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Research Article

The Effects of Homing and Movement Behaviors on Translocation: Desert Tortoises in the Western Mojave Desert

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ABSTRACT Translocation of threatened or vulnerable species is a tool increasingly used for conservation and management. However, in some species, homing and movement behaviors may undermine the success of translocation efforts. For the federally protected Agassiz's desert tortoise (*Gopherus agassizii*), translocation is a strategy used to manage declining populations, yet homing behavior in this species is poorly understood. To explore homing behavior and movement patterns after translocation, we radio tracked 80 tortoises during a 2-phase experimental translocation. Phase 1 included 40 tortoises that were translocated, then monitored for a period of 37 days (21 Sep–28 Oct 2009), and phase 2 included a different group of 40 tortoises that were translocated and then monitored for 186 days (13 Apr–20 Oct 2010). In both phases, we assigned tortoises randomly to 1 of 3 treatment groups: translocated (displaced 2, 5, or 8 km from their source location), handling control, or control. After translocation, 20% of the translocated tortoises were able to navigate to their source location, and translocation distance had an effect on their ability to navigate home. We found 44% of tortoises in the 2-km translocated group returned home; 1 tortoise in the 5-km group, and no tortoises in the 8-km translocated group returned. The time required to reach home ranged from 5 to 37 days for the 2-km group, and 34 days for the 5-km group. We deemed tortoises to have homed successfully if they returned to their source location within 37 days of translocation as this reflected the duration of phase 1 and allowed for a balanced comparison between the 2 phases. We found that translocated tortoises moved at least 1.5 times more overall than the control groups, with some individuals moving >10 km from the translocation site. These patterns persisted even after accounting for seasonal and sex differences in distance traveled. By identifying homing behaviors and quantifying post-translocation movement patterns, this experiment addressed a key data gap in tortoise behavior that may limit the efficacy of tortoise translocation efforts. Our results point to the need to account for behavioral responses of tortoises to minimize risk to translocated individuals and maximize the success of translocation projects.

KEY WORDS desert tortoise, Fort Irwin, *Gopherus agassizii*, homing, Mojave Desert, National Training Center, reintroduction, translocation.

Wildlife and resource managers are frequently tasked with maintaining or promoting population growth in species of conservation concern based on best available information. In some cases, success of a proposed management action may be limited by current knowledge of the behavioral characteristics and ecology of an organism. As a result, incorporating and accounting for behavioral responses to management strategies have been suggested as a key component to improving the success of management and conservation actions (Buchholz 2007, Caro 2007). Understanding behavioral responses such as movement patterns, changes in habitat use, or altered thermoregulatory behaviors, to specific management actions has served to improve and refine management strategies and protocols (Martins et al. 2012, Nussear et al. 2012, Abele et al. 2013, Heer et al. 2013).

Reintroductions and translocations, the human-mitigated movement of organisms from one area to release in another (International Union for Conservation of Nature 2013), are conservation management tools that provide a unique opportunity to explore these behavioral responses. Although accounting for behavior has been recognized as an important element to successful wildlife management, many reintroduction and translocation projects have occurred without understanding or consideration for behavioral responses, potentially limiting the success of translocation efforts (Letty

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et al. 2007, Sheean et al. 2012), where success may be measured by survivorship (Troy et al. 2013), breeding success (King et al. 2013), integration into an existing population (Scillitani et al. 2012), or restoration of key ecological functions (Griffiths et al. 2010). For example, a study of northern water snakes (*Nerodia sipedon sipedon*) found thermoregulatory behaviors were impaired in translocated individuals, leading to management recommendations that included matching pre- and post-translocation habitat conditions, releasing individuals into enclosures, and enriching environmental conditions for captive snakes prior to translocation (Roe et al. 2010).

Translocation, which is used to establish, re-establish, augment, or mitigate populations in decline, has yielded varied results across a broad range of taxa. Translocations have been used with fishes (Sheller et al. 2006, Vincenzi et al. 2012), birds (Reynolds et al. 2012, White et al. 2012), mammals (Van Houtan et al. 2009, Scillitani et al. 2012, Shier and Swaisgood 2012), and herpetofauna (Nelson et al. 2002, Nussear et al. 2012). For reptiles and amphibians, translocations have had limited success for some species, with survival rates of translocated animals ranging from 14% to 42% (Griffith et al. 1989, Dodd and Seigel 1991, Fischer and Lindenmayer 2000, Germano and Bishop 2009). For example, a translocation study of Gila monsters (*Heloderma suspectum*) found individuals translocated less than 1 km returned to their point of capture, and those translocated greater than 1 km demonstrated high rates of movement with increased risk of predation, thermoregulatory costs, and mortality (Sullivan et al. 2004). Similarly, studies of timber rattlesnakes (*Crotalus horridus*; Reinert and Rupert 1999) and eastern box turtles (*Terrapene carolina*; Hester et al. 2008) both found decreased survival and increased movement post-translocation relative to individuals in the resident population.

