Inter-Research Science Publisher
Endangered Species Research
Volume 59:esr01468
Published February 12, 2026
https://doi.org/10.3354/esr01468

An integrated model improves inferences about survival in the Mojave desert tortoise

Steven J. Hromada[1,12,⋆], Brian Folt[1,2], Kevin T. Shoemaker[3], Madeline Standen[1], Arielle Parsons[1], Linda J. Allison[4,†], Jacqueline Dougherty[5], K. Kristina Drake[4], Todd C. Esque[6], M. A. Walden[3], Jerry Freilich[7], Jeffrey E. Lovich[8], Ann M. McLuckie[9], Corey I. Mitchell[4], Michael S. Vamstad[7], Amy G. Vandergast[10], Elizabeth A. Hunter[11], Kenneth E. Nussear[5], Brett G. Dickson[1]

[1]Conservation Science Partners, Inc., Truckee, CA 96161, USA
[2]US Geological Survey, Nevada Cooperative Fish and Wildlife Research Unit, University of Nevada, Reno, NV 89557, USA
[3]Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV 89557, USA
[4]US Fish and Wildlife Service, Desert Tortoise Recovery Office, Las Vegas, NV 89130, USA
[5]Department of Geography, University of Nevada, Reno, NV 89557, USA
[6] Western Ecological Research Center, US Geological Survey, Boulder City, NV 89005, USA
[7]National Park Service, Joshua Tree National Park, Twentynine Palms, CA 92277, USA
[8]US Geological Survey, Southwestern Biological Science Center, Flagstaff, AZ 86001, USA
[9]Utah Division of Wildlife Resources, Washington County Field Office, Hurricane, UT 84737, USA
[10]US Geological Survey, Western Ecological Research Center, San Diego, CA 92101, USA
[11]US Geological Survey, Virginia Cooperative Fish and Wildlife Research Unit, Department of Fish and Wildlife Conservation, Virginia Tech, Blacksburg, VA 24061, USA
[12]*Present address:* Fresno Chaffee Zoo, Department of Conservation, Fresno, CA 93728, USA

ABSTRACT: The Mojave desert tortoise *Gopherus agassizii* experienced population declines during recent decades, which have persisted despite its designation as a federally protected species. A small number of populations were monitored with mark–recapture methods starting in the 1970s, but inconsistent sampling resulted in challenges estimating the range of factors influencing survival. Large amounts of tortoise telemetry data were collected in recent decades, providing an alternative source for survival estimation. Here, we describe an integrated, spatially explicit, analysis that combined mark–recapture (3923 tortoises, 35 sites, 1977–2022) and telemetry (2858 tortoises, 22 sites, 1988–2022) datasets to estimate variation in survival across tortoise populations. We produced robust estimates of annual survival conditioned on climate-related covariates and compared results to non-integrated known-fate and mark–recapture models. Integration allowed for estimation of effects on survival not recovered by non-integrated models, including higher survival of males than females, lower survival of juveniles and subadults than adults, and a positive effect of total precipitation from 2 prior winters and active seasons. The integrated analysis estimated permanent emigration rate as the difference between both true survival (via telemetry data) and apparent survival (via capture–recapture data). Annual emigration probability was ~5% in 1 km^2 plots and decreased with increasing plot size. Our results demonstrate the strength of leveraging multiple data sources in describing historical demographic rates and identifying relationships with covariates that have delayed effects on survival. Our modeling framework could be used to examine the effects of additional factors on tortoise survival and resulting population dynamics.

KEY WORDS: Emigration · Drought · *Gopherus agassizii* · Bayesian hierarchical model · Mark–recapture · Radio telemetry

---

⋆Corresponding author: stevehromada@gmail.com
† Deceased

Publisher: Inter-Research · www.int-res.com

1. INTRODUCTION

Survival is an important demographic rate for animal populations, particularly for long-lived species with low reproductive rates (Congdon et al. 1993, Heppell 1998, Spencer et al. 2017). Challenges in survival estimation limit our ability to understand important factors that influence historical or contemporary population dynamics of threatened and endangered species and what management actions may be most useful for ameliorating stressors to decrease extinction risk (Beissinger & Westphal 1998, Sibly & Hone 2002). Estimating survival can be difficult for at-risk species, which often persist at low densities, can be difficult to detect, and therefore may be challenging to monitor over large geographic ranges (Thompson 2004, Jeliazkov et al. 2022). Monitoring studies that typically focus on localized populations of a species for short periods of time can be important for understanding the demographic rates and local population dynamics but may not be appropriate for extrapolating processes across large spatial scales (e.g. range wide) that could inform population trends and shape management strategies. Additionally, different methods and data collection protocols may preclude efficient estimation of effects on survival across the range of the species. Fortunately, advances in statistical methods can facilitate use of datasets that were collected in a variety of ways to be integrated together into single, concise analyses that better estimate the historical effects of different stressors on wildlife populations (Schaub & Abadi 2011, Schaub & Kéry 2022).

Survival estimation has long been of key interest among wildlife managers, and many different field and statistical protocols have been developed to estimate survival rates in animal populations (Lebreton et al. 1992, Murray & Patterson 2006). One traditional method has been to mark animals over multiple sampling sessions and then model survival as a function of recapture (survival and detection) probabilities (Jolly 1965, Seber 1965, Pollock 1982). Further development of these methods (hereafter, mark–recapture models) allowed for consideration of the spatial patterns in animal movements among sampling occasions (Royle et al. 2014). With the adoption of radio telemetry methods to track animal movements through space, models were developed to estimate survival when the survival fate of study animals was fully known (i.e. known-fate models; White & Garrott 1990) and not confounded by imperfect detection (Mazerolle et al. 2007), as is the case for many mark–recapture models. More recently, the development of integrated demographic models has allowed for the joint modeling of demographic rates across different sampling methods, providing insight into historical demographic trends (Besbeas et al. 2002, Schaub & Abadi 2011, Schmidt et al. 2015). Although these methods are often used to estimate multiple demographic rates, they can also be used to integrate different data sources to improve estimates of a single rate (e.g. survival; Badia-Boher et al. 2023). These developments provide a potential analytical framework to re-examine and integrate analyses of different existing datasets with the goal of better estimating survival and understanding factors influencing the demography of animal populations.

Individual-level attributes (e.g. reproductive status, body condition, age) are important aspects of a species' life history and couple with time-varying environmental attributes (e.g. precipitation, temperature) to act as key predictors of survival (Delgiudice et al. 2006, Rose et al. 2018, Moiron et al. 2020). Environmental conditions often have a crucial effect on animal survival; these can be natural cycles such as weather conditions and natural disturbances or the result of human impacts on habitat quality (Coulson et al. 2001, Guimarães et al. 2020). Species are expected to be adapted to the climate they evolved in, but climatic changes often result in new population stressors that may be changing faster than natural populations can adapt to via natural selection of plasticity (Bestion et al. 2015, Iler et al. 2021), can be additive or interactive with other stressors to cause population declines (DeMars et al. 2021, Church et al. 2022), and thus are necessary to be accounted for when determining the effects of other stressors (Gaillard et al. 2013, Abrahms et al. 2023). Historical datasets were typically obtained through studies of short duration, were not typically collected with the intention of answering questions related to climatic impacts, and were not always available for further analyses (Salguero-Gómez et al. 2016) — though newly developed analyses may be able to leverage such datasets.

The Mojave desert tortoise *Gopherus agassizii* (hereafter, tortoise) is an herbivorous reptile native to the Mojave and Colorado deserts of the southwestern USA. Most tortoise populations experienced precipitous population declines in the decades preceding and following federal listing as 'threatened' in 1990 (US Fish and Wildlife Service 1990, though see Bury & Corn 1995). Suspected causes of these declines have included disease, subsidized predators, habitat degradation/fragmentation, and drought (US Fish and Wildlife Service 1994, 2011, Berry & Murphy 2019). Range-wide population monitoring with line transect distance sampling (Allison & McLuckie, 2018) was established in the early 2000s, providing insights into potential relationships between stressors and changes in tortoise occupancy and density (Kissel et al. 2023, Zylstra et al. 2023). However, due to low recapture rates for all tortoise size classes, especially juveniles, line transect distance sampling data do not provide much information on underlying demographic rates that influence population dynamics, resulting in a limited understanding of how various stressors influence specific tortoise demographic rates (Allison & McLuckie 2018). Estimating survival is an important part of the first objective in the revised recovery plan for the species, and understanding how environmental stressors influence survival can better inform management actions aimed to reverse current declines in population sizes (US Fish and Wildlife Service 2011, Allison & McLuckie 2018). Although demographic rates have been estimated for single populations of tortoises (Lovich et al. 2014, Dickson et al. 2019, Berry et al. 2020) or averaged over multiple populations (Doak et al. 1994), a better understanding of how demographic rates vary across the species' range and are influenced by environmental stressors could further help inform management actions.

In this paper, we sought to understand how Mojave desert tortoise survival is influenced by climate using integrated analysis of both mark—recapture and known-fate telemetry data from across the species' range during 1977—2022. We aggregated relatively large samples of mark—recapture data (3923 individuals from 35 survey sites) and known-fate telemetry data (2858 individuals from 22 sites). We built 2 statistical models that estimated survival using mark—recapture and known-fate telemetry data separately and then integrated them into a single model informed by both sources of information (Powell et al. 2000). We used the integrated model to describe spatial and temporal variation in survival and test for the importance of climatic variables (precipitation). Our results provide a spatially explicit parameterization of the baseline stressor of climatic variation on historical tortoise survival and also show the benefits in precision of parameter estimates that come from the integration of multiple data sources.

