Movement Ecology

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Origin of translocated animals is associated with time to settlement and post-translocation survival

Seth Harju[1*] and Scott Cambrin[2]

Abstract
Translocation of animals is a widespread tool for resolving human-wildlife conflicts and augmenting struggling wild populations. However, expected time to settlement and survival (both measures of translocation success) are often unknown, particularly as a function of the origin of translocatees. We quantified settling times using Bayesian changepoint detection models on the variance in two derived movement metrics for translocated Mojave desert tortoises (*Gopherus agassizii*) of two different origins: wild adults and adult waifs (i.e. former pets). We compared the annual home range sizes of translocated tortoises with residents, and we also compared survival of each origin group to tagged resident adults. We found that translocated tortoises from different origin groups took an average of 0.5–2.0 years, depending on origin group, to settle based on movement metrics. Waif tortoises took the longest to settle, on average, within 2 years. There was high individual heterogeneity in settling times among tortoises. Home range sizes were larger for translocated wild tortoises than for resident adults only in the year of translocation. Home range sizes of translocated waif females and males were larger than those of residents, but only for the first two years post-translocation. After accounting for a strong year effect, annual survival rates were not different between resident adults (0.91; 90% CI 0.78–0.98) and translocated wild adults (0.90; 0.67–0.99); survival of waif adults was lower than residents, albeit with overlapping confidence intervals, at an annual rate of 0.80 (0.56–0.95) over the 11-year study. We provide results and discussion of using Bayesian models to identify fundamental changes in the variance of distance from release site and directional movement rate (e.g. erratic versus deliberate movements) to determine translocation success. We also provide guidance for managers of Mojave desert tortoise translocation projects and the translocation of animals in general.

KeyWords Animal movement, *Gopherus agassizii*, Mojave desert tortoise, Dispersal distance, Directional movement rate, Settling behavior, Survival translocation

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Introduction

Translocation of animals into wild populations is an increasingly large part of management and applied conservation [1]. Translocations are often driven by three motivations: re-colonizing suitable habitats that previously supported now-extirpated populations, augmenting isolated or declining populations, and/or minimizing human-wildlife conflicts [2, 3]. These translocations can benefit both source individuals by avoiding development-driven direct mortality and habitat loss, and target populations via demographic rescue and improved genetic diversity [4, 5].

The outcome of animal translocations is often subjectively deemed unsuccessful [6]. One promising quantitativemeasure of success is some metric of animal movement, such as dispersal, site fidelity, home range size, or other derived movement metrics [7]. Animal movement is promising for the field of conservation translocation because the primary difficulty reported in translocation programs is movement itself [8]. Individual animals may leave the release site following translocation, possibly attempting to return to their original home range [9] or because they are fleeing unfamiliar habitat cues at the release site [10]. Movement also provides a mechanistic assessment of translocation success, as translocated animals may exhibit sub-optimal resource selection and fitness that is not obvious without tracking movement [11, 12].

Research on post-translocation movement has found some consistent patterns. First, that time to settlement varies across species [7]. For example, translocated marten (*Martes martes*) may settle within two weeks [13], translocated beavers (*Castor canadensis*) within 100 days [14], and greater sage-grouse (*Centrocercus urophasianus*) may take over one year to exhibit movement behaviors similar to resident animals [15]. Second, the source of translocated animals, hereafter termed 'origin', can also affect translocation success. For example, captive-born Iberian lynx (*Lynx pardinus*) were more cautious after release than translocated wild-born lynx [16].

Translocation is a prominent part of tortoise management and recovery worldwide, including the Mojave desert tortoise (*Gopherus agassizii*) in the southwestern U.S., the gopher tortoise (*Gopherus polyphemus*) in the southeastern U.S., and Hermann's tortoise (*Testudo hermanni*) in the Mediterranean region [6, 17–21]. Researchers have found similar patterns across species. Most translocated Mojave desert tortoises and gopher tortoises dispersed away from the release location, with water-supplemented tortoises moving the farthest and temporarily field-penned tortoises dispersing the least [17, 19–21]. Some Mojave desert tortoise translocatees settled down with space use metrics equivalent to residents within 3 years post-release [20], but other studies on Mojave desert tortoise and Hermann's tortoise concluded settlement within two weeks or shorter [17, 18]. Mojave desert tortoises and Hermann's tortoise often showed higher mortality post-translocation, but survival improved over time [17, 19, 22]. Field et al. [17] concluded that initial high mortality was due to drought conditions, not translocation effects (although they were not able to compare survival rates to concurrent resident tortoises). Nussear et al. [20] found no difference in survival between translocated and resident Mojave desert tortoises, and also found that survival was unrelated to previous winter precipitation.

What has been minimally addressed in the tortoise translocation literature is the fate of translocated 'waif' tortoises. Waif tortoises are individuals of unknown origin, displaced from the wild and maintained by humans as pets. The waif tortoise and freshwater turtle population is huge, with an estimated 2 million tortoises and turtles traded globally per year from 1990 to 2010, with the U.S. alone likely having 7.3 million pet tortoises and turtles in 2014 [23, 24]. This situation is also quite common for Mojave desert tortoises. Prior to federal listing, many people in the desert southwest had desert tortoises as pets and those pets were exempted from the listing decision as threatened under the rule as long as they were not part of a commercial operation [25]. This did not limit the number of tortoises that could be housed in one location and did not address future progeny, which has resulted in widespread backyard breeding and large populations of legal waif Mojave desert tortoises within the geographic region of the Mojave desert. McKee et al. [26] evaluated the fate of translocated waif gopher tortoises and found that they had survival and site fidelity rates equivalent to wild-to-wild translocated gopher tortoises. Following extensive disease testing, waif tortoises may be an under-utilized origin of translocatees to replenish depleted wild populations where the causes of population decline have been remedied.

Our objective with this study was three-fold. First, we wanted to use modern Bayesian models to quantify population and individual-level times to settlement based on movement behaviors. We chose to estimate settlement using the natural logarithm of dispersal distance, which is the squared straight-line distance between the point of release and every subsequent relocation [27]. We also used directional movement rate, which is an index combining steplengths (i.e., the straight-line distance between consecutive relocations) and turning angle, which reflects a combination of strong turns combined with long steplengths. Second, we used a simple, historic method to determine settling time based on home range size. Third, we modeled survival since release as a function of origin to compare ultimate individual fates of translocated animals versus resident tortoises.

Study area

Our study area was within the Boulder City Conservation Easement, a 35,000-ha protected area managed largely for Mojave desert tortoise habitat. The Easement ranges from 520 - 1,080 m elevation south of the metropolitan area of Las Vegas, Nevada, USA (Fig. 1). The habitat consists of Mojave Desert scrub, mesquite/acacia, and salt desert scrub with a dominant species community of creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*). The climate for the project area is typical of the Mojave Desert – hot summers, mild winters, and very little rain. Temperatures usually exceed 38 °C in the summer with average winter highs near 15 °C and annual precipitation averages less than 125 millimeters per year. Rainfall in each year post translocation was considered below normal (2.95 cm – 8.84 cm) with only 2015 (10.87 cm) exceeding the Las Vegas average of 10.54 cm according to regional flood control data.