A recent review of 91 herpetofauna translocations reported the leading causes of translocation failure (defined as failure to establish a self-sustaining population) were homing behavior, the ability to return to the place of origin, and large movements away from translocation sites (Germano and Bishop 2009). Although the mechanisms underlying these responses are poorly understood, there are a number of putative proximate factors, including stress, disease, displacement by conspecifics, avoidance of predators, habitat preference, or homing (Bertolero et al. 2007, Field et al. 2007, Teixeira et al. 2007). Ultimately these increased movements may lead to an increase in mortality (Sullivan et al. 2004, Field et al. 2007, Berry et al. 2009), increased predation risk (Bertolero et al. 2007, Esque et al. 2010), or increased exposure to disease (Wendland et al. 2010). Furthermore, post-translocation movement responses overlay existing patterns that often vary by sex (Tuberville et al. 2005, Harless et al. 2009, Nussear et al. 2012), season (Zimmerman et al. 1994, Eubanks et al. 2003), or weather and climate conditions (Duda et al. 1999, Zylstra et al. 2013). Although the success rates of herpetofaunal translocations have improved in recent years, a general lack of knowledge concerning the factors responsible for unsuccessful translocations still remains (Germano and Bishop 2009).

Increasing land use pressure is one of the primary drivers of translocations of desert species, including the desert tortoise (*Gopherus agassizii*). Ranging across the southwest United States and northwest Mexico, the desert tortoise is a species in decline despite conservation efforts (U.S. Government Accountability Office 2002, USFWS 2011). The Sonoran population (*G. morafkai*) was recently separated from the federally protected Mojave population, found northwest of the Colorado River (Murphy et al. 2011). Listed as threatened in 1990 (USFWS 1990), habitat loss (Doak et al. 1994, Heaton et al. 2008, Darst et al. 2013), disease (Brown et al. 1994, Homer et al. 1998), and predation (Bjurlin and Bissonette 2004, Boarman et al. 2006, Berry et al. 2013), have worked synergistically to erode existing populations across the entire range of both species. The revised recovery plan for the Mojave population of the desert tortoise acknowledges a large number of threats to this species, and in an effort to help recover and manage tortoise populations, translocation has been identified as a key management strategy in response to habitat loss and changes in land-use (USFWS 2011).

Recent land-use changes in the Mojave Desert have included renewable energy developments proposed at an unprecedented rate (Lovich and Ennen 2011), with United States Bureau of Land Management (BLM) processing approximately 70 solar development applications covering over 2,200 km^2 of public lands in California, Nevada, and Arizona, as of March 2014 (BLM 2014). Another land use pressure comes from expansion of military training grounds. The Marine Corps Air Ground Combat Center near Twentynine Palms, California, has approved an expansion of over 600 km^2 and is anticipated to affect over 600 adult tortoises (Department of the Navy 2013). A 2008 land expansion of the National Training Center, Fort Irwin (NTC; Public Law 107–314 2002) near Barstow, California, annexed 545 km^2 of adjacent lands, supporting an estimated 2,000 desert tortoises (Heaton et al. 2008). In an effort to protect this population, more than 500 tortoises were translocated from the NTCs southern expansion area to nearby translocation sites in April 2008.

Using the NTC as a case study, we developed an experimental approach to understand the prevalence of homing and movement behavior on desert tortoise translocation and to explore whether desert tortoises exhibit homing behavior or other behavioral responses to translocation. Desert tortoises have demonstrated a high degree of site fidelity (O'Connor et al. 1994, Harless et al. 2009) and are hypothesized to have homing abilities (Berry 1974, Field et al. 2007), suggesting some degree of spatial awareness, but neither the mechanism nor the extent of these behaviors have been studied. Our study explores the variables that may influence homing behavior and the impact that homing and related behaviors may have on tortoise survival post-translocation. This translocation experiment highlights the factors that might limit translocation success in this and other reptile species of conservation concern.

STUDY AREA

We conducted this study on approximately 90 km^2 of the western expansion area on the NTC, a 2,500-km^2 army training facility (Fig. 1). This expansion area is bounded to the north and east by active training areas of the NTC and the Naval Air Weapons Station, China Lake, and to the south and west by land primarily managed by the BLM. The study site was historically used by both the military (California-Arizona Maneuver Area, established in 1944) and the public until 2001 when the land was transferred to the NTC. The area is representative of natural Mojave creosote scrub desert habitat with minimal development and anthropogenic disturbance.

METHODS

Homing and Movement

To locate and mark tortoises on the landscape, we conducted extensive tortoise surveys at 10-m spacing on the western expansion area commencing in April 2008. As part of the survey, tortoises were weighed, measured for midline carapace length (MCL), fitted with a radio transmitter (Holohil Systems Limited, Carp, Ontario, Canada; Boarman et al. 1998), and given a preliminary health assessment. A separate research team further assessed the tortoises through a comprehensive field examination for clinical signs of health and diseases (Berry and Christopher 2001). Blood samples were submitted to the University of Florida for enzyme-linked immunosorbent assay (ELISA) testing to identify the infectious pathogens *Mycoplasma agassizii* and *M. testudineum* (K. Berry, United States Geological Survey, personal communication; Wendland et al. 2007, Jacobson and Berry 2012). We used a subset of 80 tortoises (40 males and 40 females) from this initial survey over 2 experimental phases under United States Fish and Wildlife Service research permit TE 218901. Phase 1 was conducted for 37 days, from 21 September to 28 October 2009, and phase 2 was conducted for 186 days, from 13 April to 20 October 2010; both phases included 40 tortoises each, and we translocated tortoises only once. Phase 1 was limited to 37 days because the study was designed to return tortoises to their capture location prior to winter brumation, which usually occurs by the end of October (Nussear et al. 2007). Selected tortoises were adults, (MCL >209 mm), and tested negative for exposure to *M. agassizii* and *M. testudineum*, with 4 exceptions that were of unknown disease status (K. Berry, personal communication). We randomly placed the 80 individuals into 3 treatment groups (translocated, handling control, and control) in the following male/female ratios: phase 1: translocated (12/11), handling control (4/5), control (5/3); and phase 2: translocated (12/12), handling control (4/4), control (4/4).