2. MATERIALS AND METHODS

2.1. Tortoise data

2.1.1. Mark—recapture data

We used 3 sources of mark—recapture data from tortoise populations (Table 1, Fig. 1). The first was data from 'permanent study plots' that were established between 1971 and 1994 by the US Bureau of Land Management (BLM), US Fish and Wildlife Service (USFWS), and other agencies (Tracy et al. 2004). These plots were generally 2.6 km^2 (i.e. 1 mile^2) in area and were surveyed intermittently during 1977—2012. During each survey year, researchers searched plots with 1—4 complete searches (ca. 30 person-days each) during both the spring and summer, and every live tortoise detected was marked. We digitized locations of tortoises found during surveys from published and unpublished reports when available. We used data from all of the established permanent study plots surveyed more than once in Nevada, Utah, and Arizona (data for most [14/16] of the plots established in California were not made available for this analysis). In total, we had data for multiple years at 16 historical plots, most of which had spatial records of tortoise encounters. We treated the Barrow plot in Joshua Tree National Park as 2 plots, as only the north portion of the plot was surveyed in some years (Lovich et al. 2014). We also used the data for the Desert Tortoise Research Natural Area (Entrance) plot (Berry & Yee 2021). Most sites had no records of tortoise translocations, but one plot in Utah (Woodbury—Hardy plot) received translocated tortoises in the 1970s (exact year unknown). Second, we used data from eight 1 km^2 plots established in Lake Mead National Recreation Area and surveyed in the spring (National Park Service 1997); all 1 km^2 plots had spatial encounter data. Finally, we used mark—recapture data collected from ten 1 km^2 plots in the Ivanpah Valley area on the border of California and Nevada. These plots were surveyed every 3 yr in the fall, with 3 full coverage passes being performed by crews of 20 skilled searchers on consecutive days. All adults in the Ivanpah Valley area mark—recapture plots had a radio transmitter attached, were tracked via radio telemetry, and were included in the radio telemetry datasets (see below). These plots have been used to derive density estimates using spatial capture—recapture methods (Mitchell et al. 2021b). One of these plots (Sheep Mountain) falls within the boundary of a historical 'permanent study plot'; we treated these plots as separate due to different plot size areas and no temporal overlap. Three of the Ivanpah Valley plots (ISEGS North, ISEGS South, and Silver State) occurred near where translocated tortoises were released in association with the construction of nearby utility-scale solar plants. Only 2 translocated individuals were captured during mark—recapture

Table 1. Mark–recapture datasets (n = 35) from Mojave desert tortoise *Gopherus agassizii* population monitoring efforts used in survival analyses. Metrics include: number of years surveyed, specific years surveyed, number of unique individuals captured, plot area, land management agency ownership (Mgmt. agency). The spatial data column indicates whether tortoise capture locations were available. State abbreviations: Arizona (AZ), California (CA), Nevada (NV), Utah (UT). Land management agencies: Bureau of Land Management (BLM), Boulder City Conservation Easement (BCCE), Department of Defense (DoD), National Park Service (NPS), and US Fish and Wildlife Service (USFWS). MCL: midline carapace length

Site	State	Mgmt. agency	No. of yr surveyed	Years surveyed (no. of passes yr^{-1})	Plot area (km^2)	Spatial data	No. of tortoises captured	Notes
Beaver Dam Exclosure (BDE)	AZ	BLM	7	1977(1), 1978(1), 1979(1), 1980(1), 1989(1), 1996(2), 2001(3)	1.7	No	87	No within-year recapture information; each year treated as one survey
Littlefield (LFN)	AZ	BLM	7	1977(1), 1978(1), 1980(1), 1987(1), 1993(2), 1998(2), 2002(2)	2.6	No	207	
Virgin Slope (VSN)	AZ	BLM	3	1992(2), 1997(2), 2003(1)	2.6	Yes	51	
Desert Tortoise Research Natural Area (DNA)	CA	BLM	7	1979(2), 1985(2), 1989(2), 1993(2), 1997(2), 2002(2), 2012(2)	7.8	No	1111	No MCL measurements, only age class
ISEGS North (IN)	CA	BLM	3	2016(3), 2019(3), 2022(3)	1	Yes	24	Tortoises >160 mm MCL telemetered
ISEGS South (IS)	CA	BLM	2	2017(3), 2020(3)	1	Yes	13	Tortoises >160 mm MCL telemetered
Joshua Tree National Park — Barrows Plot (BAJ)	CA	NPS	10	1978(2), 1991(N,2), 1992(N,2), 1993(B,2), 1994(B,1), 1995(B,2), 1996(B,2), 2004(N), 2005(N,4), 2012(B,1)	2.6	Partial*	271	Only the North portion of the plot was surveyed in years marked with N, the entire plot was surveyed in years marked with B; no spatial data for 2004
Nipton (NI)	CA	BLM	2	2017(3), 2020(3)	1	Yes	62	Tortoises >160 mm MCL telemetered
Sandy Valley (SV)	CA	BLM	3	2016(3), 2019(3), 2022(3)	1	Yes	37	Tortoises >160 mm MCL telemetered
Southpah (SP)	CA	BLM	3	2016(3), 2019(3), 2022(3)	1	Yes	73	Tortoises >160 mm MCL telemetered
Stateline Pass (SL)	CA	BLM	3	2016(3), 2019(3), 2022(3)	1	Yes	25	Tortoises >160 mm MCL telemetered
Bitter Springs (BSL)	NV	NPS	3	1996(2), 1997(2), 2003(2)	1	Yes	23	
Cottonwood (CWL)	NV	NPS	4	1992(2), 1993(2), 1994(3), 1995(2)	2.6	Yes	65	Animals telemetered beginning in 1993
Coyote Springs (CSN)	NV	BLM	3	1986(2), 1992(2), 1995(2)	2.6	Yes	154	
Dupont Mine (DML)	NV	NPS	2	1995(2), 1999(2)	1	Yes	2	No tortoises found in 1999

Table 1. continued on next page

Table 1. (continued)

Site	State	Mgmt. agency	No. of yr surveyed	Years surveyed (no. of passes yr^{-1})	Plot area (km^2)	Spatial data	No. of tortoises captured	Notes
Eldorado (EL)	NV	BLM	2	2017(3), 2020(3)	1	Yes	19	Tortoises > 160 mm MCL telemetered
Gold Butte (GBN)	NV	BLM	3	1986(3), 1990(2), 1994(2)	2.6	Yes	119	No spatial data in 1986
Government Wash (GWL)	NV	NPS	3	1996(2), 1997(2), 2002(2)	1	Yes	9	No live Tortoises in 2002
Grapevine (GVL)	NV	NPS	4	1992(2), 1993(2), 1994(3), 1995(2)	2.6	Yes	90	Tortoises telemetered beginning in 1993
McCullough Pass (MC)	NV	BLM	3	2015(3), 2018(3), 2021(3)	1	Yes	74	Tortoises > 160 mm MCL telemetered
Mormon Mesa (MMN)	NV	BLM	2	1989(2), 1994(2)	2.8	Yes	107	
Overton (OVL)	NV	NPS	2	1996(2), 2000(2)	1	Yes	22	
Piute Valley (PVC)	NV	BLM	5	1979(1), 1983(2), 1987(2), 1989(2), 1994(2)	2.6	Yes	200	
River Mountains (RML)	NV	NPS	3	1995(2), 1998(2), 2002(2)	1	Yes	46	
Road 42 (R4L)	NV	NPS	2	1997(2), 2001(2)	1	No	5	
Road 58 (R5L)	NV	NPS	3	1996(2), 1997(2), 2003(2)	1	Yes	17	No spatial data in 2003
Road 60 (R6L)	NV	NPS	2	1995(2), 1998(2)	1	Yes	14	No spatial data in 1998
Sand Hollow (SHN)	NV	BLM	2	1989(2), 1994(2)	2.8	Yes	15	
Sheep Mountain (SHM)	NV	BLM	4	1979(1), 1984(3), 1992(2), 1995(2)	2.6	Yes	120	
Sheep Mountain (New; SH)	NV	BLM	3	2015(3), 2018(3), 2021(3)	1	Yes	40	Animals > 160 mm MCL telemetered, boundaries inside SHM plot
Silver State (SS)	NV	BLM	3	2015(3), 2018(3), 2021(3)	1	Yes	24	Animals > 160 mm MCL telemetered; 2 translocated tortoises found on surveys
Trout Canyon (TCE)	NV	BLM	2	1987(3), 1992(2)	2.6	Yes	51	
Xmas Tree Pass (XTC)	NV	BLM	3	1985(3), 1991(2), 1994(2)	2.8	Yes	226	
City Creek (CCU)	UT	BLM	2	1988(2), 1994(2)	2.6	No	385	
Woodbury–Hardy (WHN)	UT	BLM	4	1981(2), 1986(2), 1992(2), 1998(2)	2.7	No	135	Site of Woodbury & Hardy (1948); translocated tortoises released sometime in the 1970s

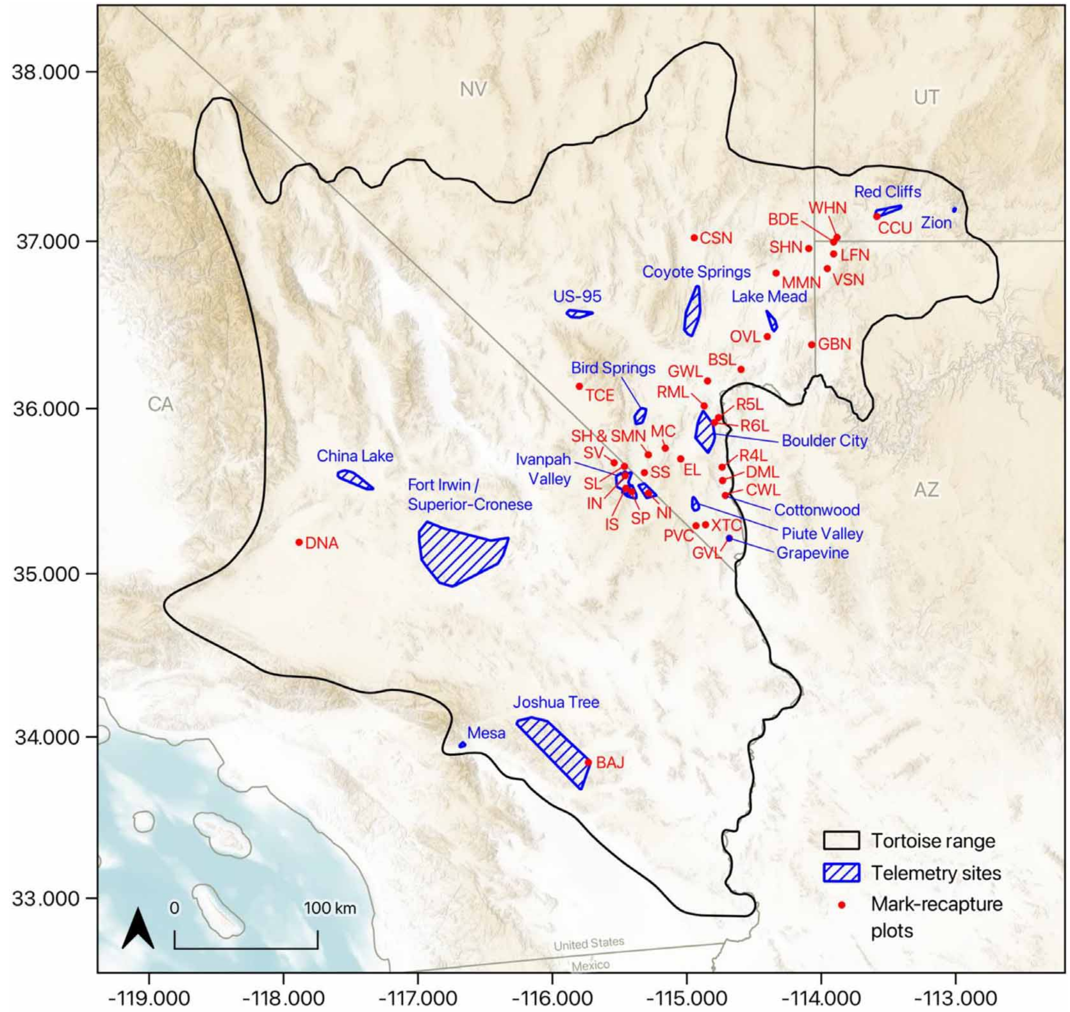

Fig. 1. Study areas where mark—recapture and telemetry methods were used to monitor Mojave desert tortoises *Gopherus agassizii* populations. Blue hashed polygons: boundaries of telemetry areas; red points: centroids of mark—recapture plots. Abbreviations for mark—recapture plots are in Table 1

surveys on one plot (Silver State). For all survey efforts every live tortoise was measured, marked uniquely, identified to sex (when possible), and released where found.