Methods

Origin of translocatees

Translocatee tortoises were obtained from two main sources. Waif tortoises (26 females, 25 males) were surrendered pet tortoises that were held at the Desert Tortoise Conservation Center (DTCC) located on the southwestern edge of Las Vegas, NV. These animals underwent rigorous testing and a minimum 90-day quarantine period before they were eligible for translocation. Full details related to health procedures and protocols can be found in the Greater Trout Canyon Area and Northeast Boulder City Conservation Easement translocation plans, but all tortoises received at least two physical examinations and were tested for *Mycoplasma agassizii* and *Mycoplasma testudineum* through an enzyme-linked immunosorbent assay and a quantitative polymerase chain reaction test [28, 29]. Other tests were completed as needed based on the results of the physical examination. Wild translocated tortoises (6 females, 3 males) were removed from construction sites in and around the Las Vegas Valley. These individuals received a 30-day quarantine and two health assessments to look for

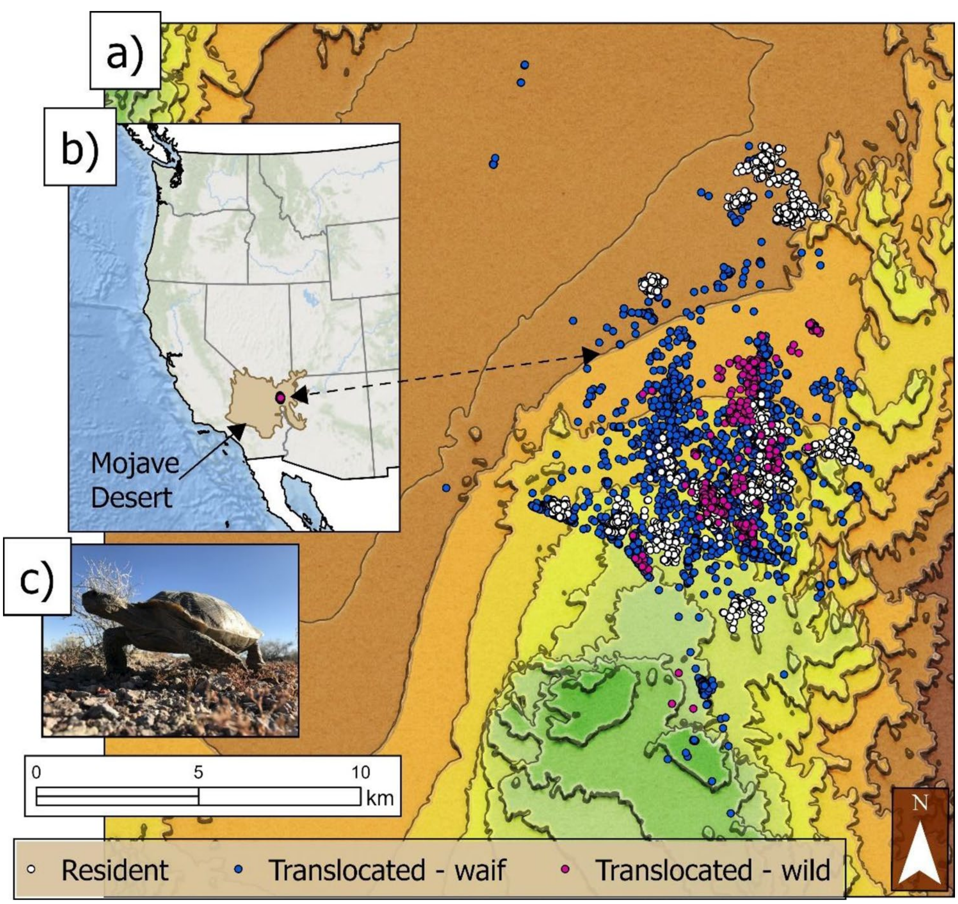

Fig. 1 Location of study on post-translocation settling times and survival of Mojave desert tortoises in southern Nevada, USA, released periodically during the period 2014–2024. The main release area (**a**) is within the Boulder City Conservation Easement in the eastern Mojave desert (**b**). Subpanel (**c**) is an adult resident male Mojave desert tortoise (photo credit S. Cambrin)

clinical signs of disease, the protocol for which is detailed in U.S. Fish and Wildlife Service [30]. Resident tortoises (12 females, 25 males) were located during pre-translocation surveys in 2014 and as incidental encounters during radio telemetry of other telemetered individuals. All tortoises used in this study were above the 180 mm midline carapace length threshold to be considered an adult. Tortoises were affixed with a 15 g transmitter (RI-2B, Holohil Systems Ltd.) with a putty epoxy (SteelStick Grey Epoxy Adhesive, J-B Weld). Transmitters were replaced every one and a half to two years to prevent the transmitter from failing, subsequently losing connection with the individual tortoise. Each individual was marked with a unique ID in the form of a small tag attached with clear epoxy. A detailed explanation of these methods is available in U.S. Fish and Wildlife Service [31].

Tortoises were released within the Boulder City Conservation Easement as they were available. Each individual received a final health assessment and was given access to water for at least 30 minutes prerelease. We translocated 35 waif tortoises in the fall of 2014, four wild tortoises in the fall of 2016, 16 waif tortoises in the fall of 2017, and five wild tortoises in the fall of 2022 (Fig. 2). Resident tortoises were captured and released more consistently, with 13, 4, 5, 3, 3, and 9 tortoises tagged and released in 2014, 2016, 2017, 2019, 2021, and 2023, respectively. We followed all release parameters set forth by the US Fish and Wildlife Service's Desert Tortoise Recovery Office for each release, including multiple health assessments and a release window where temperatures range from 18 - 30 °C and are not forecasted to exceed 32 °C within 3 hours of release or 35 °C within 1 week of release. Additionally, forecasted daily low temperatures should not be cooler than 10 °C for one-week post-release, all of which is easier to accomplish in the fall than the spring.