The tortoises in the translocated treatment were located using radio telemetry, weighed, measured, given a rapid assessment for recent trauma or signs of disease, soaked in water for 20 minutes to hydrate them, placed in a secure box in a vehicle, and transported to their release site 2 km, 5 km, or 8 km away from their capture location upon initiation of the experiment. Upon release, we placed tortoises in the shade of a creosote shrub and observed them from a distance

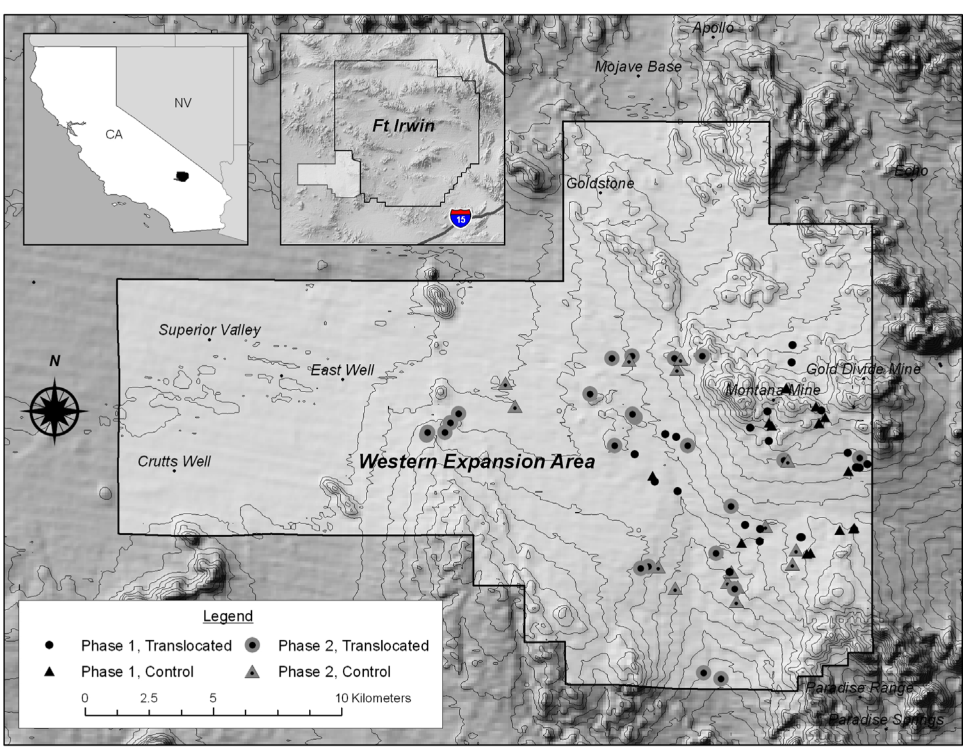

Figure 1. Map of the Western Expansion Area on the National Training Center, Fort Irwin near Barstow, California, USA. We radio-tracked 47 translocated and 33 control desert tortoises over 2 phases, 21 September–28 October 2009, and 13 April–20 October 2010. Tortoise initial capture locations for translocated (black circles for phase 1, grey circles for phase 2) and control (black triangles for phase 1 and grey triangles for phase 2) animals are indicated on the map.

of approximately 10 m, for 20 minutes. We chose release sites randomly within areas of suitable habitat, and both the capture and release areas were in creosote scrub habitat. We did not place tortoises within 50 m of previously known tortoises or active tortoise burrows. We chose this range of experimental distances based on the topography of the study area which was constrained by mountains, dry lake beds, fence line boundaries, and paved roadways. These translocation distances included sites that were in or near their home range (2 km), and sites outside of the tortoises' home ranges (8 km). In this region, desert tortoise home ranges average 16 ha for females and 44 ha for males (Harless et al. 2009). To ensure translocated tortoises were likely to be moved out of their core activity areas, we calculated the maximum linear distance (in meters) across a minimum convex polygon (MCP) activity range of 54 resident tortoises that had been monitored for 13–29 months immediately prior to the commencement of our experiment by a separate research group. This maximum linear distance ranged 309.2–2,368.7 m for females, and 400.5–1,724.9 for males. We calculated MCP and distances using Hawth's tools (Beyer 2004) in ArcGIS 9.3 (ESRI, Redlands, CA; Appendix A).

The handling group served to control for the effect of handling the tortoises during translocation and had 2 treatments: 8 tortoises were handled by researchers at their burrow for less than 1 hour (weighed, measured, and given a health assessment), and 9 tortoises were handled for up to 3 hours (weighed, measured, given a health assessment, soaked in water for 20 minutes, placed in a vehicle and transported), then returned to their initial capture site. These handling times reflected our estimated minimum and maximum times for processing a tortoise during this experiment. Control group tortoises had a radio transmitter attached at least 6 months prior to the commencement of the experiment and otherwise, were not handled at all. We eventually combined handling control and control groups for all analyses (see Results).