2.1.2. Telemetry data

We used very high frequency (VHF) radio telemetry data from numerous desert tortoise monitoring projects across the species range during 1988—2022 (Table 2, Fig. 1). Intentions for these monitoring projects ranged from (1) understanding how human and natural disturbances influence tortoise individuals, populations, and population connectivity, (2) modeling detection probability for population density monitoring across the species range, (3) studying the efficacy of tortoise translocation methods, and (4) describing other aspects of the species ecology (Longshore et al. 2003, Nussear et al. 2012, Drake et al. 2015, Allison & McLuckie 2018, Dickson et al. 2019, Mitchell et al. 2021b). Projects occurred on different land jurisdictions, but most were either on BLM, National Park Service (NPS), or US Department of Defense (DoD) lands. All tortoises were individually marked and carried a VHF radio transmitter that was less than 10% of the individual's mass. For each project, tortoises were generally radio-tracked at a minimum of once a month in accordance with USFWS permitting rules, and all mortalities were recorded. We included incidental (<10 total) encounters of tortoises after radio transmitter removal, as such encounters improve survival estimates in tortoises (Harju et al. 2020). We did not include data from translocated tortoises in our telemetry analyses.

Table 2. Telemetry datasets (n = 22) from Mojave desert tortoise *Gopherus agassizii* monitoring efforts used in survival analyses. Number of ind.: sample size of individuals monitored over all years at each site; number of mortalities: number of individuals that were known to have died during the study period at each site. Total sample of years and individuals is on the final row. See Table 1 for abbreviations of states and land management (mgmt.) agencies

Site	State	Mgmt. agency	Study period	No. of ind.	No. of mortalities
China Lake	CA	BLM/DoD	2019–2022	31	3
Fort Irwin	CA	BLM/DoD	2005–2022	1632	107
Ivanpah Valley	CA	BLM	2010–2022	370	95
Joshua Tree National Park	CA	NPS	1996–1999; 2005–2022	30	9
Mesa	CA	BLM	1997–2022	45	3
Mesquite Valley	CA	BLM	2016–2022	18	6
Stateline Pass	CA	BLM	2012–2022	28	6
Superior-Cronese	CA	BLM	2005–2022	39	13
Bird Springs Valley	NV	BLM	1996–1999	81	10
Boulder City Conservation Easement	NV	BCCE	2014–2021	25	3
Cottonwood	NV	NPS	1992–2001	58	28
Coyote Springs	NV	BLM/USFWS	2006–2022	86	34
Eldorado	NV	BLM	2017–2022	23	0
Grapevine	NV	NPS	1992–2001	56	2
Indian Springs (US95)	NV	BLM	2020–2022	16	10
McCullough Pass	NV	BLM	2012–2022	62	9
Lake Mead National Recreation Area	NV	NPS	1998–2000	17	1
Piute Valley	NV	BLM	2005–2022	66	16
Sheep Mountain	NV	BLM	2015–2022	30	9
Silver State	NV	BLM	2012–2022	18	7
Red Cliffs Desert Reserve	UT	BLM	1988–2022	101	24
Zion National Park	UT	NPS	2000–2017	17	1
Total			1988–2022	2849	396

2.1.3. Environmental covariates

Research has suggested that tortoise survival and occupancy are influenced by drought (Lovich et al. 2014) and temperature extremes (Kissel et al. 2023), potentially due to time-lagged effects (Longshore et al. 2003, Lovich et al. 2014). We therefore sought to evaluate the relative contribution of precipitation and maximum temperature on tortoise survival. We obtained spatial rasters describing monthly precipitation and temperature data each year spanning the range of the tortoise at 800 m resolution (PRISM Group, Oregon State University 2023).

2.2. Survival models

We built 3 different models (known-fate, mark–recapture, integrated survival) to estimate survival and test for differences in inference on parameters influencing tortoise survival in space and time. We built all models and performed all statistical analyses in the statistical program R v. 4.2.1 (R Core Team 2018).

For each model, we tested for both individual and environmental-level covariate effects on annual survival probability. Tortoises were categorized as adults (midline carapace length [MCL] ≥180 mm), subadults (MCL 140–179 mm), or juvenile (MCL <140 mm); (Berry & Yee 2021). Tortoise sex has also been suggested as an important driver of survival (Esque et al. 2010, Folt et al. 2021, Lovich et al. 2023), and we classified each adult tortoise by its recorded sex. Where sex information was missing (juvenile tortoises do not display secondary sex characteristics, and sex classification was missing for some adult tortoises), we used Bayesian multiple imputation to assign sex probabilistically according to a site-specific male probability (Royle 2009). Similarly, we imputed age class (juvenile, subadult, adult) for individuals first captured as juveniles or subadults by including parameters (*sub.trans*, *ad.trans*) that represented the probability that a tortoise would transition between juvenile to subadult and subadult to adult age class every year in all models.

2.2.1. Known-fate survival model

We built a known-fate survival model to estimate annual survival probability from telemetry datasets. Known-fate models can be used to estimate annual survival when the fate of every animal is known for each survival interval, as is the case when telemetry data are collected (White & Garrott 1990). We right censored (removed the last year of data) any individual that did not have a full active season of data during its final year of tracking. We modeled tortoise annual survival (S) with:

$$\mathrm{logit}(S_{i,t}) = \mathrm{logit}(S_0) + \beta_{juv} \times juv_{i,t} + \beta_{subad} \times subad_{i,t} + \beta_{male} \times male_{i,t} + \beta_{precip} \times precip_{i,t} + \beta_{precip \times \mathrm{sex}} \times male_i \times precip_{i,t} + \beta_{temp} \times temp_{i,t} + \eta_{s,t} \tag{1}$$

where S_0 was a logit-transformed intercept of S_0, *juv*, *subad*, and *male* were binary variables estimating juvenile, subadult, and male status for each tortoise, i, in each year, t, and *precip* and *temp* were continuous covariate estimates for precipitation and maximum temperature for each individual tortoise, i, in each year, t, and η was a random effect of site (s) by year (t).

2.2.2. Mark–recapture model

We built a hierarchical, spatial state-space, Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965) with a robust design (Pollock 1982, Kendall et al. 1995) to understand annual survival of tortoises using the mark–recapture datasets (Royle 2008, 2014). This model was developed for area-search surveys, conditions detection probability on whether a tortoise is located within the surveyed area (with each location drawn from an isotropic, half-normal distribution centered on a latent 'activity center' unique to each tortoise; see below) and allows temporary emigration of individuals during a survey period (Royle et al. 2011). All the plots were surveyed 1 to 3 times in a year (in close succession), providing a 'robust design' with open-population processes (i.e. survival) occurring among annual primary sessions and secondary sessions nested within each primary session during which the population is assumed to be closed (Pollock 1982). Study plots were likely too small (1–7.8 km^2) and isolated from each other to detect permanent tortoise emigration (Hromada 2022). We were unable to properly parameterize long distance movements between primary sessions from mark–recapture survey data (Efford & Schofield 2022). Thus, the CJS model estimates apparent annual survival probability (ϕ), the probability of surviving and remaining within the study area. Apparent survival is usually lower than true survival (S) (Schaub & Kéry 2022) due to permanent emigration (Schaub & Royle 2014).

Our CJS model had 3 main subcomponents: a spatial process model, an observation model, and a survival model. For the spatial process model, we modeled a latent activity center for each individual tortoise, with an activity use area determined by a Gaussian kernel with a spatial scale parameter σ that represents the radius (m) of the activity center, as done in (Mitchell et al. 2021b). We modeled σ as follows, with the assumption that the center point of activity centers is not different across years:

$$\log(\sigma_{i,t}) = \log(\sigma_0) + \beta_{juv} \times juv_{i,t} + \beta_{subad} \times subad_{i,t} + \beta_{male} \times male_i + \beta_{fall} \times fall_t \tag{2}$$

where $\log(\sigma_0)$ was an intercept, while *fall* was a binary variable representing whether survey t was done in the fall, as fall surveys were done in consecutive days while other surveys often had much longer gaps between passes.

We modeled the detection process (p) using fixed effects of sex and age class and a random site by year effect as follows:

$$p_{i,s,t,surv} = p_0 + \beta_{juv} \times juv_{i,t} + \beta_{subad} \times subad_{i,t} + \beta_{male} \times male_{i,t} + \beta_{effort} \times effort_{s,t,surv} + \beta_{fall} \times fall_{s,t,surv} + \eta_s + \eta_t \tag{3}$$

where p_0 was an intercept, *effort* was the reported effort (person-days) for each survey, *surv*, at each site, s, and in each year, t, η_s was a random effect of site, s, and η_t a random effect of year, t.

We estimated apparent survival (ϕ) using the same logit-linear model structure (i.e. effects) as in the known-fate model:

$$\mathrm{logit}(\phi_{i,t}) = \mathrm{logit}(\phi_0) + \beta_{juv} \times juv_{i,t} + \beta_{subad} \times subad_{i,t} + \beta_{male} \times male_{i,t} + \beta_{precip} \times precip_{s,t} + \beta_{precip \times sex} \times male_{i,t} \times precip_{s,t} + \beta_{temp} \times temp_{s,t} + \eta_{s,t} \tag{4}$$

2.2.3. Integrated survival model

We built a third model where we integrated the survival process model between the known-fate and CJS models. Because the integrated model estimated both apparent (ϕ) and true survival (S), we used the difference between ϕ and S to measure permanent emigration probability (ε). Because we expected smaller plots to have greater emigration and lower ϕ compared to larger plots, we also included a linear effect of plot area on emigration (β_{area}). To do so, we shared the intercept of the true survival parameter from the known-fate sub-model (S_0) in the mark–recapture sub-model, estimated ε as the difference between S

and ϕ, and shared all linear effect parameters (e.g. β_{juv}, β_{male}, β_{precip}) to benefit from information sharing with:

$$\operatorname{logit}(\phi_{i,t}) = \operatorname{logit}(S_0) + (\varepsilon_i + \beta_{area} \times area_s) + \ldots + \eta_{s,t} \qquad (5)$$

where the ε was estimated at each plot, s, and the survival model included the same linear effect structure as with the 2 single-data-source models previously described.