Field data collection

Tortoises were located via a VHF radio receiver and a handheld antenna by a radio telemetry technician. Tortoises were located twice a week for the first month post-release, followed by weekly during the active season (March – October) and monthly during brumation (November – February). Tortoises that went missing

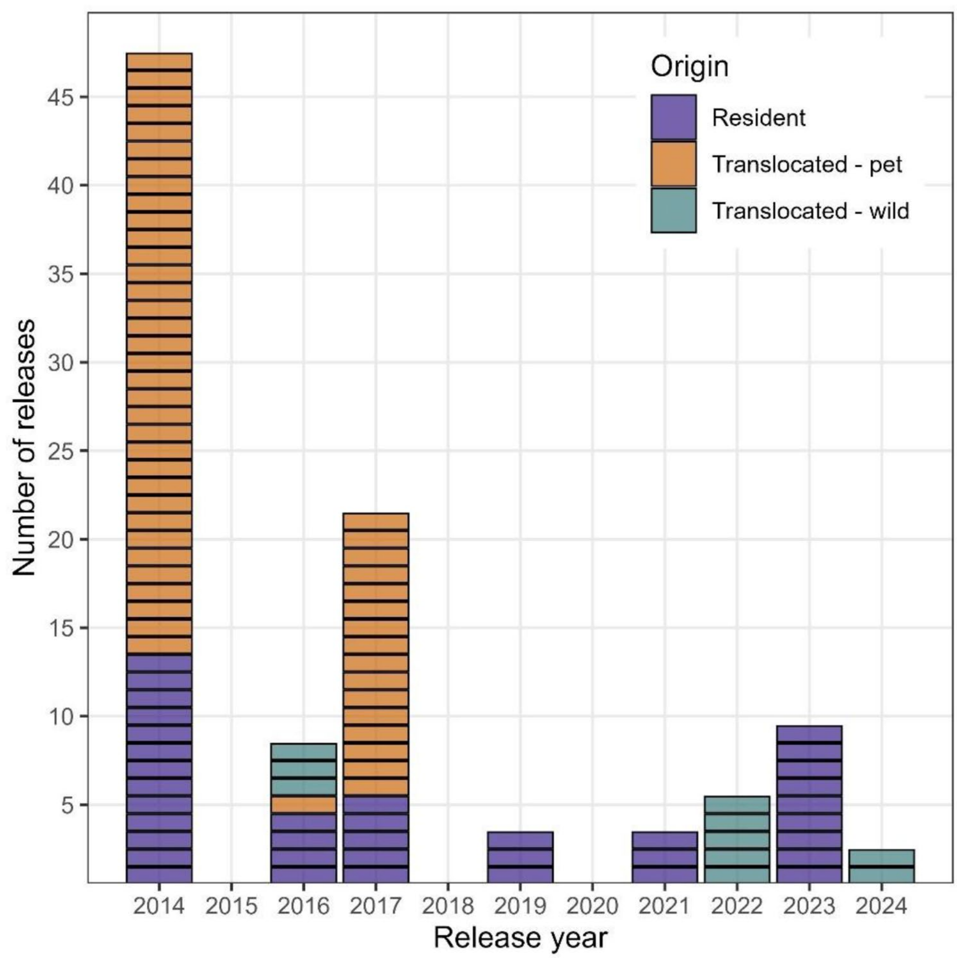

Fig. 2 Sample sizes across release years of released translocated and mark-release resident Mojave desert tortoises in southern Nevada, USA, 2014–2024

were searched for on a weekly basis for at least one year before we considered them "disappeared, fate unknown".

Statistical analysis

We used the GPS locations from individual tortoises to calculate basic movement metrics, including steplength (Γ) based on location coordinates (Z) and turning angle (Ψ) based on compass angle (Φ) between consecutive locations *t-1* and *t*:

$$\Gamma_t = |Z_t - Z_{t-1}|$$

$$\Psi_t = \Phi_t - \Phi_{t-1}$$

We then used steplength (Γ) and turning angle (Ψ) to calculate persistence velocity, which reflects how directed versus erratic an individual's movement is [32]. A high value indicates fast, straight-line travel, whereas a low or negative value reflects slow or highly tortuous movement. Persistence velocity (*PV*) at time *t* was defined as the product of steplength and the cosine of the turning angle:

$$PV_t = \Gamma_t * \cos(\Psi_t)$$

For clarity, we refer to this measure as directional movement rate throughout the manuscript.

We also calculated Net Squared Displacement (NSD) to characterize movement away from the release site and settlement in a final home range [33]. NSD is the square of the distance of each successive location from the first location:

$$NSD_t = (Z_t - Z_0)^2$$

This metric describes the tortoise's cumulative dispersal distance from its release point over time. For clarity, we refer to this measure as dispersal distance throughout the manuscript.

We then used behavioral changepoint analysis to identify a single changepoint demarcating a fundamental change in variance separately for directional movement rate (i.e., persistence velocity) and dispersal distance (i.e., log(NSD)) as a function of time since release. We chose variance in both metrics because we hypothesized that variance in these metrics would be higher before versus after the changepoint. Behavioral changepoint analysis is an efficient analytical method that is robust to temporally gappy movement data, makes minimal assumptions, and can be applied to a wide variety of movement metrics [32]. We used a Bayesian formulation and focused on the change in variance in our two movement metrics as a function of days since release. We set an uninformative uniform prior on the population-level changepoint value between 0 and the maximum observed days since release *x*, defined for each origin group *i*:

$$cp_i \sim dunif\left(0, \max(x_i)\right)$$

and set a normal prior for individual tortoise *j* changepoints zero-centered on the population-level changepoint:

$$cp\_ind_{ij} \sim \ dnorm\left(0, tau\_ind_i\right)$$

Our Bayesian normal prior was parameterized in terms of mean and precision tau_i, where tau_i was a function of standard deviation:

$$tau_i = \frac{1}{cp\_sd_i{}^2}$$

and the prior for the standard deviation was truncated to be positive-definite as:

$$cp\_sd_i \sim \ dnorm\left(0, tau_{cp_i}\right) T\left(0,\right)$$

$$tau\_cp_i = \frac{1}{\left(2 * \left(\max\left(x_i\right) - \min\left(x_i\right)\right)\right)^2}$$

with separate priors for the variance before and after the changepoint truncated to be positive-definite as:

$$var = (sigma)^2$$

$$sigma \sim \ dnorm\left(0, tau\_sigma\right) T\left(0,\right)$$

$$tau\_sigma = \left(\frac{1}{\left(SD\left(y\right)\right)^2}\right)$$

We present variance in movement metrics before and after the changepoint but did not conduct traditional tests for statistical significance in variances before and after the changepoint because we did not think that such null hypothesis tests would add to the biological understanding of the research questions.

We used a simple, historic method to estimate settling time, the size of a minimum convex polygon around annual locations of resident and translocated tortoises. We separated locations from each tortoise into calendar years for analysis of post-translocation home range size. We then used Bayesian log-normal generalized linear regression models to compare each origin group's annual home range size, for each year following translocation, with annual resident home range sizes of males or females. We did not include the final year in home range calculations for individuals that died in order to avoid biasing low annual home range sizes as a function of fewer locations due to death.

We modeled survival as a time-to-event process using a Cox proportional hazards model. Time was represented by days since release of translocated or tagged resident tortoises, where the event was either death or last-seen-alive (i.e., alive at the end of monitoring, a.k.a. censored). We used origin group (pooling sexes) as a predictor variable on the instantaneous hazard rate to compare whether the probability of dying after release differed between resident tortoises and translocated wild or waif tortoises.

We analyzed post-release survival as a function of tortoise origin (resident, translocated-pet, translocated-wild) while accounting for temporal variation in environmental conditions. Specifically, overall desert tortoise survival can differ dramatically across years in response to environmental conditions [34, 35]. We wanted to explicitly account for this in the survival model to accommodate 'bad' years and the effect of this on group-level survival estimates given the ragged translocation timeline across origin groups. Survival time was measured as the duration from release until death or censoring (end of study). To control for year-to-year variation in mortality risk that could confound comparisons among groups released in different years, we employed a Cox proportional hazards model with random year effects (a shared frailty model).

