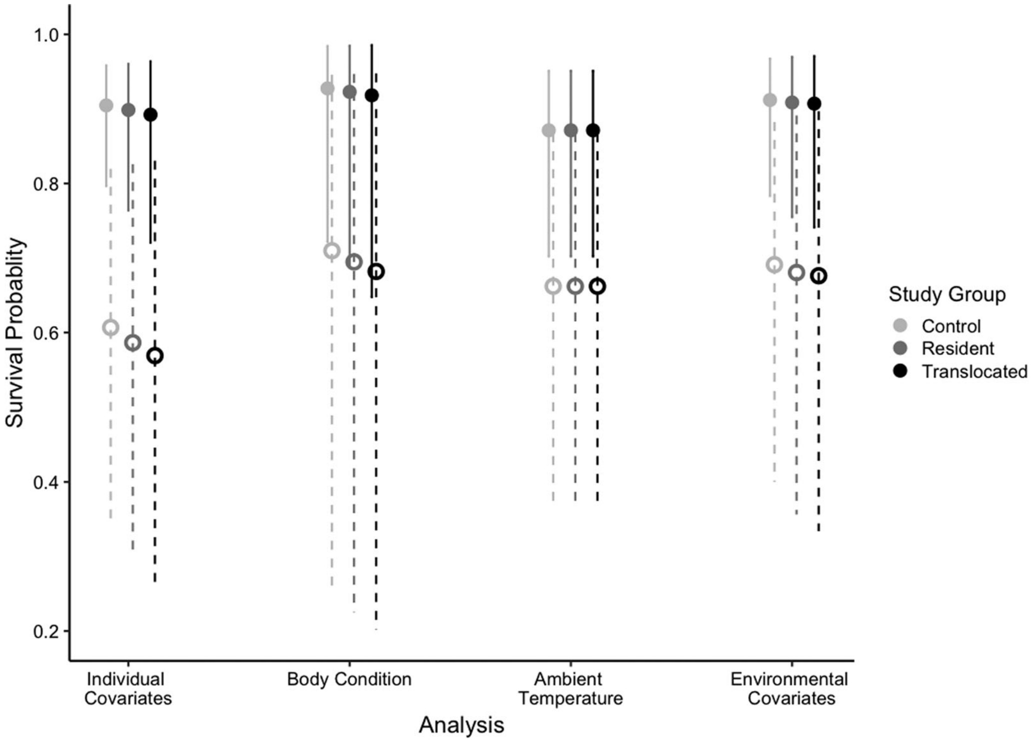

Figure 3. Average annual (filled circles) and cumulative (2012–2017) (open circles) survival estimates for Mojave desert tortoises with a midline carapace length of 120–160 mm (small-tortoise data set) in 3 study groups (control, resident, translocated) and for 4 analyses with different sets of covariates (Table 1) (dashed lines, 95% CI).

that included only a group effect had slightly more support than the model with no covariates ($\Delta \mathrm{AIC_c} = 1.6$).

Ambient Temperature Covariates

Based on the ambient temperature covariates, estimates of model-averaged annual survival probability for the large tortoises ranged from 0.96 to 0.98, and model-averaged cumulative survival estimates were ≥ 0.80 for all groups (Fig. 2 & Supporting Information). For the small-tortoise data set, we did not include a group covariate due to small sample size, and the model-averaged annual survival probability was 0.87 and cumulative survival probability was 0.66 (Fig. 3 & Supporting Information).

There was no support for interactions between temperature variables and study group for the large tortoise size class, indicating that translocated tortoises were not differentially affected by variation in ambient thermal conditions (Supporting Information). Furthermore, although models with covariates describing ambient temperatures (or group or size) were among the highest ranked, none of these models were substantially better than the model with no covariates ($\Delta \mathrm{AIC_C}$ always <7.0).

Environmental Covariates

For the large tortoises, estimates of model-averaged annual survival probability using the environmental covariates were 0.98 for all groups. Model-averaged cumulative survival estimates were ≥ 0.90 for all groups (Fig. 2 & Supporting Information). For the small tortoises, model-averaged annual survival probability was 0.91 for all groups, and cumulative survival ranged from 0.68 to 0.69 (Fig. 3 & Supporting Information).