We radiotracked tortoises in all treatment groups 2–7 times per week, using hand-held radio receivers (R-1000 Communication Specialist Inc., Orange, CA) and a Yagi-Uda directional hand-held antenna (AFAntronics, Champaign, IL). We had no interruptions in our tracking efforts due to equipment failure. At each tracking event, we recorded geographic location (Universal Transverse Mercator, UTM) with Garmin GPSMap76Cx and Garmin GPSMap76CSx units (Garmin Inc., Olathe, KS), which were calibrated daily and had an estimated error of 3–6 m. We used ambient temperature data collected from the weather station at the Barstow-Daggett airport, located approximately 45 km from our study site (Weather Underground 2011). We categorized the temperatures into 3 blocks: block 1 $\leq 20^{\circ}$C, 20°C < block 2 < 32°C, and block 3 $\geq 32^{\circ}$C where reduced tortoise activity levels roughly corresponded with lower temperatures in block 1 and higher temperatures in block 3. Upon conclusion of the 2 experimental phases (28 Oct 2009 and 20 Oct 2010), we returned all translocated tortoises to their capture location, and monitored them for a week to ensure their well-being. All tortoises were in good condition upon conclusion of our experiment, and these animals continued to be monitored monthly at a minimum by a separate research group.

Statistical Analysis

We evaluated movement behavior using 4 metrics: 1) the ability of tortoises to find their way home, where home was any location within 500 m of their original capture location; 2) directionality, assessing if the animal traveled in the direction of their capture location and how direct their path was; 3) the total distance traveled, calculated as the sum of the straight line distances between radio tracking point locations over time; and 4) net displacement, calculated as the straight-line distance between the tortoises' initial release point and the capture location on day 37 for both experimental periods. To allow for balanced comparisons, we conducted analyses for homing ability, directionality, total distance traveled, and net displacement between the first 37 days of both experimental phases (21 Sept–28 Oct 2009 and 13 April–20 May 2010) using SYSTAT (SYSTAT Software Inc. San Jose, CA). We conducted an additional analysis of total distance traveled on the full phase 2 data set to capture movement patterns across different temperatures, and over time.

To assess ability to home, we used Pearson's chi-square and Cochrane's test of linear trend for ordered data to determine if translocated distance affected the number of tortoises that returned to their original location. We explored directionality using 2 metrics of circular statistics: angular dispersion (r), a measure of how direct the movement path was, and average directionality (θ), the mean angle of travel (Zar 1999). We standardized the mean angle of travel to 0 for all tortoises so it was not influenced by the relative position of the release versus the capture location. Tortoises moving in the opposite direction of home with no angular concentration would have θ and r values of 180 and 0 respectively, whereas those exhibiting perfect homing ability would have θ and r values of 0 and 1.0. We used Pearson's correlation to determine how average θ and r were related to one another. We used analysis of covariance (ANCOVA) to analyze average θ, where the factors were experimental phase (1 or 2) and distance (2, 5, or 8 km), and the covariate was average r. We used a 2-sample t-test to investigate differences in θ and r between tortoises that arrived home and those that did not.

We used general linear models (GLM) to determine whether there were differences of total distance traveled (square root transformed) or net displacement (log transformed) within the first 37 days after translocation between the translocated and control groups for both phases. We used the independent variables experimental treatment and sex, and we found no significant interaction between them. To further analyze the phase 2 data set, we used a generalized linear mixed model (GLMM) to test total distance traveled (square root transformed) for differences among treatment, sex, and temperature blocks using the PROC GLMMIX command with a variance component structure (SAS Institute Inc. Cary, NC). Our full model included the fixed effects of treatment, sex, temperature block, with all interactions, and the random effects of tortoise identification number and week, to account for repeated measures of individual animals over time. To test differences across significant fixed effects, we used post-hoc least squares mean Tukey-Kramer pairwise comparisons. We applied a Pearson chi-square to further investigate categorical differences in net-displacement (as being greater or less than 1 km) between translocated and control groups. We set significance levels to $\alpha < 0.05$.

RESULTS

We found no difference in total distance traveled or net displacement between the 2 handling control regimes (distance: $F_{1,\ 15} > 1.337$ $P > 0.266$; displacement: $F_{1,\ 15} > 0.541$ $P > 0.474$) or between our handling control and control groups ($F_{1,\ 31} > 1.404$ $P > 0.245$); therefore, we combined these 2 treatments for all analyses, and categorized them all as controls.

Homing Movements

We found a statistically significant number of tortoises navigated home among our 3 distance groups. In total, 9 out of 47 tortoises returned home, 5 in phase 1 ($n = 23$; 2 km: 4/10; 5 km: 1/7; 8 km: 0/6) and 4 in phase 2 ($n = 24$; 2 km: 4/8; 5 km: 0/8; 8 km: 0/8). Eight of these were in the 2-km distance group, and 1 was in the 5-km distance group (phase 1: $\chi^2 = 3.76$, $P = 0.052$; phase 2: $\chi^2 = 7.2$, $P = 0.007$). The time required to reach home ranged from 5–37 days for the 2-km distance, and 34 days for the 5-km distance group. Although not categorized as homing in this analysis, in phase 2 we had 1 female tortoise in the 8-km distance group navigate to within 670 m of her previously known location, 20 days post-translocation. No tortoises returned home after day 37, despite phase 2 continuing for 186 days, and we observed no mortality throughout the duration of both experimental phases.

Directionality and Angular Dispersion in Movement

We found a negative correlation between average directionality (θ) and average angular dispersion (r), where low θ was associated with a high r value ($r = -0.434$, $P = 0.002$). We found θ was predicted by distance ($F_{2,\ 42} = 8.526$, $P = 0.001$), experimental phase ($F_{1,\ 42} = 5.416$, $P = 0.025$), and r ($F_{1,\ 42} = 10.970$, $P = 0.002$), where translocated tortoises that arrived home traveled in both the correct direction of home, and with less angular dispersion (e.g., in straighter paths). We found translocated tortoises that homed had a lower θ and higher r values than translocated tortoises that did not (r: $t_{11.708} = -3.497$, $P = 0.005$, θ: $t_{12.675} = 4.345$, $P = 0.001$; Figs. 2, 3).