The baseline model was specified as:

$$h_i\left(t|g_i, w_j\right) = w_j h_0\left(t\right)\exp\left(g_i^T\beta\right)$$

where $h_i(t)$ is the hazard function for individual *i* at time *t* since release, $h_0(t)$ is the baseline hazard function, g_i is the origin group for individual *i*, β is the regression coefficient for each origin group, and w_j represents the multiplicative frailty (random effect) for year *j*. Year frailties were assumed to follow a gamma distribution with mean 1 and variance θ to maintain identifiability, where θ quantifies the degree of between-year variation in baseline mortality risk. We then calculated the survival *S* at time *t* based on the hazard model, such that:

$$S\left(t\right) = \exp\left(-h\left(t\right)\right)$$

Because standard Cox frailty models do not permit direct computation of marginal survival curves (survival predictions averaged over the distribution of random effects, i.e., survival in an 'average' year), we used a bootstrap resampling approach to marginalize over year effects. For each of B = 500 bootstrap iterations, we: (1) sampled year-specific random effects from a normal distribution with mean 0 and variance equal to the estimated frailty variance from the fitted model; (2) fit a Cox model with the sampled year effects included as fixed offsets, allowing prediction of group-specific survival curves conditional on those particular year effects; and (3) computed survival curves for each origin group. We then calculated the mean and 90% percentile-based confidence intervals of the survival probabilities across all bootstrap samples at each time point. This procedure yields survival curves that represent expected post-release survival for each group in an "average" year, effectively controlling for the confounding influence of differential exposure to favorable or unfavorable environmental conditions. For comparison, we also computed standard Kaplan-Meier survival curves stratified by origin group, which do not account for year effects.

We monitored model convergence for the Bayesian behavioral changepoint analyses using Gelman-Rubin r-hat diagnostics and effective sample sizes. We used the 'mcp' package [36] to conduct the Bayesian behavioral changepoint analysis, the 'brms' package [37] for generalized linear models on annual home range size, the 'survival' package [38] for Kaplan-Meier survival analysis, and custom code for bootstrap marginalization over the shared frailty effect in Program R (v4.4.1).

Results

We obtained an average of 39.3 to 184.8 locations per origin and sex grouping (Table 1). The relocation interval was generally maintained, with weekly relocations from March through October and monthly relocations from November through February (Fig. S1 in Additional File S1). Some relocation intervals were larger than planned if a tortoise could not be located during a planned survey

Table 1 Relocation sample sizes summary statistics for resident and translocated waif (i.e., former pets) and wild Mojave desert tortoises in southern Nevada, USA, released periodically during the period 2014–2024

Class	Sex	Mean	SD	Min.	Max.	Sum	Individ.[a]
Resident	Female	145.8	115.4	24	318	1749	12
Resident	Male	184.8	118.5	36	392	4805	25
Waif	Female	147.1	123.6	13	406	3824	26
Waif	Male	130.1	107.2	12	290	3252	25
Wild	Female	174.2	152.4	15	318	1045	6
Wild	Male	39.3	14.6	29	56	118	3

[a]Number of individual tortoises

Table 2 Estimated population-level changepoints in movement metrics for translocated waif (i.e., former pets) and wild Mojave desert tortoises in southern Nevada, USA, released periodically during the period 2014–2024. Changepoint units are days since release of translocated tortoises

Movement metric	Origin	Changepoint (days after release)	L 95% CrI	U 95% CrI	n_eff[a]	rhat[b]
Dispersal distance (log(m^2))	Waif - female	376.4	293.6	475.1	25	1.97
	Waif - male	193.7	164.0	227.4	50	1.27
	Wild - female	137.2	102.9	184.8	112	1.28
	Wild - male	335.4	127.4	539.4	309	3.72
Directional movement rate	Waif - female	697.0	604.4	800.0	8	1.24
	Waif - male	721.7	548.5	889.9	9	5.72
	Wild - female	362.1	143.0	799.9	135	9.67
	Wild - male	232.0	167.2	298.6	862	1.50

[a]Number of effective draws from the posterior distribution. [b]Gelman-Rubin rhat statistic for MCMC chain convergence

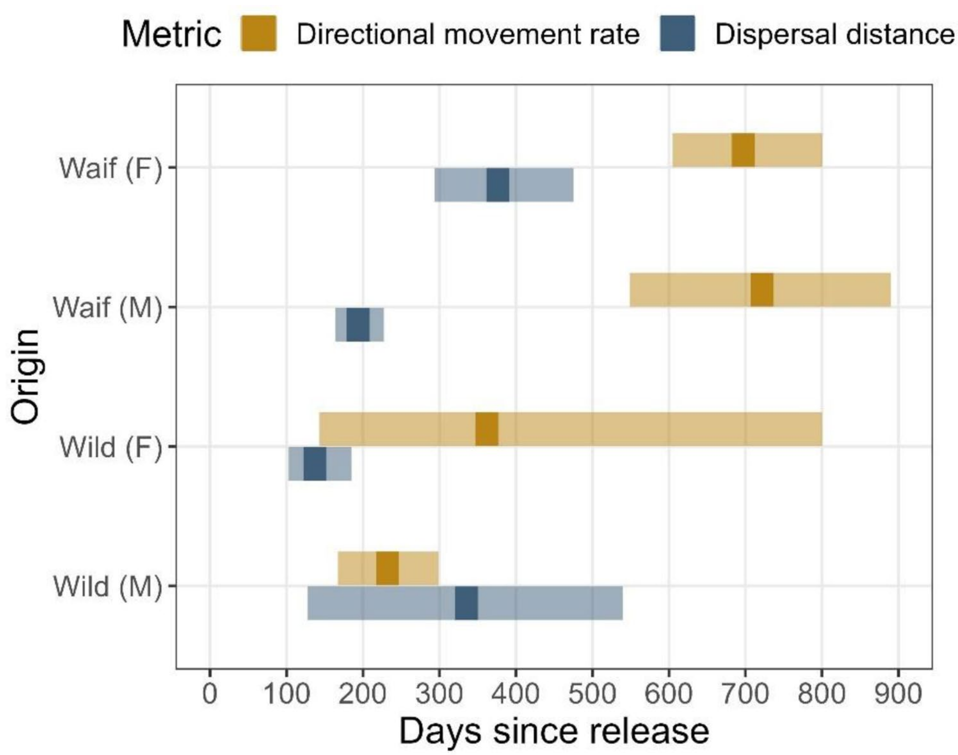

Fig. 3 Estimated population-level changepoints (opaque squares) in the variance of log(dispersal distance) and directional movement rate for four origin groups of translocated Mojave desert tortoises in southern Nevada, USA, released periodically during the period 2014–2024. Error bars are 95% Bayesian credible intervals

(e.g., it was in a burrow underground and the transmitter signal did not propagate). Other relocation intervals were occasionally more frequent than planned, due to incidental encounters while surveying for other individual tortoises.