For large tortoises, we found little support for the effects of environmental covariates on survival, though some evidence for a positive effect of MCL ($w_+[j] = 0.99$), including a top model with the additive, negative effect of area of home range (Supporting Information). For tortoises in the smaller size class, we found little support for the effects of environmental covariates on survival (Supporting Information). There was some evidence ($w_+[j] = 0.85$) for a negative relationship between topographic roughness within the home range and survival, although the models with this covariate were within 8.0 $\Delta \mathrm{AIC_c}$ units of the model with no covariates.

Discussion

Translocation has become a common mitigation technique to reduce negative effects of human activities on protected species. However, the technique has had mixed results and relatively few studies conduct multi-year monitoring following translocation to detect impacts on survival (Germano et al. 2015). Numerous translocations have been conducted on *Gopherus* spp. tortoises (e.g., Mojave desert tortoises, Sonoran desert tortoises [*G. morafkai*], gopher tortoises [*G. polyphemus*]) following exurban or military development; follow-up studies found no effect on short-term indicators of stress (Drake et al. 2012), reproductive output (Nussear et al. 2012), or survival (Field et al. 2007; Nussear et al. 2012), but possible effects on paternal genetic integration (Mulder et al. 2017). For both long-distance (Field et al. 2007; Nussear et al. 2012) and short-distance (Tuberville et al. 2005; Hinderle et al. 2015) translocations, the most consistently-observed effect has been an increase in movement immediately following translocation. Our previous work (Farnsworth et al. 2015; Brand et al. 2016) was consistent with these findings: translocated tortoises in the Ivanpah Valley exhibited increased movement and experienced higher ambient temperatures than did resident and control tortoises in the months immediately post-translocation. We found that those short-term behavioral and environmental impacts on translocated tortoises did not result in increased mortality in the 5 years over which individuals were monitored.

Our survival estimates for immature and adult tortoises in the Ivanpah Valley are among the highest annual survival probabilities for *Gopherus* spp. (including *G. agassizii*) of any published study in the last 3 decades (Doak et al. 1994; Tuberville et al. 2008; Nussear et al. 2012; Zylstra et al. 2013; Nafus et al. 2017). Our results suggested that in a given year, the probability of survival ranged from 89% to 99% for large tortoises (>160 mm MCL) in the vicinity of the ISEGS site, regardless of whether they had been translocated; larger (i.e., adult) tortoises were at the higher end of the range. These high survival rates are important for population persistence and potential recovery because desert tortoises have long lifespans (~50 years; sexual maturity at ~20 years [Medica et al. 2012]) and survival of older age classes disproportionately affects population dynamics in turtles generally (Heppell 1998) and desert tortoises in particular (Doak et al. 1994; Reed et al. 2009). Our study did not include years with extreme drought—which could increase mortality (Field et al. 2007; Esque et al. 2010; Zylstra et al. 2013; Lovich et al. 2014)—so our estimates of annual survival from 2012 to 2017 may be higher than the longer-term average for this population. Recent (2004-2014) declines in tortoise abundance reported for critical habitats in the eastern Mojave could reflect drought-related impacts, in particular, that are not captured by the study area or data we analyzed (USFWS 2015). Continued monitoring of such long-lived individuals would provide greater insights about drivers of long-term survival (Tuberville et al. 2008).

Although we found no differences in survival rates among study groups, we did identify covariates that had apparent effects on survival. Across candidate models for the larger tortoises, our results indicated that survival estimates increased with body size. This result is consistent with the well-established tenet of turtle demography that larger individuals have higher survival rates, mainly because predation risk is lower (Doak et al. 1994; Heppell 1998; Tuberville et al. 2008; Reed et al. 2009). Our study was not designed to monitor predator populations (namely, coyotes [*Canis latrans*] and ravens [*Corvus corax*]) or the influence of subsidized predation on the survival of the individual tortoises (large and small) we studied. Because proximity to anthropogenic features and food items may increase risk of predation on desert tortoises, including translocated individuals (Esque et al. 2010; Cypher et al. 2018), and because our study area was proximate to ISEGS, the I-15 corridor, and a large golf course, the impact of subsidized predators on tortoise survival warrants further investigation.