Total Distance Moved

We found an effect of both treatment (phase 1: $F_{3,\ 35} = 21.946$, $P < 0.001$; phase 2: $F_{3,\ 35} = 3.782$, $P = 0.019$) and sex (phase 1: $F_{1,\ 35} = 9.416$, $P < 0.004$; phase 2: $F_{1,\ 35} = 11.255$, $P = 0.002$) in both experimental phases where translocated tortoises moved more than controls, and male tortoises moved more than female tortoises with no interaction between treatment and sex. Tukey's post hoc test showed different means across treatment groups ($P < 0.05$) where in phase 1, the 2-km, 5-km, and 8-km distance treatments all moved more than the control treatment, and in phase 2, only 5-km and 8-km distance treatments moved more than the control group (means of total distance traveled, phase 1: 2 km = 3,192 m, 5 km = 7,589 m, 8 km = 5,436 m, control = 1,361 m; phase 2: 2 km = 6,920 m, 5 km = 12,750 m, 8 km = 11,293 m, control = 6,994 m). Our analysis of the phase 2 data using a GLMM found an effect of temperature block, sex, and the 2-way interactions of temperature block by sex, and temperature block by treatment, where males moved farther than females regardless of temperature block (block 1: $t_{64} = 5.26$, $P < 0.001$; block 2: $t_{64} = 6.38$, $P < 0.001$; block 3: $t_{64} = 3.62$, $P = 0.008$), and translocated tortoises moved more than control tortoises only at the mid-range ambient temperatures (block 2: $t_{64} = 6.20$, $P < 0.001$; Fig. 4).

Net Displacement

We found a difference in net displacement among groups, with the translocated groups displacing longer distances than the control groups in both phase 1 ($F_{3,\ 35} = 9.242$, $P < 0.001$) and phase 2 ($F_{3,\ 35} = 6.624$, $P = 0.001$; Fig. 5). We found no difference between sexes ($P > 0.05$) in either phase. We further analyzed the net displacement data to consider whether there were categorical differences in net displacement distance between tortoises that moved and the tortoises that did not move. We found a difference in both phase 1 ($\chi^2_3 = 13.737$, $P < 0.003$) and phase 2 ($\chi^2_3 = 21.845$, $P < 0.001$) where the translocated treatment had proportionally more tortoises that moved greater than 1 km.

DISCUSSION

Translocation has been identified as a key, and often preferred, management strategy for desert tortoises in response to habitat loss and changes in land-use (USFWS 2011). However, choosing appropriate translocation sites for desert tortoises is challenging, and must take into account population densities, disease status of both recipient and donor populations, present and future anthropogenic influences, predator densities, and habitat structure. Assuming that the goal is to keep translocated individuals away from their home range of origin, our data suggest that moving tortoises a short distance, <2 km, is unlikely to result in successful translocation. Relocating tortoises short distances may have advantages, such as keeping tortoises in or near their home range or within a similar habitat type, and increasing the probability of maintaining social and genetic ties with neighboring tortoises (Berry 1986). However, based on our results, this strategy may increase the likelihood of a tortoise returning home and thus undermine this management strategy unless an effective barrier fence is in place. Furthermore, homing tortoises are more likely to encounter fence line boundaries built to exclude tortoises from their site of origin during some translocation efforts (D. Hinderle, San Diego State University, personal observation). Tortoise exclusion fencing may increase vulnerability to predation, mortality, or thermal stress, and such physical obstacles have been shown to limit dispersal, impede gene flow, and/or increase mortality in other taxa (Aresco 2005*a*, *b*; Clark et al. 2010).

In an effort to minimize successful homing, an alternative may be to move tortoises more than 2 km from their source location during translocation efforts. Although longer distance translocations may reduce the likelihood of individuals returning to their source location, we found some evidence that homing may occur with translocation distances >2 km; 1 tortoise returned home from 5 km away, and another, who was moved 8 km away, navigated to within 670 m of home. Our results also point to another cost of long distance translocations; the data suggest that increased total movement and net displacement may correspond to increased translocation distance, although this trend was not statistically significant. In areas where tortoises are translocated >5 km from their original site, increased movements and net displacement could dramatically heighten vulnerability to predation, mortality, disease, and aggressive conspecific interactions (Berry et al. 2009, Germano and Bishop 2009), and may increase the likelihood of encountering an anthropogenic landscape, including fence lines, roads, or developed areas (Sullivan et al. 2004).

Regardless of the distance moved, we found that all translocated tortoises moved longer distances and had greater net displacement than the control group within the first 5 weeks of translocation, and increased movements persisted over time in more than 80% of the translocated tortoises (32/38 translocated tortoises, excluding those that navigated to their capture location). This measureable behavioral response to translocation may challenge translocation efforts irrespective of whether a tortoise exhibits homing. Such increased movements may influence ability to breed successfully (Tuberville et al. 2011), affect survivorship (Tuberville et al. 2008) or have physiological consequences (Moulherat et al. 2014).