The movement changepoint analyses showed high variation in estimated changepoints among origin groups, ranging from 137.2 to 721.7 days post-release (Table 2). In general, population-level changepoints based on directional movement rate were later than changepoints for dispersal distance, indicating that translocated tortoises from most origin groups settled on a 'home range' but continued erratic movements within their home range for a time, differently than expected distributions of mostly short and occasionally long movements (Fig. 3 [39]). The exception to this pattern was translocated wild males, who showed similar changepoints for both movement metrics, possibly with an earlier settling point based on directional movement rate than with dispersal distance. Unfortunately, for both movement metrics, some origin groups had poor model convergence via low effective posterior sample size and high rhat diagnostics (Table 2). Nonetheless, changepoint estimates were consistent across independent model runs (S. Harju, unpublished data).

We found that variance in dispersal distance was overwhelmingly higher before the changepoint but was extremely small after the changepoint (Table S1 in Additional file S1). Variance in directional movement rate also showed this same pattern for waifs and wild females. For wild males, the point estimate for variance was lower after the changepoint, but credible intervals were wide and overlapping for pre- and post-changepoint.

Viewing observed directional movement rate across individuals as a function of the number of days since translocation highlighted a general dampening over time. For example, translocated waif males showed that most individuals reduced variance in directional movement rate by ~ 721 days after release (i.e., 2 years), although there was high variability in individual changepoints, ranging from 186 to 1,400 days after release (Fig. 4a, Table 2, Table S2 in Additional file S1). Similarly, translocated waif females had highly variable individual changepoints in directional movement rate, ranging from 14 to 1896 days, although on average females had settled in their post-release home range within 376.4 days (i.e., 1 year; Fig. 4b, Table 2, Table S3 in Additional file S1). Individual changepoints in dispersal distance for both waif males (Fig. 4c) and waif females (Fig. 4d) were more closely concentrated around the mean than they were for directional movement rate. The estimated changepoints were often clear when back-applied to raw movement tracks, as illustrated by two representative waif tortoises (Fig. 5), providing a visual demarcation of settling time.

Home range size of translocated waif females and males appeared considerably larger than resident females and males, respectively, for the first three years following translocation, after which they fell within the range of residents (females 4.16 ha [95% CrI 0.04–8.23], males

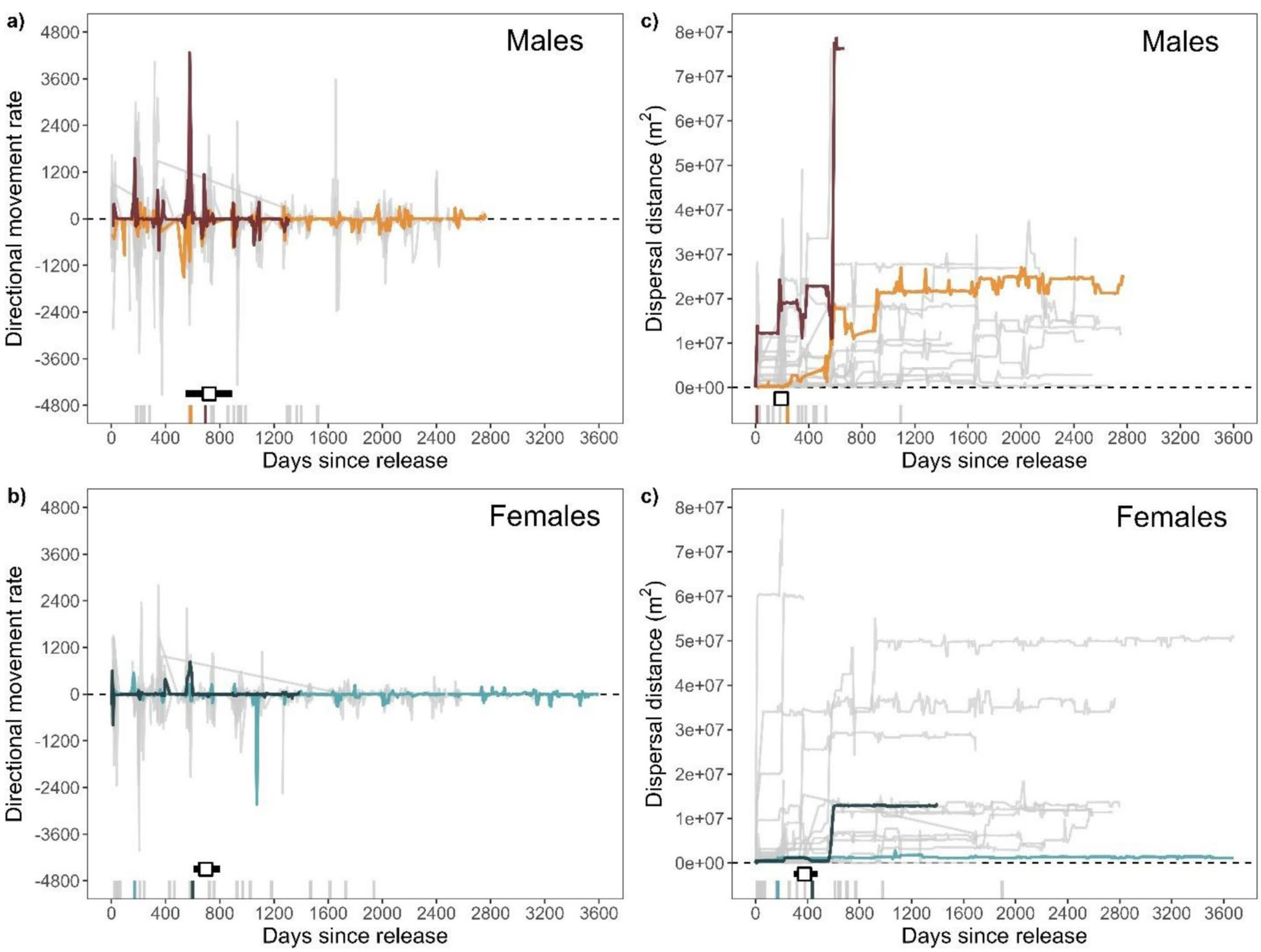

Fig. 4 Individual line graphs (gray) of observed directional movement rate of adult male (**a**) and female (**b**) waif Mojave desert tortoises and dispersal distance of adult male (**c**) and female (**d**) waifs following translocation in southern Nevada, USA, released periodically during the period 2014–2024. Two individuals are highlighted in each subplot via colored lines: those with the median and the maximum number of days since release. Vertical hashes along the x-axes mark individual tortoise changepoints. Black outlined boxes are the population-level changepoints; horizontal error bars are 95% Bayesian credible intervals