We found some evidence for survival rates in all study groups decreasing as time spent in ambient temperatures ≥35 °C, home range sizes, and topographical roughness increased, although the latter only applied to tortoises in the smaller size class. Although the ecological mechanisms driving these results are unclear, our results may reflect the importance of habitat quality. For example, some individuals may be forced to spend more time searching for resources (e.g., food, water, shelter) in exposed areas with reduced access to shelter sites, thereby increasing energy expenditure, thermal stress, or both (Sieg et al. 2015; Brand et al. 2016) and negatively influencing survival. However, this effect did not differentially affect translocated tortoises—despite their increased movements and time spent in high ambient temperatures during the months following translocation (Farnsworth et al. 2015; Brand et al. 2016)—nor did it significantly depress survival within or across years. Regardless of the underlying mechanism, these results suggest that translocation methods that minimize stress and place tortoises in high-quality habitat (e.g., areas with abundant shelter sites and preferred forage) can be expected to result in positive outcomes, at least in the short-term. These approaches should be required for translocation projects (Nussear et al. 2012).

Our study was not designed to establish a new population or augment an existing population (e.g., Griffith et al. 1989; Germano et al. 2015), but to avoid mortality of individuals located in an area of high-quality habitat and slated for alterations. Although our design could cause reduced survival of individuals that were already living in the release area (through density-dependent processes), translocation did not appear to negatively affect resident individuals because those tortoises had similar levels of survival as control tortoises. If density dependence had been stronger in the release area, we might have expected lower survival rates for the translocated and resident tortoises in that area compared to controls (Germano et al. 2015).

Our results suggest a number of factors related to our translocation procedure contributed to the high survivorship we observed in translocated tortoises. First, releasing tortoises within 500 m of their original home range may have helped to ensure some familiarity with their surroundings and minimize the degree to which translocated individuals exhibited homing behavior (as in Hinderle et al. 2015). Second, translocating individuals in early spring (i.e., March–April) may have been important for giving tortoises time to dig burrows and familiarize themselves with their surroundings prior to being exposed to hot summer temperatures (Field et al. 2007; Farnsworth et al. 2015). Finally, taking steps to maximize hydration (e.g., by soaking or offering drinking water) of individual tortoises just prior to their release may have lessened the potential for dehydration in the days immediately following translocation (sensu Field et al. 2007).

Like many arid regions of the world, human activities are increasing in the Mojave Desert, including renewable energy development, but relatively little is known about how such developments will affect local populations or species of conservation concern. Our study serves as an important case study of how mitigation-driven translocations can be combined with intensive monitoring to understand the potential effects of development on sensitive species (Tuberville et al. 2008; Germano et al. 2015). We recommend that post-translocation monitoring focus not only on fine-scale behaviors and survival immediately following translocation, but also on other important life-history parameters, such as growth, age- or stage-specific recruitment, and reproductive success (Germano et al. 2015; Mulder et al. 2017), and predation risk (Teixeira et al. 2007; Esque et al. 2010) to assess the long-term ecological success of wildlife translocation and recovery efforts.

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Supporting Information

Table S1. Mean (and SD) plant species richness across 100 × 100 m vegetation plots sampled in the spring and fall within the Ivanpah Valley study area.

Table S2. Summary of temperature based on 6 on-site weather stations established in the Ivanpah Valley study area.

Table S3. Summary of rainfall based on 6 on-site weather stations within the Ivanpah Valley study area.

Table S4. Candidate model-selection results for the evaluation of effects of treatment group, midline carapace length, and body condition score using (a) the large-tortoise dataset and (b) the small-tortoise dataset.

Table S5. Candidate model-selection results for the evaluation of effects of ambient temperature covariates using (a) the large-tortoise dataset and (b) the small-tortoise dataset.

Table S6. Candidate model-selection results for the evaluation of effects of treatment group, environmental covariates, and midline carapace length using (a) the large-tortoise dataset and (b) the small-tortoise dataset.

Table S7. Model averaged estimates of annual probability of survival for the large tortoise size class for each group and each analysis.

Table S8. Model averaged estimates of cumulative probability of survival for the large tortoise size class for each group and each analysis.

Table S9. Model averaged estimates of annual probability of survival for the small tortoise size class for each group and each analysis.

Table S10. Model averaged estimates of cumulative probability of survival for the small tortoise size class for each group and each analysis.

Figure S1. Scatter plot of Landsat NDVI and plot-level vegetation cover in the fall and spring of 2013-2015.

Figure S2. Scatter plot of daily gridded 4-km temperature data and daily weather station data from 2013-2015.