2.3. Analyses

2.3.1. Climatic sliding window analysis

To estimate the best lagged temporal window of climatic variables that may influence annual survival, we used a sliding window analysis on tortoise telemetry data. We used the telemetry data summarized annually (whether a tortoise died in a year or not) because the monthly assessments of whether tortoises were alive or dead with telemetry provided an opportunity to test for covariate effects with known-fate understanding of survival. We used the package 'climwin' (Bailey & van de Pol 2016) to assess sliding windows of monthly total precipitation and average maximum temperature. We fit competing models with all possible window options and compared support for resulting models using Akaike's information criterion adjusted for small sample sizes (AIC_c; Burnham & Anderson 2002). We used November 30 as our reference date and examined all possible monthly windows that went back in time up to 36 mo. Thus, our potential climatic windows referenced a date when most tortoises had entered winter hibernation (Nussear et al. 2007, Cummings 2020) and included the past 3 winter and active seasons of weather data. For these exploratory models, we used a generalized linear mixed model as our 'base' model with annual survival treated as a binary response variable, sex as a fixed effect predictor, and study site as a random effect using the 'lme4' package (Bates et al. 2017). For all climatic windows for each variable, we calculated model support using AIC_c and selected the climatic window model with the lowest AIC_c value for inference. We compared this to the base model to ensure that the best climatic window also outperformed the base model with no climatic information. To ensure our detected climate windows were not the result of Type I errors, we used the 'randwin()' and 'pvalue()' functions in 'climwin' to calculate the likelihood that our results could have occurred from random chance. We used the time-lagged window and summarization approach to create raster layers for each climatic variable (precipitation, maximum temperature).

2.3.2. Survival models

Our analysis involved estimating survival using each of the 3 models: the CJS mark—recapture model, the known-fate telemetry model, and the integrated model. We fit the CJS model using mark—recapture data from each of the 36 plots (3923 individuals; Table 1) and fit the known-fate model using telemetry data from all individuals tracked in the 22 study areas (2858 individuals; Table 2). However, most adult tortoises in some mark—recapture plots were also tracked and included in the radiotelemetry datasets (Table 2). For the integrated model analysis, we removed individuals from the telemetry dataset that were also included in the mark—recapture datasets to avoid 'double counting' individuals during that analysis. We chose to remove them from the telemetry dataset in the integrated analysis because the telemetry dataset included a relatively large number of individuals with detailed data compared to the mark—recapture datasets (Tables 1 & 2), and we thought that removing captures from the mark—recapture datasets would significantly reduce inference capability from the CJS sub-model in the integrated analysis. This resulted in a slightly smaller telemetry dataset for the integrated model (2662 individuals). We calculated geometric means for estimated survival from the mark—recapture plots across all sites and years to assess how including the known-fate data changed the estimates. We tested for goodness of fit using the 'overall_cjs()' function in the 'R2ucare' package (Gimenez et al. 2018b) for all mark—recapture sites with sufficient data. This function combines 2 tests: 'Test 3.SR' for detecting transients and 'Test 2.CT' for detecting trap-dependence. We tested capture histories at each site separately, first conducting a test including all individuals captured at the site. Where those tests were significant ($\alpha = 0.05$), we tested again by separating males and females to determine if our use of effects in our model was adequate to account for transience and/or trap-dependence where it occurred.

We related climatic spatial data layers to individuals and populations in different ways for each model. For analysis of telemetry data in the known-fate model, we used the median location of each individual in each year to extract point estimates for each climatic variable. For analysis of mark—recapture data with the CJS model, we extracted the average value from within plot boundaries for each climatic variable in each year. We standardized each extracted covariate with a *z*-score centering before model fitting except for survey effort, which was standardized using min-max standardization. We checked for correlations between transformed covariates using a Pearson's correlation coefficient (r) between each pair of covariates. When pairwise r values were greater than 0.6 (or less than −0.6), we removed one covariate from our analyses to reduce potential collinearity issues; this required maximum temperature to be removed from the known-fate, CJS, and integrated models.

We used uniform priors that spanned 0–1 for survival, detection, and juvenile-to-adult transition parameter and 10–700 m for the spatial parameter σ. We used slightly regularized priors [Normal(0,1)] for all β parameters. All random effects had a mean = 0 and a standard deviation shared among the level of the strata. Priors for random effect standard deviations were Gamma(0.1, 0.1).

We fit models using Markov chain Monte Carlo (MCMC) sampling in JAGS software (Plummer 2003) through the 'jagsUI' package (Kellner & Meredith 2021). We ran 3 chains of 30 000 iterations following an adaptation phase of 1000 iterations and burn-in of 2000 iterations with a thin rate of 10 for the known-fate model. We ran 3 chains of 60 000 iterations following an adaptation phase of 1000 iterations and a burn-in phase of 25 000 iterations with a thin rate of 4 for the CJS model. We ran 3 chains for 60 000 iterations for the integrated model but required 45 000 burn-in iterations for satisfactory convergence. We assessed convergence by examining trace and density plots and calculating the Gelman-Rubin diagnostic for each parameter and ensuring that all values fell <1.1 (Gelman & Rubin 1992). We identified a parameter(s) as having a significant effect on survival if the 95% confidence limits (CL) did not overlap zero.

3. RESULTS

3.1. Climatic sliding window analysis

Climatic sliding window analysis identified support for meaningful temporal windows that differed among climatic variables (Table 3). Prior to the reference date of November 30, survival was best explained by the sum of monthly total precipitation during the previous 6–34 mo (i.e. 3 winters and 2 active seasons prior to a given record), and the average monthly maximum temperature during the previous 12–21 mo (i.e. spring of the year prior to the record through the summer of the record) compared to all other temporal windows for each variable. The best window for average monthly maximum temperature was highly correlated with sum of monthly total precipitation (r = 0.72) and monthly maximum temperature was therefore excluded from further analysis.

3.2. Survival models

The known-fate model measured an average annual true survival probability (S_0) of 0.97 (0.96–0.98, 95% CL) for adult females (Table 4); the geometric mean for annual female survival across all populations and years was 0.929. Male (β_{male} = 0.49; 0.27–0.70, 95% CL) status had significant effects on annual survival probability (Table 4), resulting in adult males having higher derived estimates of mean survival (S_{male} = 0.98; 0.97–0.99, 95% CL; Table 5) than adult females. Neither juvenile (β_{juv} = −0.46; −0.97–0.07, 95% CL) nor subadult (β_{subad} = −0.18; −0.65–0.33, 95% CL) status had a significant effect on annual survival probability, though apparent effects were in the predicted direction. Among covariates included in the model, cumulative precipitation in the previous 6–34 mo had the largest effect on survival ($\beta_{precip =}$ 0.72; 0.47–0.98, 95% CL), resulting in average adult female survival increasing from 0.90–0.99 as cumulative precipitation increased from 32–993 mm (Fig. 2). The effect of precipitation on survival did not differ sub-

Table 3. Top models from 2 climate window analyses identifying the best-supported time-lagged temporal windows for precipitation and maximum temperature influence survival of Mojave desert tortoises *Gopherus agassizii*. Summarization is the summary statistic used to summarize each variable over the lagged time frame. Temporal window is the range of previous months that each variable was summarized. AIC_c: Akaike's information criterion adjusted for small sample size. ΔAIC_c: difference in AIC_c from the null model that did not include a climatic variable. We determined windows of time (months prior to the status or 'record' of an individual, e.g. on November 30 of each year). Each model had lower AIC_c than the baseline model (status ~ sex + (1|site)) and thus outperformed the baseline model in addition to all other temporal windows considered. NA: not applicable

Climate variable	Summarization	Temporal window	AIC_c	ΔAIC_c
Monthly sum precipitation	Sum	34–6 mo prior to a given record	4835.4	285.7
Monthly maximum temperature	Mean	21–12 mo prior to a given record	5010.2	110.9
None	NA	NA	5121.1	0

Table 4. Posterior mean ± SD for parameters estimated from a known-fate model, a Cormack-Jolly-Seber model, and an integrated model of Mojave desert tortoise *Gopherus agassizii* survival during 1988–2022. S_0: intercept of each known-fate survival model, ϕ_0: intercept of apparent survival, p_0: intercept of detection during a survey; CL: 95% confidence limits, $\hat{R}$: Gelman-Rubin statistic