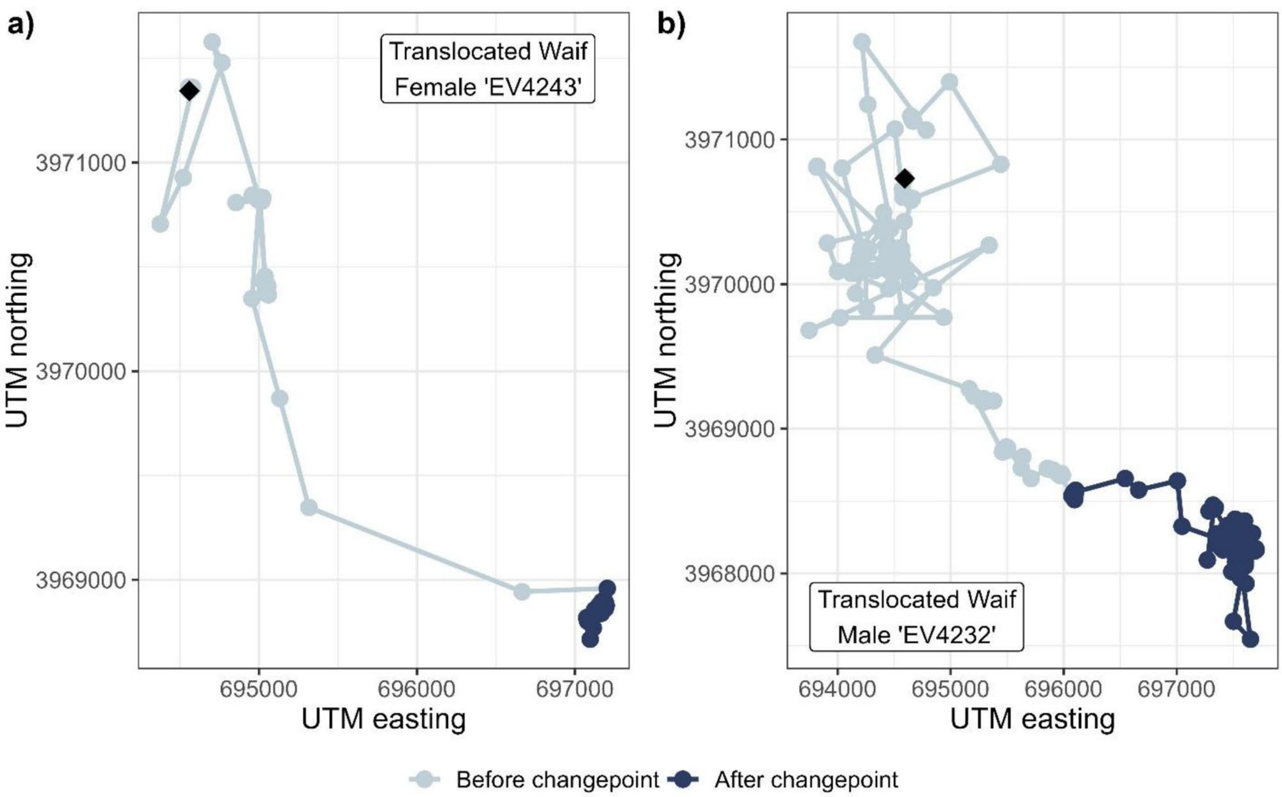

Fig. 5 Movement paths of two randomly chosen translocated waif Mojave desert tortoises released in southern Nevada, USA, in September 2017 until the tortoise's ultimate fate. The female (**a**) died in July 2021 and the male (**b**) was last seen alive in October 2024. Movement paths are symbolized by whether they were before or after the individual changepoint in directional movement rate (**a**) or log(dispersal distance)(**b**). Black diamonds are the release locations. UTM coordinates are shifted by a fixed value to protect locational information

14.50 ha [95% CrI 11.50–17.66]; Fig. 6). However, this difference was only significant (i.e., 95% credible intervals not overlapping zero difference) for female waifs for the year of translocation (1.76 times larger home range, 95% CrI 0.76 - 2.76), year 1 post-translocation (2.09 times larger, 0.67 - 3.47), and year 2 (2.36 times larger, 0.98–3.75). In year 3, female waifs had home ranges 0.98 (–0.41 - 2.36) times larger than resident females, but credible intervals broadly overlapped zero. For translocated male waifs, home range size in the year of translocation was 1.20 times (–0.34 - 2.75) as large as resident males, but the difference was not statistically significant. However, in year 1 post-translocation male waif home ranges were 2.15 times larger (0.35 - 3.91) and in year 2 were 2.00 times larger (0.20 - 3.80). By year 3 post-translocation, male waif home ranges were not significantly larger than resident males (0.56 times larger, –1.28 - 2.34). Translocated wild females had home ranges 2.91 times larger (1.54 - 4.30) than resident females in the year of translocation, but did not have larger home ranges by the year following translocation (Fig. 6). Translocated wild males also had larger home ranges the year of translocation (3.21 times larger, 1.00 - 5.37) than resident males. No translocated wild males remained in the study past the first year post-translocation (one disappeared, one had the transmitter removed and was released, and one died).

Origin of translocated tortoises was associated with increased mortality compared to resident tortoises, but only for translocated waifs (Fig. 7). Resident adults (males and females combined) had frailty-adjusted annual survival rates of 0.91 (90% CI 0.78–0.98), similar to translocated wild tortoises (annual survival rate = 0.90, 90% CI 0.67–0.99). Translocated waifs had considerably lower annual survival rates than residents, at 0.80 (90% CI 0.56–0.95), albeit with confidence broadly overlapping among the three tortoise groups. There was strong annual variation in the hazard of mortality, such that an average 'bad' year could have ~4.2x higher mortality rates than the average across all years ($\chi^2 = 96.87$, $p < 0.001$). The same general pattern in mortality was present in the naïve Kaplan-Meier curves, even though these curves did not account for strong annual variability in mortality (Fig. S2 in Additional File S1). By calendar year, waif tortoises had mortality pulses in 2015 and 2022, whereas resident tortoises had a high mortality pulse in 2022 (Fig. S3 in Additional file S1).