Our study also indicates that males and females exhibit different responses to translocation, consistent with other translocation research (Field et al. 2007, Nussear et al. 2012). Although we found the ability to navigate home was the same for males and females, given the importance of females to population growth (Doak et al. 1994), female homing may have a disproportionate impact on the population if this behavior were to increase mortality in females, although this was not observed during the short duration of this study. In terms of total movement, males moved more than females in all treatment groups, a finding consistent with males having larger home ranges (O'Connor et al. 1994, Harless et al. 2009). In the phase 2 experimental period, males consistently moved more than females across all temperature blocks, but this was most pronounced at temperatures between 20–32°C, which was also the temperature range where translocated tortoises moved more than control animals. Our data indicates this effect of sex across all temperatures is primarily driven by the increased movement of males from August through October, and is consistent with peak spermatogenesis and mating (Rostal et al. 1994, Lance and Rostal 2002). Such increased movement may cause males to disperse into areas of disease or heavy anthropogenic use at a higher rate than females, and suggests that the success of translocation efforts may vary seasonally. However, even with characteristic seasonal variability, translocated animals moved more than the control groups, indicating translocation may elicit atypical movement in this species irrespective of season. There also appeared to be a critical distance between 2 km and 5 km where tortoises were no longer able to locate home, and repeating this experiment with a suite of translocation distances between 1 km and 5 km would help identify these critical distances and aid to inform future translocations.

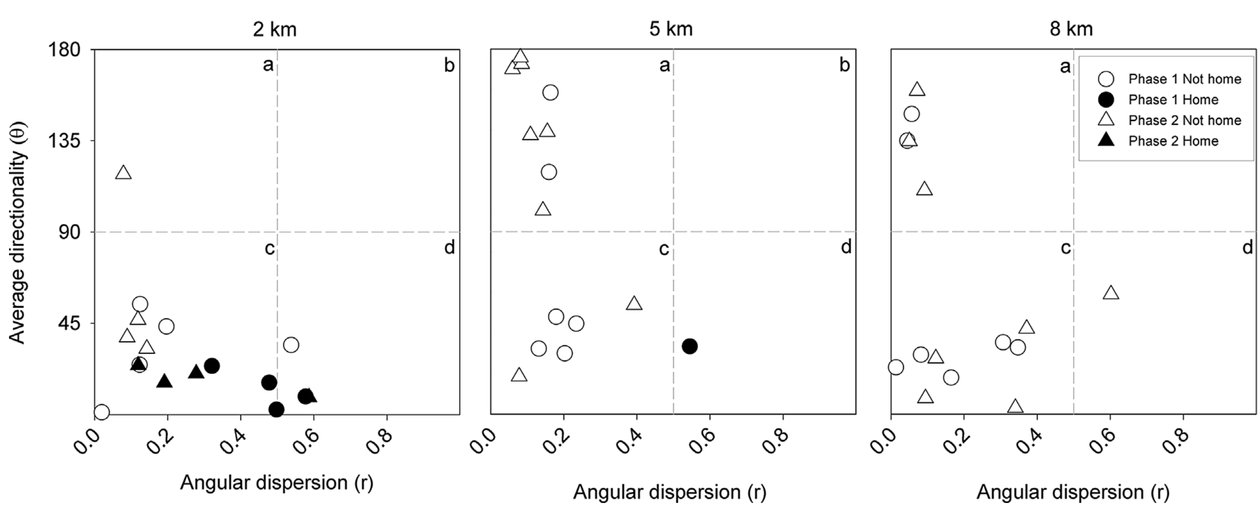

Figure 2. Directionality (θ) and angular dispersion (*r*) of desert tortoises in 3 translocation distance groups occurring at the National Training Center, Fort Irwin near Barstow, California, USA, in 2009 and 2010. Tortoises able to navigate home had higher *r* values and lower θ values than tortoises not able to navigate home. Tortoises moving in the opposite direction of home with no angular concentration would have θ and *r* values of 180 and 0, respectively. Tortoises exhibiting perfect homing ability would have θ and *r* values of 0 and 1.0, respectively. Quadrants generally correspond with different movement patterns, where tortoises in quadrant (a) traveled in the wrong direction and were not concentrated in their movement bearings; (b) moved in the wrong direction toward a concentrated bearing; (c) exhibited some directionality; and (d) demonstrated homing, with both directionality and minimal angular dispersion. Solid symbols indicate tortoises that arrived home (defined as within 500 m of their capture location within 37 days of experimental translocation). Open symbols indicate tortoises that did not return home. Phase 1 occurred from 21 September to 28 October 2009, and phase 2 occurred from 13 April to 20 October 2010.