Model	Parameter	Mean	SD	95% CL	$\hat{R}$
Known-fate model	S_0	0.967	0.005	0.957–0.976	1.00
	$\beta_{S,male}$	0.486	0.11	0.271–0.703	1.00
	$\beta_{S,juv}$	−0.466	0.267	−0.97–0.07	1.00
	$\beta_{S,sub}$	−0.178	0.25	−0.646–0.328	1.00
	$\beta_{S,precip}$	0.72	0.13	0.471–0.982	1.00
	$\beta_{S,precip \times sex}$	0.111	0.121	−0.123–0.353	1.00
	sub.trans	0.21	0.031	0.153–0.272	1.00
	ad.trans	0.244	0.03	0.187–0.304	1.00
	$\mathrm{sd}(\eta_S)$	1.356	0.136	1.113–1.645	1.00
Cormack-Jolly-Seber model	ϕ_0	0.968	0.005	0.957–0.977	1.00
	$\beta_{\phi,male}$	−0.097	0.091	−0.274–0.081	1.00
	$\beta_{\phi,juv}$	−1.153	0.194	−1.517 to −0.762	1.02
	$\beta_{\phi,sub}$	−0.622	0.263	−1.112 to −0.085	1.00
	$\beta_{\phi,\mathrm{precip}}$	0.288	0.191	−0.087–0.659	1.01
	$\beta_{\phi,precip \times sex}$	−0.079	0.096	−0.268–0.105	1.00
	sub.trans	0.142	0.015	0.114–0.174	1.02
	ad.trans	0.268	0.024	0.223–0.315	1.00
	p_0	0.376	0.076	0.234–0.535	1.01
	$\beta_{p,male}$	−0.195	0.095	−0.381 to −0.01	1.00
	$\beta_{p,juv}$	−2.07	0.146	−2.357 to −1.785	1.00
	$\beta_{p,sub}$	−0.839	0.155	−1.145 to −0.539	1.00
	$\beta_{p,effort}$	2.382	0.595	1.191–3.535	1.00
	$\beta_{p,fall}$	0.998	1.001	−0.939–2.966	1.00
	$\mathrm{sd}(\eta_\phi)$	1.96	0.037	1.862–1.999	1.00
	σ_0	168.208	3.314	161.929–174.878	1.00
	$\beta_{\sigma,male}$	0.335	0.03	0.275–0.394	1.00
	$\beta_{\sigma,sub}$	−0.104	0.065	−0.232–0.022	1.00
	$\beta_{\sigma,\mathrm{juv}}$	−0.498	0.067	−0.626 to −0.364	1.00
	$\beta_{\sigma,fall}$	0.002	0.99	−1.947–1.949	1.00
Integrated model	S_0	0.973	0.004	0.965–0.981	1.01
	$\beta_{\mathrm{m}ale}$	0.135	0.063	0.011–0.258	1.04
	$\beta_{S,juv}$	−1.002	0.148	−1.294 to −0.713	1.01
	$\beta_{S,sub}$	−0.553	0.178	−0.889 to −0.188	1.01
	$\beta_{S,precip}$	0.742	0.108	0.533–0.956	1.00
	$\beta_{S,precip \times sex}$	−0.161	0.064	−0.286 to −0.034	1.00
	sub.trans	0.154	0.014	0.128–0.184	1.05
	ad.trans	0.254	0.019	0.217–0.293	1.02
	p_0	0.386	0.075	0.248–0.539	1.04
	$\beta_{p,male}$	−0.221	0.096	−0.412 to −0.033	1.01
	$\beta_{p,juv}$	−2.073	0.141	−2.351 to −1.801	1.00
	$\beta_{p,sub}$	−0.908	0.152	−1.202 to −0.604	1.00
	$\beta_{p,effort}$	2.38	0.592	1.244–3.544	1.05
	$\beta_{p,fallt}$	0.992	0.998	-0.954–2.942	1.00
	σ_0	168.373	3.511	161.541–175.417	1.00
	$\beta_{\sigma,male}$	0.333	0.031	0.273–0.395	1.00
	$\beta_{\sigma,juv}$	−0.49	0.066	−0.611 to −0.357	1.02
	$\beta_{\sigma,sub}$	−0.113	0.06	−0.232–0.006	1.01
	$\beta_{\sigma,fall}$	0.011	0.993	−1.915–1.992	1.00
	$\mathrm{sd}(\eta_\phi)$	1.96	0.038	1.859–1.999	1.00
	$\mathrm{sd}(\eta_s)$	1.39	0.142	1.134–1.685	1.00
	ε_0	−0.769	0.224	−1.218 to −0.346	1.00
	$\beta_{\varepsilon,area}$	0.376	0.106	0.179–0.591	1.02

stantially for males versus females ($\beta_{precip \times sex}$ = 0.11; −0.12–0.35, 95% CL). The known-fate model estimated that the annual juvenile to subadult transition rate was 0.21 (0.15–0.27, 95% CL), and the subadult to adult transition rate was 0.24 (0.19–0.30, 95% CL).

For the mark–recapture ('CJS') model, the intercept of the apparent survival (ϕ_0) model was 0.97 (0.96–0.98, 95% CI), which was the baseline apparent annual survival probability for an average adult female in an average year (Table 4); the geometric mean of all predicted survival estimates across sites and years was 0.873. We observed an effect of juvenile status (β_{juv} = −1.15; −1.51 to −0.76, 95% CI) and subadult status (β_{subad} = −0.62; −1.11 to −0.09, 95% CI) on annual survival probability (Table 4), where juveniles and subadults had lower derived estimates of ϕ (e.g. ϕ for juvenile female = 0.90; 0.86–0.94, 95% CL; ϕ for subadult females = 0.94; 0.91–0.97, 95% CL; Table 5) than adults. We did not observe effects of sex (β_{male} = −0.10; −0.27–0.08, 95% CL) or precipitation ($\beta_{precip\,=}$ 0.29; −0.09–0.66, 95% CL) on apparent survival, though we did find a weak effect of the male-precipitation interaction term ($\beta_{precip \times sex}$ = −0.08; −0.27–0.011, 95% CL; Table 4). The mark–recapture model estimated that the annual juvenile to subadult transition rate was 0.14 (0.11–0.17, 95% CL) and the subadult to adult transition rate was 0.27 (0.22–0.32, 95% CL). We observed an average detection probability of 0.38 (0.23–0.54, 95% CL) for tortoises during mark–recapture surveys; males had lower detection rates (β_{male} = −0.20; −0.38 to −0.01, 95% CL), juveniles and subadults had lower detection than adults (β_{juv} = −2.07; −2.36 to −1.79, 95% CL, β_{subad} = −0.84; −1.15 to −0.54, 95% CL; Table 4). Increased survey effort was associated with higher detection values (β_{effort} = 2.38; 1.20–3.54, 95% CL). The mean radius of activity areas (σ_0) was 168.2 m (161.93–174.88 m, 95% CL) for adult females,

Table 5. Posterior mean ± SD for derived survival estimates from 3 survival estimation models for the Mojave desert tortoise *Gopherus agassizii* in the Mojave desert during 1988–2022: a known-fate model using telemetry data, a Cormack-Jolly-Seber model of mark–recapture data, and an integrated model with both datasets. S: true survival; ϕ: apparent survival; 95% CL: 95% confidence limits; $\hat{R}$: Gelman-Rubin statistic

Model	Parameter	Mean	SD	95% CL	$\hat{R}$
Known-fate model	S_{female}	0.967	0.005	0.967–0.976	1
	S_{male}	0.98	0.003	0.973–0.985	1
	$S_{\text{female,sub}}$	0.96	0.01	0.936–0.978	1
	$S_{\text{female,juv}}$	0.948	0.015	0.915–0.971	1
Cormack-Jolly-Seber model	ϕ_{female}	0.968	0.005	0.958–0.971	1
	ϕ_{male}	0.965	0.006	0.953–0.975	1
	$\phi_{\text{female,sub}}$	0.941	0.016	0.906–0.967	1
	$\phi_{\text{female,juv}}$	0.904	0.021	0.858–0.940	1
Integrated model	S_{female}	0.973	0.004	0.965–0.981	1
	S_{male}	0.977	0.004	0.969–0.983	1
	$S_{\text{female,sub}}$	0.954	0.01	0.931–0.971	1
	$S_{\text{female,juv}}$	0.930	0.014	0.900–0.953	1

and we also observed significant effects of male (β_{male} = 0.34; 0.28–0.39, 95% CL) and juvenile statuses (β_{juv} = −0.50; −0.63 to −0.36, 95% CL) on σ, such that males and juveniles had larger and smaller activity use areas than females, respectively. The effect of subadult status on activity area was not significant (β_{subad} = −0.10; −0.23–0.02, 95% CL). Goodness-of-fit testing was performed for 17 sites with sufficient data. Of these, 16 sites showed no significant evidence of either transience or trap-dependence (Table S1 in the Supplement at www.int-res.com/articles/suppl/esr01468_supp.pdf). A single site exhibited a significant signal of transience when analyzing all individuals together; however, this effect disappeared when capture histories were analyzed separately by sex (Table S1).

The integrated model estimated average annual true survival for adult females (S_0) of 0.97 (0.97–0.98, 95% CL; Tables 4 & 5) and the geometric mean of estimated survival across sites and years for the mark–recapture datasets was 0.898. The integrated model detected real effects of male (β_{male} = 0.14; 0.01–0.26, 95% CL), juvenile (β_{juv} = −1.00; −1.30 to −0.71, 95% CL), and subadult status (β_{subad} = −0.55; −0.89 to −0.19, 95% CL) on survival (Table 4). This suggested that males had higher survival than females, and both juveniles and subadults had lower survival than adults (Table 5). Estimates for ε suggested that emigration accounts for a real and considerable difference between true and apparent survival (ε = −0.769; −1.22 to −0.35, 95% CL) and that the difference between ϕ_0 and S_0 decreased with plot size area (β_{area} = 0.38; 0.18–0.59, 95% CL; Fig. 3). For a

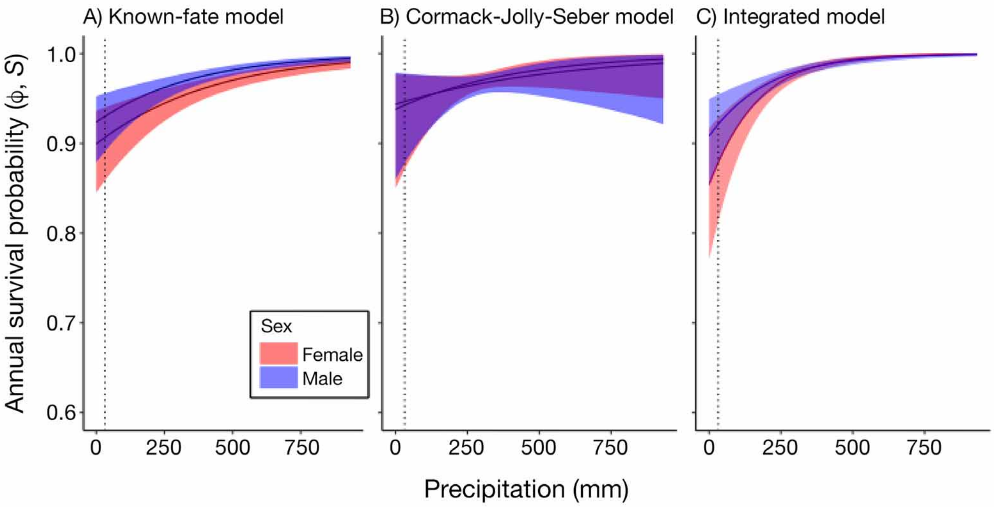

Fig. 2. Effects of precipitation on survival estimates of male and female Mojave desert tortoise *Gopherus agassizii* using 3 hierarchical survival models: (A) a known-fate model that estimated true survival (S) using telemetry data, (B) a Cormack-Jolly-Seber model that estimated apparent survival probability (ϕ) using mark–recapture data, and (C) an integrated model that estimate S using both telemetry and mark–recapture data. Precipitation is the sum of the prior 2 active and 3 winter seasons. The Cormack-Jolly-Seber model failed to detect the important effect of precipitation, but the integrated analysis resolved this effect using information from both known-fate and Cormack-Jolly-Seber models. Ribbons represent 95% confidence limits for parameter estimates; vertical dashed line represents the lowest observed precipitation

1 km^2 plot, the difference between ϕ_0 and S_0 was 0.03 (0.02–0.04; 95% CL). Detection and activity center parameter estimates were similar between both the integrated and CJS model (Table 4). The integrated model suggested a significant effect of precipitation ($\beta = 0.74$; 0.53–0.96, 95% CL) on survival, and a weak interaction between sex and precipitation ($\beta = -0.16$; –0.29–0.03, 95% CL, Fig. 2). The integrated model returned similar estimates of the stage transition probabilities (juvenile-to-subadult: 0.16; 0.13–0.18, 95% CL; subadult-to-adult: 0.25; 0.22–0.29, 95% CL) as the 2, non-integrated models. The integrated model produced true survival estimates with less uncertainty (smaller CLs) compared to apparent survival estimates from the non-integrated CJS model (Fig. S1).