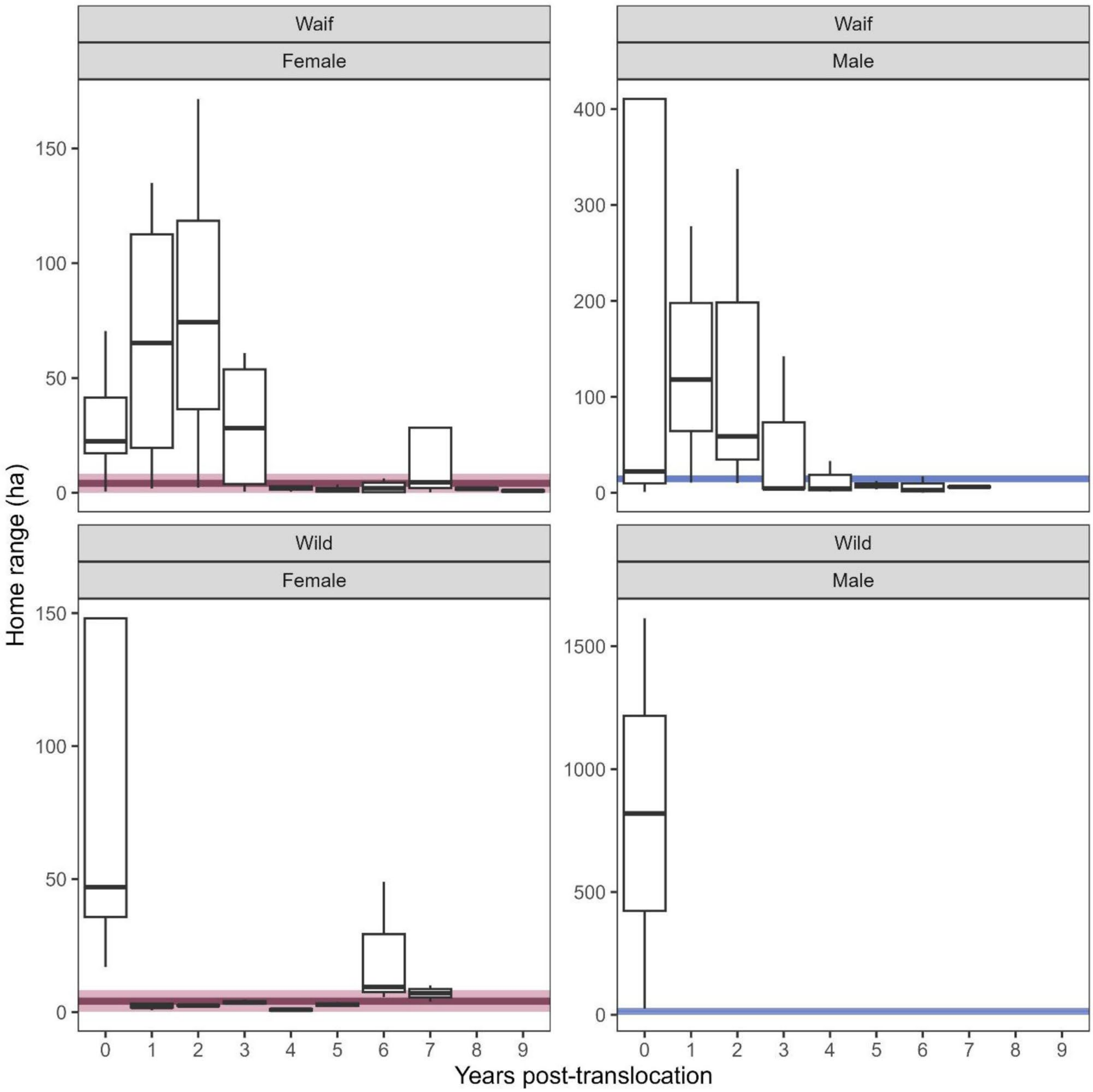

Fig. 6 Post-translocation minimum convex polygon home range size of translocated waif and wild Mojave desert tortoises in southern Nevada, USA, released periodically during the period 2014–2024. Outliers are excluded for display purposes. Horizontal red and blue lines are mean annual home range sizes for resident female and male desert tortoises, respectively. Shaded horizontal bands are 95% credible intervals

Discussion

We found that origin of translocated tortoises significantly affected their movement and settlement dynamics. Based on dispersal distance (i.e., home range establishment), waif tortoises and wild female tortoises evidenced settlement within 0.5–1.0 years after translocation. Those three origin groups also took considerably longer to settle based on directional movement rate, reflecting erratic movement within the established home range until 1–2 years after release. Waif tortoises (i.e., former pets) took the longest time for settlement based on directional movement rate, at 2 years on average. Importantly, for most origin groups and movement metrics, there was high inter-individual variability in time-to-settling.

These settlement times are considerably longer than previous studies reporting post-translocation movement of Mojave desert tortoises. While we found average settlement times pf 0.5- 2.0 years based on movement metrics, previous researchers have qualitatively concluded that settlement occurred within two months [17,

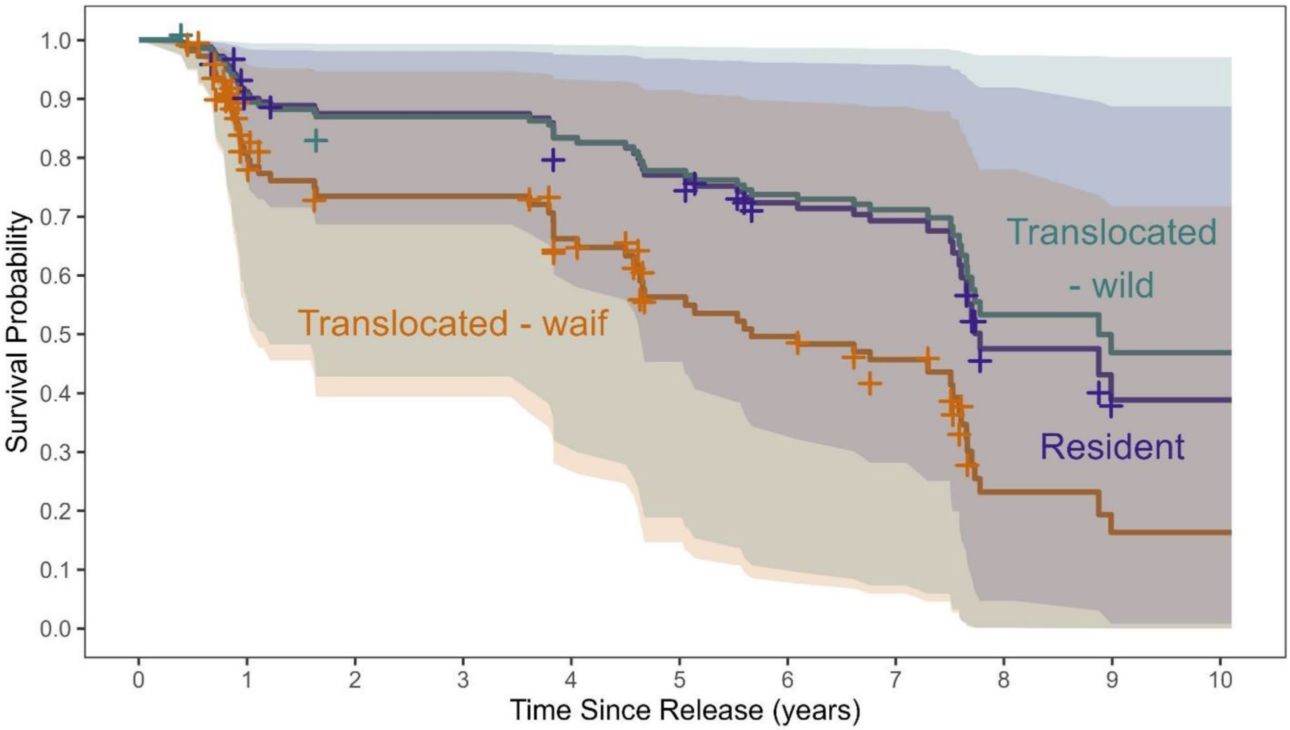

Fig. 7 Shared frailty cox proportional hazard survival curves following release for three origin groups of resident and translocated Mojave desert tortoises (pooling males and females) in southern Nevada, USA, released periodically during the period 2014–2024. Cross marks are mortality events (jittered vertically for visibility). Error ribbons are 90% confidence intervals. Wide confidence intervals are due to uncertainty in the shared frailty effect

40, 41]. Similar to this study, previous research on home range size has evidenced longer settlement times, up to two or three years [17, 20]. We found the translocated wild females only had larger home ranges the year of translocation, but translocated waif females and males had larger home ranges through the second year post-translocation, having 'settled' by the third year. We found congruence between home range size and directional movement rate, with all measures indicating 'settlement' 2 years post-translocation for waif tortoises. We think that the results presented here represent a novel detailed picture of settlement based on two meaningful measures of post-translocation movement in addition to the traditional metric of annual home range size, with the primary conclusion being that origin affects post-translocation settlement, and that settlement can be quantified and understood via multiple metrics.