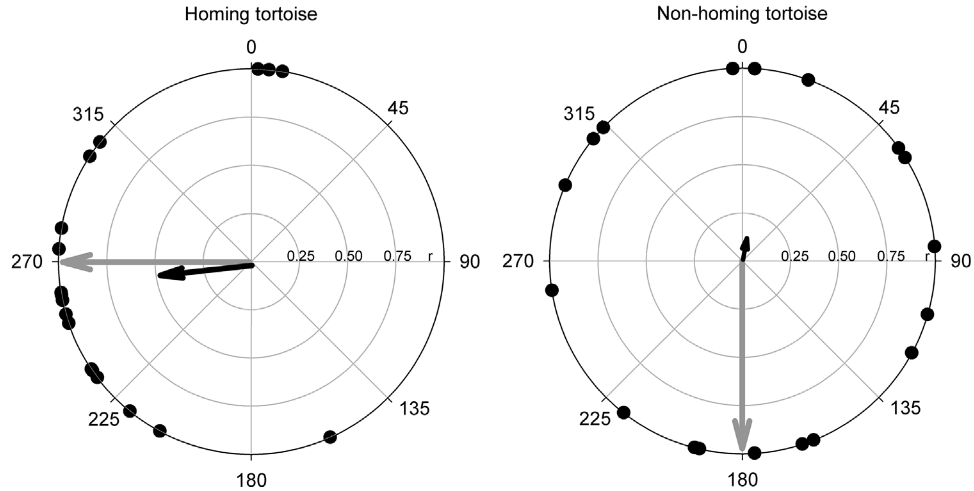

Figure 3. Examples of orientation of 2 translocated desert tortoises during an experiment on National Training Center, Fort Irwin, California, USA in 2009; 1 that returned home in 18 days, and another that did not. Both were female tortoises in the 2-km distance group in phase 1 of the experiment. Movement bearings are indicated on the outside of the circle, and angular dispersion (*r*) values are indicated by the open concentric rings. Solid circles represent desert tortoise movement bearings from release site to final location; direction and length of black arrow indicates mean angle of travel and angular dispersion (*r*), respectively; and grey arrow indicates homeward direction. The tortoise that returned home had a mean angle of travel of 266°, similar to the homeward direction of 270°, and minimal angular dispersion ($r = 0.49$). The tortoise that did not return home had a homeward direction of 180°, a mean angle of travel of 7°, and angular dispersion of $r = 0.08$.

As with all in situ experiments, uncontrolled factors may have influenced our results. In this study, neither behavioral, nor genetic data were available to account for how existing social structure may have affected the behavior of translocated tortoises. Translocations are known to disrupt social structures (Bertolero et al. 2007, Haydon et al. 2008) and translocation distance possibly served as a proxy for social structure. Individuals translocated greater than 2 km away may have exhibited increased movement in response to different and unfamiliar conspecifics rather than the new environment. Tortoises in this experiment may have been particularly habituated to human activity and presence, as all tortoises had been previously handled. Although we did not detect obvious differences between the control and handling treatment groups, we cannot discount potential effects of human activity and presence. We also were unable to account for or measure the impact of translocation on the resident tortoises in the translocated sites. As with translocated individuals, resident tortoises at recipient sites may be indirectly affected by translocation and experience higher rates of disease transmission or increased likelihood of conspecific aggression, both of which may have negative effects on survival (Haydon et al. 2008, Wendland et al. 2010).

Translocation is becoming a common instrument for conservation, mitigation, management, and restoration in many ecosystems and across many taxa (Seddon et al. 2007, Teixeira et al. 2007, Germano and Bishop 2009). The synergistic effects of disease (Brown et al. 1994, Christopher et al. 2003), habitat loss (Boarman and Sazaki 2006), predation (Esque et al. 2010) and the likely effect of climate change (Weltzin et al. 2003, Seager et al. 2007, Lovich et al.

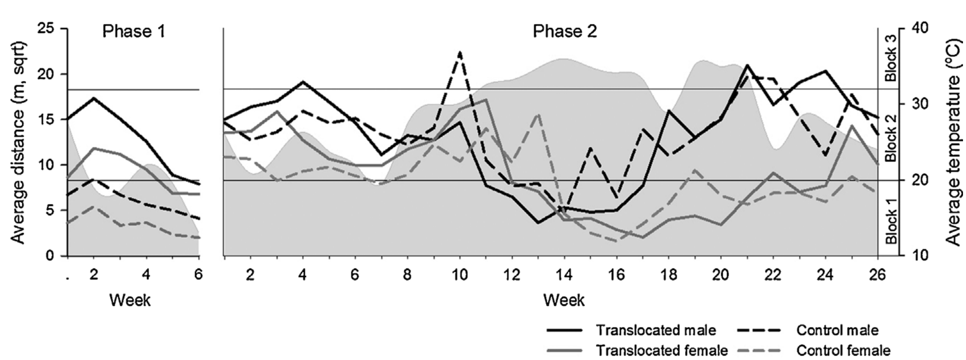

Figure 4. Mean distance (meters, square root-transformed) traveled by tortoises during a homing experiment in Fort Irwin, California. We experimentally translocated desert tortoises from their capture location and monitored their movements and ability to travel home. Phase 1 began 21 September 2009 (left panel) and lasted 37 days ($n = 35$), and phase 2 began 13 April 2010 (right panel) and lasted 186 days ($n = 36$). The average weekly ambient temperature (°C) shown in the grey profile, was obtained from the weather station at the Barstow-Daggett airport, located approximately 45 km from the study site. Temperatures blocks 1 and 3 roughly correspond with reduced tortoise activity. Tortoises in the phase 1 and phase 2 experiments were different individuals, and this graph only includes individuals who did not return home.

2014) have substantially influenced desert tortoises and the population continues to decline despite over 2 decades of federal protection. Translocations are employed to meet a range of management goals, including population re-establishment (Macmillan 1995), moderating habitat-use conflicts (Sullivan et al. 2004), and mitigating pending threats (Guyot and Clobert 1997, Heaton et al. 2008), as in the case of the Fort Irwin Expansion project. A better understanding of the long-term consequences of these, and other behavioral responses to translocation and the impact these responses may have on individual survival rates of translocated individuals is essential to improve the likelihood of success of this strategy for the desert tortoise and other reptiles at risk of extirpation.