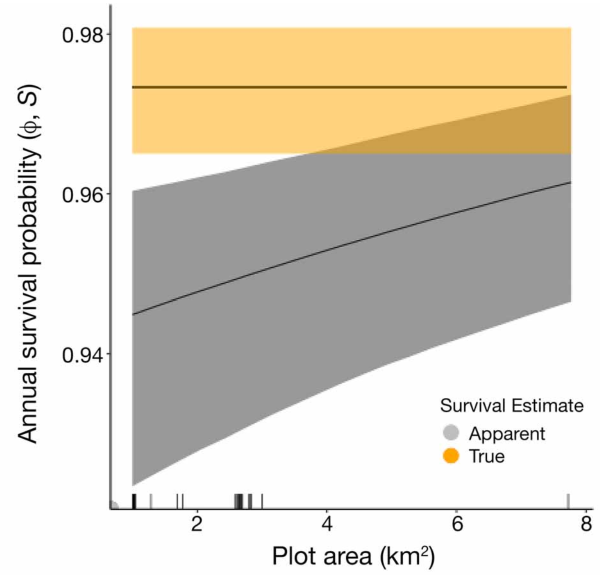

Fig. 3. Effect of plot size on apparent survival probability (grey ribbon, ϕ) estimates from the integrated model. Tick marks above the *x*-axis are plot areas from the data. As plot area increased, apparent survival increased until it became comparable to the mean estimate of true survival (orange ribbon, *S*), suggesting that emigration (the difference between apparent and true survival) is negligible at the largest plot size (7.8 km^2). Ribbons represent 95% confidence limits for parameter estimates

4. DISCUSSION

Here we demonstrated the usefulness of an integrated analytical framework for sharing information between multiple data sources to produce more robust and precise estimates of survival for a declining, imperiled species, the Mojave desert tortoise. We described and compared 3 different modeling approaches that each returned realistic estimates of tortoise survival (or apparent survival) that were comparable to previous similar efforts (Lovich et al. 2014, Dickson et al. 2019). However, our integrated modeling approach allowed us to overcome limitations of single data-source models, such that data integration between telemetry and mark–recapture datasets allowed us to estimate effects of age, sex, and precipitation on tortoise survival that were not detectable in the single data-source analyses of mark–recapture data (no effect of precipitation) or telemetry data (no effect of age). Moreover, our integrated model leveraged information about true survival to adjust for emigration from mark–recapture data — a key parameter that often vexes demographers working with mark–recapture data (Schaub & Royle 2014). Therefore, we have provided an integrated framework that leverages information from different data sources to better understand tortoise demographic rates and factors that influence them.

The Mojave desert tortoise is a declining species that may benefit from population viability analysis (PVA) efforts to understand extinction risk, but most survival estimates for the species to date have relied on Cormack-Jolly-Seber models that have estimated apparent survival (Doak et al. 1994, Lovich et al. 2014, Berry et al. 2020). This is not ideal because PVAs that use estimates of apparent survival can make inaccurate, negatively biased predictions, because apparent survival estimates are lower than true survival (Badia-Boher et al. 2024) and populations of long-lived species like tortoises are sensitive to adult survival rates (Heppell 1998). For example, one notable population viability analysis for the Mojave desert tortoise that appeared to have used estimates of apparent survival probability (Doak et al. 1994) predicted great uncertainty and low persistence probability for populations in the western Mojave. However, those populations remain extant 3 decades later (Allison & McLuckie 2018, Berry et al. 2020), though have undergone steep declines in recent decades (Zylstra et al. 2023). Those original predictions of great extinction risk (Doak et al. 1994) may have been due to using apparent survival probabilities that were considerably lower than true survival rates experienced by tortoises. Indeed, robust population viability analyses require adequate estimates of demographic parameters (Beissinger & Westphal 1998, Chaudhary & Oli 2020), and our integrated model found that true survival was considerably higher than apparent survival at most study sites. By leveraging both known-fate telemetry and mark–recapture data to simultaneously estimate both true and apparent survival and important environmental variables influencing survival, our integrated modeling approach provides true survival estimates that might be most realistic and useful for future PVA efforts for the tortoise, especially when done at the local population scale.

Immigration and emigration processes are difficult to measure for animal populations (Lebreton et al. 1992, Schaub & Royle 2014), and despite decades of research, are still not well understood in *Gopherus* spp. (e.g. Guyer et al. 2024). To our knowledge, our integrated model is the first to provide empirical estimates of annual emigration probabilities for tortoises measured at the local population scale. Specifically, we estimated a mean emigration probability suggesting that ca. 3% of the local population may permanently emigrate from a 1 km^2 plot during any year, such that emigration is a considerable component of local population dynamics at this spatial scale. We also observed that emigration rate decreased in larger plots, perhaps because these plots were more likely to encompass entire home ranges and dispersal distances for individuals to the point where the apparent survival estimates were nearly indistinguishable from true in the largest plot (Desert Tortoise Research Natural Area; 7.77 km^2, Fig. 3). Thus, our model provides information about migration rates that might be useful as a framework for developing spatially explicit population models, especially for species monitored in plots of differing sizes.

An advantage of an integrated approach is that combining information from across different datasets increased precision in the estimation of demographic rates and covariate effects. The known-fate model was able to detect a significant positive relationship with the cumulative precipitation and higher survival of males, while the CJS model was unable to measure significant effects for these parameters. Conversely, the known-fate model was unable to detect a significant effect of the 2 younger age classes that the CJS model detected. This suggests that information sharing during integrated modeling benefited parameter estimation compared to non-integrated approaches that failed to measure effects, either due to increased sample sizes (captures of juvenile and subadult tortoises bolstering low sample sizes in the telemetry datasets) or providing more consistent sampling with perfect detection (irregular sampling events in the mark—recapture plots). The integrated approach also allowed us to understand historical patterns of tortoise survival, revealing that even after accounting for precipitation, tortoise survival was lower during the decades preceding the listing of the species (Fig. S1). This coincides with noted population declines (Berry & Murphy 2019) and indicates that other factors may have played an important role in historical tortoise population declines. Future work could use our analytical framework to test other hypotheses related to tortoise demographic rates (e.g. anthropogenic stressors; Darst et al. 2013), potentially using other historical datasets that were not available for this effort (e.g. permanent study plots in the western Mojave Desert; Tracy et al. 2004).

Drought has been a persistent disturbance to the ecosystems and species of the southwestern USA and is likely to increase in intensity and duration as human-caused climate change progresses (Williams et al. 2022). Our results indicate that precipitation over a 6—32 mo period prior to the end of an active season is an important driver of desert tortoise survival, such that low total precipitation over the prior 3 winters and 2 active seasons can drastically reduce tortoise survival. This finding provides further evidence that long-term drought conditions alter tortoise survival across the range, supporting previous studies that have shown similar effects on localized populations (Longshore et al. 2003, Esque et al. 2010, Lovich et al. 2014). Drought reduces germination of annual plants that are important tortoise forage (Beatley 1969). While tortoises can withstand periods of drought by restricting activity and tolerating departures from homeostasis (Peterson 1996, Henen et al. 1998), lack of drinking water can cause tortoises to exceed physiological limits and cause mortality due to dehydration (Peterson 1994, Berry et al. 2002) or may increase susceptibility to upper respiratory tract diseases (Jacobson et al. 2014). Previous research suggested that female tortoises may be more sensitive to drought than males due to the costs of reproduction (Mitchell et al. 2021a, Lovich et al. 2023), but we did not find support for a time-lagged precipitation-by-sex interaction effect in our global, integrated model. However, we did observe overall lower survival rates for females than males, potentially due to costs associated with reproductive activity, yet the confidence limits of the predicted relationship between annual survival, sex, and preceding precipitation overlapped heavily (Fig. 2), suggesting that females are not particularly more sensitive to drought than males. It is possible that females in certain populations experience greater effects of precipitation than males, such that more careful examination of site-specific interactions between precipitation and sex might reveal support for this effect at local scales (i.e. interaction between site, drought, and sex).

Potentially more important than direct dehydration and physiological effects on tortoises are the pressures that drought causes on the Mojave Desert ecosystem as a whole. Drought can reduce populations of small mammals and therefore reduce typical prey availability for mesocarnivores, such as coyotes *Canis latrans* and badgers *Taxidea taxu* (Beatley 1969, Simes et al. 2015), leading to targeting of atypical food sources such as the desert tortoise (Emblidge et al. 2015, Cypher et al. 2018). This drought-induced prey-switching effect may be higher in areas that provide anthropogenic subsidies (e.g. surface water, trash) and support higher-than-natural mesocarnivore populations (Agha et al. 2017) compared to typical climatic conditions; in this way, drought could cause a larger predator population to exert more predation pressure on tortoises in the area (Esque et al. 2010). As stable *Gopherus* demography is dependent on high adult survival (Folt et al. 2021), a single high adult tortoise mortality event from excessive meso-carnivore predation has the potential to result in depressed tortoise populations for multiple tortoise generations. A better understanding of how anthropogenic subsidies contribute to meso-carnivore population regulation and foraging patterns could help develop management strategies that can better protect tortoise populations, especially in long-term droughts.

One key difference among our model results was estimates of juvenile survival, an important parameter that has been implicated as a potential driver of the slow or no recovery in tortoise populations (US Fish and Wildlife Service 2011, Allison & McLuckie 2018). Annual true survival probability estimates of juvenile tortoises from the telemetry data were higher than apparent juvenile survival from the mark—recapture datasets, likely due to differences in data collection between the mark—recapture and known fate datasets. Specifically, juvenile tortoises are notoriously difficult to detect during surveys (Anderson et al. 2001, Nussear et al. 2008), and our results estimated a median juvenile detection rate of 0.07. This low detection rate may prevent precise estimation of juvenile survival rates from non-integrated mark—recapture analysis. Another likely reason for this difference is that telemetry datasets were usually limited to larger juvenile tortoises due to logistical issues with finding and tracking smaller tortoises (Boarman et al. 2006). Previous research on tortoises as well as other Testudines species has suggested that smaller juveniles are expected to have lower survival rates than larger juveniles, and the exclusion of these smaller age classes in the telemetry data may have biased results from the non-integrated known-fate analysis (Turner et al. 1987, Doak et al. 1994). In addition, because juvenile tortoises may have higher rates of dispersal than adult tortoises (Averill-Murray et al. 2020, Hromada 2022), higher juvenile emigration may be reflected in the magnitude of difference between real and apparent juvenile survival estimates. There are research opportunities to better understand variation of survival rates within the juvenile age class (e.g. size-dependent survival) and what factors cause reduced juvenile survival (e.g. human-subsidized raven populations; Boarman et al. 2006, Holcomb et al. 2021).