Figure S3. The average difference in monthly rainfall between (1) local measures derived from 18 rain gauges within the Ivanpah Valley study area, and (2) remotely-derived measures based on daily gridded 4-km rainfall data.

Literature Cited

Abatzoglou JT. 2011. Development of gridded surface meteorological data for ecological applications and modelling. International Journal of Climatology **33:**121–131.

Anderson DR. 2008. Model based inference in the life sciences: a primer on evidence. Springer Publishing, New York.

Batson WG, Gordon IJ, Fletcher DB, Manning AD. 2015. Translocation tactics: a framework to support the IUCN Guidelines for wildlife translocations and improve the quality of applied methods. Journal of Applied Ecology **52:**1598–1607.

Boarman WL, Goodlett T, Goodlett G, Hamilton P. 1998. Review of radio transmitter attachment techniques for turtle research and recommendations for improvement. Herpetological Review **29:**26–33.

Brand LA, Farnsworth ML, Meyers J, Dickson BG, Grouios C, Scheib AF, Scherer RD. 2016. Mitigation-driven translocation effects on temperature, condition, growth, and mortality of Mojave desert tortoise (*Gopherus agassizii*) in the face of solar energy development. Biological Conservation **200:**104–111.

Burnham KP, Anderson DR. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer Publishing, New York.

Cypher BL, Kelly EC, Westall TL, Van Horn Job CL. 2018. Coyote diet patterns in the Mojave Desert: implications for threatened desert tortoises. Pacific Conservation Biology **24:**44–54.

Dickson BG, Wallace BP, Scherer RD, Gray ME, Kissel A. 2017. Process- and scale-based determinants of survival for translocated Mojave desert tortoises in the Ivanpah Valley, California; April 2011 through May 2017. Final report prepared for Solar Partners I; Solar Partners II; Solar Partners VIII, Oakland. Available from https://www.csp-inc.org/public/CSP_ISEGS_Tortoise_Report_5yr_FINAL.pdf (accessed April 2018).

Doak D, Kareiva P, Klepetka B. 1994. Modeling population viability for the desert tortoise in the western Mojave Desert. Ecological Applications **4:**446–460.

Drake KK, Nussear KE, Esque TC, Barber AM, Vittum KM, Medica PA, Tracy CR, Hunter KW. 2012. Does translocation influence physiological stress in the desert tortoise? Animal Conservation **15:**560–570.

Esque TC, et al. 2010. Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave Desert, USA. Endangered Species Research **12:**167–177.

Farnsworth ML, Dickson BG, Zachmann LJ, Hegeman EE, Cangelosi AR, Jackson TG, Scheib AF. 2015. Short-term space-use patterns of translocated Mojave desert tortoise in southern California. PLOS ONE **10** (e0134250) https://doi.org/10.1371/journal.pone.0134250.

Field KJ, Tracy CR, Medica PA, Marlow RW, Corn PS. 2007. Return to the wild: translocation as a tool in conservation of the desert tortoise (*Gopherus agassizii*). Biological Conservation **136:**232–245.

Germano JM, Field KJ, Griffiths RA, Clulow S, Foster J, Harding G, Swaisgood RR. 2015. Mitigation-dirven translocations: Are we moving wildlife in the right direction? Frontiers in Ecology and the Environment **13:**100–105.

Griffith B, Scott J, Carpenter J, Reed C. 1989. Translocation as a species conservation tool: status and strategy. Science **245:**477–480.

Heppell SS. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia **1:**367–375.

Hinderle D, Lewison RL, Walde AD, Deutschman D, Boarman WI. 2015. The effects of homing and movement behaviors on translocation: desert tortoises in the western Mojave Desert. Journal of Wildlife Management **79:**137–147.

Laake JL. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01. Alaska Fisheries Science Center, National Oceanic and Atmospheric Adminstration, National Marine Fisheries Service, Seattle.

Lamberski N. 2013. Body condition scores of desert tortoises. U.S. Fish and Wildlife Service report. Available from https://www.fws.gov/nevada/desert_tortoise/documents/reports/2013/assess/Desert-Tortoise-BCS-2013-lamberski-po.pdf (accessed April 2018).

Lovich JE, Yackulic CB, Freilich J, Agha M, Austin M, Meyer KP, Arundel TR, Hansen J, Vamstad MS, Root SA. 2014. Climatic variation and tortoise survival: Has a desert species met its match? Biological Conservation **169:**214–224.