MANAGEMENT IMPLICATIONS

Curtailing impacts that would require the translocation of desert tortoises is critical to conserve desert tortoises and their habitat. If translocation is required, our study indicates its success may be impeded by homing behavior and large movements after translocation assuming the goal is for tortoises to remain within the recipient site. Results from this experiment provide strong evidence that some desert tortoises in the NTC region exhibit homing behavior, and, if translocated, they are more likely to return home when their recipient site is less than 2 km away from their original home range. We found all tortoises that were able to get home, did so within 37 days, and that their trajectories towards home were generally straighter than those that did not get home. We also found increased movements persisted over time and therefore recipient sites should be large enough to support a translocated population with movement patterns and net displacement distances which, based on our findings, may be substantial. We recommend that tortoises should be monitored more closely during the first weeks or months post-translocation for homing behaviors and potentially fence-walking, should their original home range be excluded by a physical barrier.

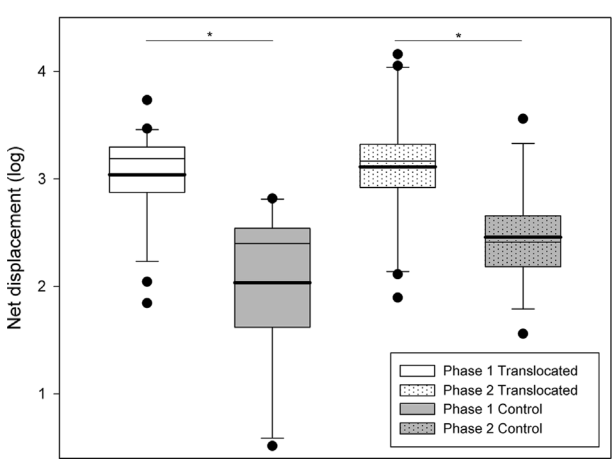

Figure 5. Mean net displacement distance (meters; log_{10} transformed) traveled by desert tortoises after experimental translocation at National Training Center, Fort Irwin, California, in 2009 and 2010. The boundary of the box closest to 0 indicates the 25th percentile, the thin line within the box marks the median, and thick line within the box marks the mean, the boundary of the box farthest from 0 indicates the 75th percentile, whiskers indicate 90th and 10th percentile, and outliers beyond are shown as points. A significant difference in net displacement between groups within each phase is indicated with an *.

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APPENDIX A. Demographic and activity area calculations for desert tortoises on the western expansion area.Tortoise unique identifying number (ID), sex, midline carapace length (MCL), number of months radio tracked, area (m^2), perimeter (m) and maximum linear distance (m) across the minimum convex polygon (MCP) of 54 desert tortoises on the western expansion area in 2009 and 2010. We calculated the minimum convex polygon from all monthly locations to establish activity areas of resident tortoises on the western expansion area and completed analysis using Hawth's tools in ArcGIS 9.3.

Tortoise ID	Sex	MCL (mm)	Months tracked	MCP area ($m^{2)}$	Maximum distance (m)
1	Female	210	20	44,526.2	309.2
2	Male	266	24	543,258.7	400.5
3	Male	236	22	16,686.0	432.0
4	Female	232	23	52,734.7	475.1
5	Female	235	22	60,552.9	482.1
6	Female	246	19	64,377.9	490.7
7	Male	226	22	114,202.8	504.4
8	Female	221	21	97,278.6	512.6
9	Male	268	24	69,354.2	524.9
10	Male	223	18	76,582.9	526.4
11	Female	229	25	138,696.1	548.2
12	Female	234	23	81,397.4	564.3
13	Female	215	22	80,116.6	579.4
14	Female	251	23	65,634.1	610.8
15	Male	270	20	151,278.7	617.9
16	Female	252	20	116,554.4	627.5
17	Male	270	16	70,347.0	646.2
18	Female	240	16	142,849.3	654.0
19	Female	242	20	94,510.0	658.1
20	Female	232	22	149,995.0	661.9
21	Male	288	20	221,063.6	668.6
22	Male	285	13	151,959.6	688.3
23	Male	225	15	85,623.5	693.6
24	Male	264	20	149,990.8	694.9
25	Male	242	20	231,530.1	704.7
26	Female	253	22	165,283.9	737.1
27	Male	276	21	77,498.7	743.6
28	Male	260	20	277,941.8	758.0
29	Male	288	21	271,448.3	768.4
30	Male	278	22	40,037.7	775.2
31	Male	260	21	110,918.7	782.1
32	Male	277	21	132,092.2	810.2
33	Female	237	17	114,594.1	834.7
34	Female	227	21	119,056.2	846.9
35	Male	272	20	235,180.6	853.6
36	Male	259	20	171,232.7	861.1
37	Male	260	22	282,741.2	890.7
38	Male	281	20	98,583.9	925.0
39	Male	211	22	278,810.0	969.0
40	Male	276	21	451,632.3	1,032.3
41	Male	254	29	276,322.7	1,040.7
42	Female	244	21	146,881.1	1,053.3
43	Male	271	16	238,365.7	1,066.7
44	Female	213	19	88,202.0	1,083.6
45	Female	226	24	109,268.6	1,188.6
46	Male	258	20	227,815.0	1,240.7
47	Female	242	23	415,687.9	1,278.5
48	Female	239	22	134,395.1	1,449.3
49	Female	219	17	295,719.8	1,515.5
50	Female	254	23	735,967.3	1,542.7
51	Female	219	15	464,834.5	1,611.9
52	Male	276	15	195,589.5	1,648.8
53	Male	267	17	1398,071.4	1,724.9
54	Female	214	17	1583,987.0	2,368.7