Assessing model assumptions is an important aspect in building ecological models. Our mark—recapture dataset did not meet the sample size and temporal requirements necessary to apply formal tests for capture heterogeneity (Jeyam et al. 2018). Nonetheless, we acknowledge that individual-level variation in capture probability may be present and can bias survival estimates low if unaccounted for. Our inclusion of fixed effects for sex, and age, in addition to random effects for site, and year, helps address this by capturing several known sources of heterogeneity. However, as Gimenez et al. (2018a) note, even models with a broad set of covariates and random effects cannot fully capture the extent of individual heterogeneity, much of which remains unmeasured. Although other approaches to addressing individual heterogeneity exist, such as individual-level random effects and finite mixture models, these methods are prone to identifiability issues (Pledger 2000, Jasra et al. 2005) and substantially increase model dimensionality (Gimenez et al. 2018a), complicating convergence and mixing. Given the already high dimensionality of our model, we deemed these approaches impractical given our data limitations. However, these approaches could be explored more thoroughly in future iterations of this model.

To this end, we hope the survival estimation framework described here may be useful for survival estimation using additional tortoise data currently being collected and exploring relationships with other stressors. For example, to complement ongoing population monitoring across the species' range using line transect distance sampling and radiotelemetry, the USFWS has begun monitoring tortoise populations at additional plots across the species range (Mitchell 2024) using the same mark—recapture methods as the plots analyzed here. Our integrated survival model could be used to update estimates and monitor tortoise survival using ongoing and future telemetry and mark—recapture efforts. These plots are in the same general area that tortoises are monitored with telemetry for range-wide density monitoring (Allison

& McLuckie, 2018). Additional data may allow for estimating differences in survival in the different portions of the species' range, leading to better understanding of factors influencing survival, thereby highlighting opportunities for management recommendations. Future extensions of these models could be made to integrate other data sources and estimate other parameters such as population size and recruitment to allow for holistic understanding of population trends (Schaub & Kéry 2022). Finally, we believe that the framework provided here will likely be useful in informing survival analysis of other species that have been monitored with different survey methods across time and space.

Data availability. We provide R scripts and anonymized datasets (sites and coordinates obscured) to recreate our analyses on a Github repository (https://github.com/csp-inc/Tortoise_Survival_MS). For other inquiries, please contact Brett Dickson (brett@csp-inc.org).

Acknowledgements. This work would not have been possible but for the efforts of many biologists across many studies. While this list is likely incomplete, we recognize the following people for their data, expertise, or other project contributions: F. Chen, B. Gottsacker, J. Swart, R. Inman, P. Medica, R. Averill-Murray, K. Dutcher, A. Modlin, A. Macdonald, B. Cunningham, S. Murray, G. Berry, E. Gaylord, G. Gantz, R. Van Gaalen, S. Lewicki, S. Dahl, B. Smith, S. Thomson, C. Silva, C. Quick, A. Poage, K. Nolte, C. Phillips, S. Snyder, B. Jacobs, G. Olson, V. Van Zerr, R. Kunicki, A. Terry, J. Willand, E. Sinnott, A. Chaney, D. Essary, T. Carmona, B. Reynolds, J. Jay, R. Lamkin, A. Berger, M. Kang, P. Cosmann, P. Emblidge, C. Aiello, R. Saulino, R. Lamkin, K. Bauer, A. Smith, S. Steel, A. Collins, M. Spangler, E. Olimpi, M. Agha, J. Ennen, J. Stroud-Settles, S. Cambrin, P. Woodman and others. This project was funded through a cooperative agreement with the California State Office of the Bureau of Land Management (agreement number L21AC10475) and through contracts with the Department of Defense Strategic Environmental Research and Development Program (project numbers RC18-1103 and RC22-3182). All authors claim no conflict of interest. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the US Fish and Wildlife Service.

LITERATURE CITED

Abrahms B, Carter NH, Clark-Wolf TJ, Gaynor KM and others (2023) Climate change as a global amplifier of human–wildlife conflict. Nat Clim Chang 13: 224–234

Agha M, Smith AL, Lovich JE, Delaney D and others (2017) Mammalian mesocarnivore visitation at tortoise burrows in a wind farm. J Wildl Manag 81:1117–1124

Allison LJ, McLuckie AM (2018) Population trends in Mojave Desert tortoises (*Gopherus agassizii*). Herpetol Conserv Biol 13:433–452

Anderson DR, Burnham KP, Lubow BC, Thomas L, Corn PS, Medica PA, Marlow RW (2001) Field trials of line transect methods applied to estimation of desert tortoise abundance. J Wildl Manag 65:583

Averill-Murray RC, Fleming CH, Riedle JD (2020) Reptile home ranges revisited: a case study of space use of Sonoran Desert tortoises (*Gopherus morafkai*). Herpetol Conserv Biol 15:253–271

Badia-Boher JA, Real J, Riera JL, Bartumeus F, Parés F, Bas JM, Hernández-Matías A (2023) Joint estimation of survival and dispersal effectively corrects the permanent emigration bias in mark–recapture analyses. Sci Rep 13: 6970

Badia-Boher JA, Real J, Hernández-Matías A (2024) Assumptions about survival estimates and dispersal processes can have severe impacts on population viability assessments. Biol Conserv 292:110550

Bailey LD, van de Pol M (2016) Climwin: an R toolbox for climate window analysis. PLOS ONE 11:e0167980

Bates D, Maechler M, Bolker B, Walker S and others (2017) Package 'lme4', v. 1.1-35. https://cran.r-project.org/web/packages/lme4/index.html

Beatley JC (1969) Dependence of desert rodents on winter annuals and precipitation. Ecology 50:721–724

Beissinger SR, Westphal MI (1998) On the use of demographic models of population viability in endangered species management. J Wildl Manag 62:821

Berry KH, Murphy RW (2019) *Gopherus agassizii* (Cooper 1861) — Mojave Desert tortoise, Agassiz's desert tortoise. Chelonian Res Monogr 5:1–45

Berry KH, Yee JL (2021) Development of demographic models to analyze populations with multi-year data — using Agassiz's desert tortoise (*Gopherus agassizii*) as a case study. United States Geological Survey, Reston, VA

Berry KH, Spangenberg EK, Homer BL, Jacobson ER (2002) Deaths of desert tortoises following periods of drought and research manipulation. Chelonian Conserv Biol 4: 436–448

Berry KH, Yee JL, Shields TA, Stockton L (2020) The catastrophic decline of tortoises at a fenced natural area. Wild Monogr 205:1–53

Besbeas P, Freeman SN, Morgan BJT, Catchpole EA (2002) Integrating mark–recapture–recovery and census data to estimate animal abundance and demographic parameters. Biometrics 58:540–547

Bestion E, Teyssier A, Richard M, Clobert J, Cote J (2015) Live fast, die young: experimental evidence of population extinction risk due to climate change. PLOS BIOL 13:e1002281

Boarman WI, Patten MA, Camp RJ, Collis SJ (2006) Ecology of a population of subsidized predators: common ravens in the central Mojave Desert, California. J Arid Environ 67:248–261

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer Science + Business Media, New York, NY

Bury RB, Corn PS (1995) Have desert tortoises undergone a long-term decline in abundance? Wildl Soc Bull 23: 41–47

Chaudhary V, Oli MK (2020) A critical appraisal of population viability analysis. Conserv Biol 34:26–40

Church DR, Bailey LL, Wilbur HM, Green JH, Hiby L (2022) Salamander demography at isolated wetlands within mature and regenerating forests. Diversity (Basel) 14:309

Congdon JD, Dunham AE, Van Loben Sels RC (1993) Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conserv Biol 7:826–833

Cormack RM (1964) Estimates of survival from the sighting of marked animals. Biometrika 51:429–438

Coulson T, Catchpole EA, Albon SD, Morgan BJT and others (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531

Cummings K (2020) Micro-geographic variation in burrow use of Agassiz's desert tortoises in the Sonoran Desert of California. Herpetol J 30:177–188

Cypher BL, Kelly EC, Westall TL, Van Horn Job CL (2018) Coyote diet patterns in the Mojave Desert: implications for threatened desert tortoises. Pac Conserv Biol 24:44

Darst CR, Murphy PJ, Strout NW, Campbell SP, Field KJ, Allison L, Averill-Murray RC (2013) A strategy for prioritizing threats and recovery actions for at-risk species. Environ Manage 51:786–800

Delgiudice GD, Fieberg J, Riggs MR, Powell MC, Pan W (2006) A long-term age-specific survival analysis of female white-tailed deer. J Wildl Manag 70:1556–1568

DeMars CA, Gilbert S, Serrouya R, Kelly AP, Larter NC, Hervieux D, Boutin S (2021) Demographic responses of a threatened, low-density ungulate to annual variation in meteorological and phenological conditions. PLOS ONE 16:e0258136

Dickson BG, Scherer RD, Kissel AM, Wallace BP and others (2019) Multiyear monitoring of survival following mitigation-driven translocation of a long-lived threatened reptile. Conserv Biol 33:1094–1105

Doak D, Kareiva P, Klepetka B (1994) Modeling population viability for the desert tortoise in the western Mojave Desert. Ecol Appl 4:446–460

Drake KK, Esque TC, Nussear KE, Defalco LA, Scoles-Sciulla SJ, Modlin AT, Medica PA (2015) Desert tortoise use of burned habitat in the eastern Mojave desert. J Wildl Manag 79:618–629

Efford MG, Schofield MR (2022) A review of movement models in open population capture–recapture. Methods Ecol Evol 13:2106–2118

Emblidge PG, Nussear KE, Esque TC, Aiello CM, Walde AD (2015) Severe mortality of a population of threatened Agassiz's desert tortoises: the American badger as a potential predator. Endang Species Res 28:109–116

Esque TC, Nussear KE, Drake KK, Walde A and others (2010) Effects of subsidized predators, resource variability, and human population density on desert tortoise populations in the Mojave desert, USA. Endang Species Res 12:167–177

Folt B, Goessling JM, College E, Tucker A and others (2021) Contrasting patterns of demography and population viability among gopher tortoise populations in Alabama. J Wildl Manag 85:617–630

Gaillard JM, Mark Hewison AJ, Klein F, Plard F, Douhard M, Davison R, Bonenfant C (2013) How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. Ecol Lett 16:48–57

Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. Stat Sci 7:457–511

Gimenez O, Cam E, Gaillard JM (2018a) Individual heterogeneity and capture–recapture models: What, why and how? Oikos 127:664–686

Gimenez O, Lebreton J, Choquet R, Pradel R (2018b) R2ucare: an R package to perform goodness-of-fit tests for capture–recapture models. Methods Ecol Evol 9: 1749–1754

Guimarães M, Correa DT, Gaiarsa MP, Kéry M (2020) Full-annual demography and seasonal cycles in a resident vertebrate. PeerJ 8:e8658

Guyer C, Goessling JM, Folt B (2024) Annual and lifetime home ranges reveal movement patterns within and among local populations of gopher tortoises (*Gopherus polyphemus*). Chelonian Conserv Biol 23:81–91

Harju SM, Cambrin SM, Averill-Murray RC, Nafus M, Field KJ, Allison LJ (2020) Using incidental mark–encounter data to improve survival estimation. Ecol Evol 10:360–370

Henen BT, Peterson CC, Wallis IR, Berry KH, Nagy KA (1998) Effects of climatic variation on field metabolism and water relations of desert tortoises. Oecologia 117: 365–373

Heppell SS (1998) Application of life-history theory and population model analysis to turtle conservation. Copeia 1998:367

Holcomb KL, Coates PS, Prochazka B, Shields TA, Boarman WI (2021) A desert tortoise–common raven viable conflict threshold. Hum Wildl Interact 15:405–421

Hromada SJ (2022) The genes must flow: using movement ecology to understand connectivity of Mojave desert tortoise (*Gopherus agassizii*) populations in altered landscapes. University of Nevada, Reno, Reno, NV

Iler AM, CaraDonna PJ, Forrest JRK, Post E (2021) Demographic consequences of phenological shifts in response to climate change. Annu Rev Ecol Evol Syst 52: 221–245

Jacobson ER, Brown MB, Wendland LD, Brown DR, Klein PA, Christopher MM, Berry KH (2014) Mycoplasmosis and upper respiratory tract disease of tortoises: a review and update. Vet J 201:257–264

Jasra A, Holmes CC, Stephens DA (2005) Markov chain Monte Carlo methods and the label switching problem in Bayesian mixture modeling. Stat Sci 20:50–67

Jeliazkov A, Gavish Y, Marsh CJ, Geschke J and others (2022) Sampling and modelling rare species: conceptual guidelines for the neglected majority. Glob Chang Biol 28:3754–3777

Jeyam A, McCrea RS, Bregnballe T, Frederiksen M, Pradel R (2018) A test of positive association for detecting heterogeneity in capture for capture–recapture data. J Agric Biol Environ Stat 23:1–19

Jolly GM (1965) Explicit estimates from capture-recapture data with both death and immigration–stochastic model. Biometrika 52:225–247

Kellner K, Meredith M (2021) jagsUI: a wrapper around 'rjags' to streamline 'JAGS' analyses, v. 1.6.2. https://cran.rstudio.com/web/packages/jagsUI/

Kendall WL, Pollock KH, Brownie C (1995) A likelihood-based approach to capture–recapture estimation of demographic parameters under the robust design. Biometrics 51:293

Kissel AM, Wallace B, Anderson J, Dickson BG and others (2023) Range-wide occupancy trends for the Mojave desert tortoise (*Gopherus agassizii*). Ecosphere 14: e4462

Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol Monogr 62:67–118

Longshore KM, Jaeger JR, Sappington JM (2003) Desert tortoise (*Gopherus agassizii*) survival at two eastern Mojave Desert sites: death by short-term drought? J Herpetol 37: 169–177

Lovich JE, Yackulic CB, Freilich J, Agha M and others (2014) Climatic variation and tortoise survival: Has a desert species met its match? Biol Conserv 169:214–224

Lovich JE, Puffer SR, Cummings K, Arundel TR, Vamstad MS, Brundige KD (2023) High female desert tortoise mortality in the western Sonoran Desert during California's epic 2012–2016 drought. Endang Species Res 50: 1–16

Mazerolle MJ, Bailey LL, Kendall WL, Andrew Royle J, Converse SJ, Nichols JD (2007) Making great leaps forward: accounting for detectability in herpetological field studies. J Herpetol 41:672–689

Mitchell CI (2024) Using demographic study plots to inform range-wide status for the Mojave desert tortoise. In: Forty-Ninth Annual Meeting and Symposium of the Desert Tortoise Council. Las Vegas, NV, p 18–19

Mitchell CI, Friend DA, Phillips LT, Hunter EA and others (2021a) 'Unscrambling' the drivers of egg production in Agassiz's desert tortoise: climate and individual attributes predict reproductive output. Endang Species Res 44: 217–230

Mitchell CI, Shoemaker KT, Esque TC, Vandergast AG and others (2021b) Integrating telemetry data at several scales with spatial capture–recapture to improve density estimates. Ecosphere 12:e03689

Moiron M, Laskowski KL, Niemelä PT (2020) Individual differences in behaviour explain variation in survival: a meta-analysis. Ecol Lett 23:399–408

Murray DL, Patterson BR (2006) Wildlife survival estimation: recent advances and future directions. J Wildl Manag 70: 1499–1503

National Park Service (1997) Protecting the threatened desert tortoise: a multi-park plan for primary survey, management, and monitoring. Lake Mead NRA

Nussear KE, Esque TC, Haines DF, Richard Tracy C (2007) Desert tortoise hibernation: temperatures, timing, and environment. Copeia 2007:378–386

Nussear KE, Esque TC, Heaton JS, Cablk ME and others (2008) Are wildlife detector dogs or people better at finding desert tortoises (*Gopherus agassizii*)? Herpetol Conserv Biol 3:103–115

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. J Wildl Manag 76:1341–1353

Peterson CC (1994) Different rates and causes of high mortality in two populations of the threatened desert tortoise *Gopherus agassizii*. Biol Conserv 70:101–108

Peterson CC (1996) Ecological energetics of the desert tortoise (*Gopherus agassizii*): effects of rainfall and drought. Ecology 77:1831–1844

Pledger S (2000) Unified maximum likelihood estimates for closed capture–recapture models using mixtures. Biometrics 56:434–442

Plummer M (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Hornik K, Leisch F, Zeileis A (eds). Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003). DSC, Vienna, p 1–8

Pollock KH (1982) A capture–recapture design robust to unequal probability of capture. J Wildl Manag 46:752

Powell LA, Conroy MJ, Hines JE, Nichols JD, Krementz DG (2000) Simultaneous use of mark–recapture and radiotelemetry to estimate survival, movement, and capture rates. J Wildl Manag 64:302

PRISM Group, Oregon State University (2023) PRISM gridded climate data. https://prism.oregonstate.edu (accessed Feb 2023)

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rose JP, Wylie GD, Casazza ML, Halstead BJ (2018) Integrating growth and capture–mark–recapture models reveals size-dependent survival in an elusive species. Ecosphere 9:e02384

Royle JA (2008) Modeling individual effects in the Cormack-Jolly-Seber model: a state–space formulation. Biometrics 64:364–370

Royle JA (2009) Analysis of capture–recapture models with individual covariates using data augmentation. Biometrics 65:267–274

Royle JA, Kéry M, Guélat J (2011) Spatial capture–recapture models for search-encounter data. Methods Ecol Evol 2:602–611

Royle JA, Chandler RB, Sollmann R, Gardner B (2014) Fully spatial capture–recapture models. In: Spatial capture–recapture. Academic Press, Waltham, MA, p 125–170

Salguero-Gómez R, Jones OR, Archer CR, Bein C and others (2016) COMADRE: a global data base of animal demography. J Anim Ecol 85:371–384

Schaub M, Abadi F (2011) Integrated population models: a novel analysis framework for deeper insights into population dynamics. J Ornithol 152:227–237

Schaub M, Kéry M (2022) Integrated population models: theory and ecological applications with R and JAGS. Academic Press, Cambridge, MA

Schaub M, Royle JA (2014) Estimating true instead of apparent survival using spatial Cormack-Jolly-Seber models. Methods Ecol Evol 5:1316–1326

Schmidt JH, Johnson DS, Lindberg MS, Adams LG (2015) Estimating demographic parameters using a combination of known-fate and open *N*-mixture models. Ecology 96: 2583–2589

Seber GAF (1965) A note on the multiple-recapture census. Biometrika 52:249–259

Sibly RM, Hone J (2002) Population growth rate and its determinants: an overview. Philos Trans R Soc Lond B Biol Sci 357:1153–1170

Simes MT, Longshore KM, Nussear KE, Beatty GL, Brown DE, Esque TC (2015) Black-tailed and white-tailed jackrabbits in the American West: history, ecology, ecological significance, and survey methods. West N Am Nat 75: 491–519

Spencer RJ, Van Dyke JU, Thompson MB (2017) Critically evaluating best management practices for preventing freshwater turtle extinctions. Conserv Biol 31: 1340–1349

Thompson WL (ed) (2004) Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters. Island Press, WA

Tracy CR, Averill-Murray RC, Boarman WI, Delehanty DJ and others (2004) Desert tortoise recovery plan assessment. Reno, NV

Turner FB, Medica PA, Bury RB (1987) Age-size relationships of desert tortoises (*Gopherus agassizi*) in southern Nevada. Copeia 1987:974

US Fish and Wildlife Service (1990) Endangered and threatened wildlife and plants; determination of threatened status for the Mojave population of the desert tortoise. Fed Regist 55:12178–12191

US Fish and Wildlife Service (1994) Desert tortoise (Mojave population) recovery plan. US Fish and Wildlife Service, Portland, OR

US Fish and Wildlife Service (2011) Revised recovery plan for the Mojave population of the desert tortoise (*Gopherus agassizii*). US Fish and Wildlife Service, Pacific Southwest Region, Sacramento, CA

White GC, Garrott RA (1990) Analysis of wildlife radio-tracking data, 1st edn. Academic Press, San Diego, CA

Williams AP, Cook BI, Smerdon JE (2022) Rapid intensification of the emerging southwestern North American megadrought in 2020–2021. Nat Clim Change 12:232–234

Woodbury AM, Hardy R (1948) Studies of the desert tortoise, *Gopherus agassizii*. Ecol Monogr 18:145–200

Zylstra ER, Allison LJ, Averill-Murray RC, Landau V, Pope NS, Steidl RJ (2023) A spatially explicit model for density that accounts for availability: a case study with Mojave desert tortoises. Ecosphere 14:e4448

Editorial responsibility: Leonardo Vignoli,
Rome, Italy
Reviewed by: H. Cayuela and 2 anonymous referees
Submitted: December 24, 2024; Accepted: October 30, 2025
Proofs received from author(s): February 3, 2026