Medica PA, Nussear KE, Esque TC, Saethre MB. 2012. Long-term growth of desert tortoises (*Gopherus agassizii*) in a southern Nevada population. Journal of Herpetology **46:**213–220.

Mulder KP, Walde AD, Boarman WI, Woodman AP, Latch EK, Fleischer RC. 2017. No paternal genetic integration in desert tortoises (*Gopherus agassizii*) following translocation into an existing population. Biological Conservation **210:**318–324.

Nafus MG, Esque TC, Averill-Murray RC, Nussear KE, Swaisgood RR. 2017. Habitat drives dispersal and survival of translocated juvenile desert tortoises. Journal of Applied Ecology **54:**430–438.

Nussear KE, Tracy CR, Medica PA, Wilson DS, Marlow RW, Corn PS. 2012. Translocation as a conservation tool for Agassiz's desert tortoises: survivorship, reproduction, and movements. Journal of Wildlife Management **76:**1341–1353.

Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jędrzejewska B, Lima M, Kausrud K. 2011. The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. Climate Research **46:**15–27.

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL, Joppa LN, Raven PH, Roberts CM, Sexton JO. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science **344:**1246752.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Reed JM, Fefferman N, Averill-Murray RC. 2009. Vital rate sensitivity analysis as a tool for assessing management actions for the desert tortoise. Biological Conservation **142:**2710–2717.

Sadoti G, Gray ME, Farnsworth ML, Dickson BG. 2017. Discriminating patterns and drivers of multiscale movement in herpetofauna: the dynamic and changing environment of the Mojave desert tortoise. Ecology and Evolution **7:**7010–7022.

Seddon PJ, Armstrong DP, Maloney RF. 2007. Developing the science of reintroduction biology. Conservation Biology **21:**303–312.

Sieg AE, Gambone MM, Wallace BP, Clusella S, Spotila JR, Avery HW. 2015. Mojave desert tortoise (*Gopherus agassizii*) thermal ecology and reproductive success along a rainfall cline. Integrative Zoology **10:**282–294.

Sullivan BK, Nowak EM, Kwiatkowski MA. 2015. Problems with mitigation translocation of herpetofauna. Conservation Biology **29:**12–18.

Teixeira CP, De Azevedo CS, Mendl M, Cipreste CF, Young RJ. 2007. Revisiting translocation and reintroduction programmes: the importance of considering stress. Animal Behaviour **73:**1–13.

Tuberville TD, Clark EE, Buhlmann KA, Gibbons JW. 2005. Translocation as a conservation tool: site fidelity and movement of repatriated gopher tortoises (*Gopherus polyphemus*). Animal Conservation **8:**349–358.

Tuberville TD, Norton TM, Todd BD, Spratt JS. 2008. Long-term apparent survival of translocated gopher tortoises: A comparison of newly released and previously established animals. Biological Conservation **141:**2690–2697.

United States Fish & Wildlife Service (USFWS). 2011*a*. Revised recovery plan for the Mojave population of the desert tortoise (*Gopherus agassizii*). USFWS, Pacific Southwest Region, Sacramento.

United States Fish & Wildlife Service (USFWS). 2011*b*. Revised biological opinion on BrightSource Energy's Ivanpah Solar Electric Generating System Project, San Bernardino County, California [CACA- 48668, 49502, 49503, 49504] (8-8-10-F-24). Memorandum to the district manager, Bureau of Land Management, California. Available from https://www.csp-inc.org/public/CON_8-8-10-F-24R_BLM_Ivanpah_SEGS_Reinitiation_Final_BO.pdf (accessed April 2018).

United States Fish & Wildlife Service (USFWS). 2011*c*. Health assessment handbook. USFWS, Desert Tortoise Recovery Office, Reno, Nevada.

United States Fish & Wildlife Service (USFWS). 2015. Range-wide monitoring of the Mojave desert tortoise (*Gopherus agassizii*): 2013 and 2014 annual reports. Report by the Desert Tortoise Recovery Office, U.S. Fish and Wildlife Service, Reno, Nevada.

White GC, Garrott RA. 1990. Analysis of wildlife radio-tracking data, Academic Press, San Diego.

Zylstra ER, Steidl RJ, Jones CA, Averill-Murray RC. 2013. Spatial and temporal variation in survival of a rare reptile: A 22-year study of Sonoran desert tortoises. Oecologia. **173:**107–116.