We note the caveat that we did not include seasonal weather effects on the movement behaviors of Mojave desert tortoises. For example, adult and juvenile Mojave desert tortoises usually move more and have larger home ranges following wet winters to capitalize on higher abundance and quality of ephemeral forage [19, 41, 42], although this pattern is not universal [43]. Although seasonal weather patterns influence some aspects of tortoise movement—particularly step length and time above ground—we suggest that dispersal distance and directional movement rate are more strongly affected by the translocation process to a novel environment than by seasonal weather. Regardless, translocations following wet winters may facilitate tortoise survival via the higher availability of quality forage.

Origin appeared to impact post-translocation survival, with inexperienced waifs having higher mortality rates than wild resident tortoises, whereas survival of translocated wild adults did not differ from adult residents [44] note wide overlapping confidence intervals in our study). Equivalent survival between wild translocated and resident tortoises agrees with previous research, possibly because the translocation process itself is not physiologically stressful to Mojave desert tortoises [20, 45–47]. Juvenile gopher tortoises also showed non-significant differences in survival based on translocation origin [48]. Our finding that waif translocated tortoises had an average annual survival rate of 0.8 is novel, given that other long-term studies have observed long-term annual survival rates of 0.9–1.0 [34, 35, 45, 46, 49, 50]. We hypothesize that the lower survival of waif Mojave desert tortoises may be due to an interaction between their lack of experience in natural environments (i.e., a life in captivity, with food and water regularly provided) combined with a long-term megadrought across the southwestern U.S. within which the translocations occurred [51, 52]. Again, we note that the survival confidence intervals overlapped broadly among groups, suggesting limited confidence in the strength of lower survival among translocated waifs.

Although not part of this study, we would be remiss to omit other concerns of using waif tortoises as a source population for translocations. One major concern with the use of waif tortoises for translocation is genetics [53–55]. For example, translocated gopher tortoises show outbreeding depression in the form of lower hatching success in individuals separated by further distances, even if translocation distance does not influence adult survival [56, 57]. Contrary to this concern, Scott et al. [58] showed that heterozygosity was the driver of survival for translocated tortoises. A second genetic concern is translocating waifs from the wrong species. Edwards and Berry [54], did find one instance of a Sonoran desert tortoise (*Gopherus morafkai*) within the geographic range of the Mojave desert tortoise, highlighting the importance of pre-release genetic testing of waifs. A third genetic concern is that translocatees may not contribute to reproduction or genetic diversity in the resident population [59]. For Mojave desert tortoises, this only seems to be a potential issue for males [60], as translocated wild and waif females reproduce in as little as 4 years from release [20].

Disease transmission is another major concern for translocation projects. Diseases such as upper respiratory tract disease and herpesvirus occur in wild populations may be further spread by highly mobile translocated animals [61]. Novel diseases may be transmitted to a wild population from waifs housed with different species of tortoises [54, 62]. While this is an important concern, it can be mitigated through careful screening of individuals included in a translocation program as well as monitoring and testing during a quarantine period.

These findings provide some guidance for managers of Mojave desert tortoise populations. First, translocating waif tortoises can be successful, albeit with longer settling times and possibly higher mortality rates. Second, settlement time differed by source population; wild adults settled most quickly, followed by waif tortoises. Third, mortality for the two largest origin groups in this study, residents and waifs, showed clear pulses in mortality in some years, indicating that environmental context was a strong moderator of translocation outcomes. Translocations followed by particularly difficult environmental conditions may benefit from resource supplementation, such as re-capture and providing supplemental water [17, 63]. Additionally, managers may wish to postpone translocation events during or preceding expected 'bad' years. For example, when the El Niño-Southern Oscillation (ENSO) is in its cold phase (i.e., La Niña), winter and spring droughts are more common in the Mojave Desert [64, 65]. As ENSO forecasting improves (e.g., there is a current 20-month ENSO forecast lead [66]), managers should plan for translocations in El Niño years when winter and spring precipitation conditions are favorable, resulting in improved nutritional forage for Mojave desert tortoises [67]. Guidance aside, we do note that we did not have balanced release sample sizes in each year, and that although we averaged movement metrics over years and explicitly incorporated year-specific mortality rates, we may have missed other year-specific effects on movement and survival of some individual tortoises.

For translocation programs with other species, this study supports the conclusion that translocating waif individuals can benefit local populations [26, 68]. However, it is critically important to screen translocatees for infectious diseases, lest local populations are ultimately harmed via introduced epidemics [69, 70]. Settlement times of translocatees may be longer and survival rates may be lower. Nonetheless, movement-based metrics proved useful in reflecting individual and population-level settlement times and successful movement-based integration into the resident population.

Supplementary information

The online version contains supplementary material available at https://doi.org/10.1186/s40462-026-00624-2.

Supplementary Material 1

Acknowledgements

We would like to thank The Great Basin Institute, especially Terry Christopher and Brent Sparks for their work on this project. We would also like to thank the U.S. Geological Survey, San Diego Zoo Global, and all the countless volunteers that helped care for and translocate these tortoises. We would like to thank the US Fish and Wildlife Service's Desert Tortoise Recovery office specifically Kim Fields and Roy Averill-Murray for their help in developing the translocation plan for this area and for help with the translocation process. We thank Tarita Harju for insightful discussions on visualizing and interpreting settling rates and two anonymous reviewers for constructive comments and feedback on earlier versions of the manuscript. All animal handling was completed under the MSHCP 10(a)1(B) permit # TE 034927–0 from the U.S. Fish and Wildlife Service.

Author contributions

SC and SH conceived the ideas and designed the methodology; SC collected the data; SH analysed the data; SH led the writing of the manuscript; all authors contributed critically to the drafts and gave final approval for publication.

Funding

This project was funded by the Clark County NV, Desert Conservation Program through Section 10 funding.

Data availability

Data are not yet provided, but will be archived on Data Dryad if manuscript is accepted for publication. Locational data will be withheld to avoid collection of a threatened species.

Declaration

Ethics and Consent to Participate

Not applicable.

Consent to publish
Not applicable.

Competing interests
The authors declare no competing interests.

Received: 10 July 2025 / Accepted: 6 January 2026
Published online: 18 January 2026

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