



Research Article

Desert Tortoise Use of Burned Habitat in the Eastern Mojave Desert

K. KRISTINA DRAKE, *United States Geological Survey, Western Ecological Research Center, 160 North Stephanie Street, Henderson, NV 89074, USA*

TODD C. ESQUE,¹ *United States Geological Survey, Western Ecological Research Center, 160 North Stephanie Street, Henderson, NV 89074, USA*

KENNETH E. NUSSEAR, *Department of Geography, University of Nevada, Reno, NV 89557, USA*

LESLEY A. DEFALCO, *United States Geological Survey, Western Ecological Research Center, 160 North Stephanie Street, Henderson, NV 89074, USA*

SARA J. SCOLES-SCIULLA, *United States Geological Survey, Western Ecological Research Center, 160 North Stephanie Street, Henderson, NV 89074, USA*

ANDREW T. MODLIN, *United States Geological Survey, Western Ecological Research Center, 160 North Stephanie Street, Henderson, NV 89074, USA*

PHILIP A. MEDICA, *United States Geological Survey, Western Ecological Research Center, 160 North Stephanie Street, Henderson, NV 89074, USA*

ABSTRACT Wildfires burned 24,254 ha of critical habitat designated for the recovery of the threatened Mojave desert tortoise (*Gopherus agassizii*) in southern Nevada during 2005. The proliferation of non-native annual grasses has increased wildfire frequency and extent in recent decades and continues to accelerate the conversion of tortoise habitat across the Mojave Desert. Immediate changes to vegetation are expected to reduce quality of critical habitat, yet whether tortoises will use burned and recovering habitat differently from intact unburned habitat is unknown. We compared movement patterns, home-range size, behavior, microhabitat use, reproduction, and survival for adult desert tortoises located in, and adjacent to, burned habitat to understand how tortoises respond to recovering burned habitat. Approximately 45% of home ranges in the post-fire environment contained burned habitat, and numerous observations ($n = 12,223$) corroborated tortoise use of both habitat types (52% unburned, 48% burned). Tortoises moved progressively deeper into burned habitat during the first 5 years following the fire, frequently foraging in burned habitats that had abundant annual plants, and returning to adjacent unburned habitat for cover provided by intact perennial vegetation. However, by years 6 and 7, the live cover of the short-lived herbaceous perennial desert globemallow (*Sphaeralcea ambigua*) that typically re-colonizes burned areas declined, resulting in a contraction of tortoise movements from the burned areas. Health and egg production were similar between burned and unburned areas indicating that tortoises were able to acquire necessary resources using both areas. This study documents that adult Mojave desert tortoises continue to use habitat burned once by wildfire. Thus, continued management of this burned habitat may contribute toward the recovery of the species in the face of many sources of habitat loss. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS behavior, critical habitat, *Gopherus agassizii*, habitat use, invasive annuals, movement, Nevada, wildfire.

Understanding how wildfires affect the persistence of threatened or endangered animal populations is essential to sound conservation and management (Webb and Shine 2008), particularly for tortoise species faced with wildfire as a novel threat. The Mojave desert tortoise (*Gopherus agassizii*) is listed in the United States as a threatened species, and its persistence remains challenged by numerous threats, including wildfire (Esque et al. 2003, Tracy et al. 2005, U.S. Fish and Wildlife Service [USFWS] 2011b).

Desert wildfires in North America are more frequent and larger now than ever in recorded history (Brooks and Matchett 2006) and in recent decades constitute one of the most common causes of land-use conversion across basin and range grasslands and shrublands (Soulard and Sleeter 2012). Desert fires are promoted by the invasion of non-native annual grasses that increase fine fuels (Brooks and Esque 2002, Esque and Schwalbe 2002) and ignition sources that are associated with areas of human population growth (Swantek et al. 1999, Brooks and Matchett 2006). Desert wildfires fundamentally alter community dynamics by changing physical processes and biotic interactions (Billings 1990, D'Antonio and Vitousek 1992). Loss of perennial vegetation reduces soil stability thus increasing erosion by

Received: 21 May 2014; Accepted: 1 March 2015

¹E-mail: todd_esque@usgs.gov

wind and water (Soulard et al. 2013). The combustion of vegetation alters soil chemistry, and hot surface temperatures incinerate seeds often promoting the dominance of non-native plant species following wildfire (Esque et al. 2010a,b). Once they dominate burned areas, non-native annual grasses increase the susceptibility of these areas to re-burn during subsequent fires, and thereby diminish plant species richness, composition, canopy cover, and structure important to wildlife and the potential for their habitats to recover (Brown and Minnich 1986, Brooks 1999, Abella 2009, Esque et al. 2010a).

The direct impacts of fire to wildlife are well known including incineration, exposure to lethal temperatures, and smoke inhalation (Lyon et al. 1978, Huff and Kapler Smith 2000, Lyon et al. 2000). However, the indirect effects of fire on desert ecosystems may have far-reaching impacts on tortoise and other wildlife populations but to date are largely speculative. Wildfires change food availability and quality, and by altering habitat structure and loss of shelter sites, could increase exposure of herbivores to predators and environmental extremes (Lowe and Hinds 1971, Fox 1982, Esque et al. 2003). Perennial shrubs provide important habitat structure for Mojave desert tortoises (Luckenbach 1982) and other wildlife (Vamstad and Rotenberry 2010). Burning reduces shrub canopy cover (O'Leary and Minnich 1981, Brown and Minnich 1986, Brooks and Esque 2002) and by potentially altering thermoregulatory options, may push tortoises toward their environmental limits (Hillard 1996, Nussear et al. 2012). Furthermore, granivorous ants and rodents can reduce native annual plant production and diversity through selective seed harvesting (Esque 2004, Suazo et al. 2013). Diverse native annual plant diets are important for tortoises comprising >90% of Mojave desert tortoise diets (Esque 1994, DeFalco 1995, Jennings 2002). Shrub canopy cover can take up to 50 years to return to pre-fire levels in desert environments (Webb et al. 2003, Shryock et al. 2014), and human-mediated restoration of plant species composition is estimated to require centuries (Webb et al. 1983, Abella 2010, Turner et al. 2010).

On 22 June 2005, lightning strikes started numerous wildfires in the northeast Mojave Desert, collectively called the Southern Nevada Complex (SNC). The SNC comprises over 24,254 ha of critical habitat for the desert tortoise and 163,089 ha of potentially suitable habitat (Nussear et al. 2009, Derasary et al. 2011, USFWS 2011b). Similar to other fires in tortoise habitat (Esque et al. 2003, Lovich et al. 2011), these wildfires resulted in the injury and death of desert tortoises and dramatic changes in plant species richness, composition, and structure. Despite the importance of wildfire and habitat alteration as stressors, the indirect effects of fire on desert tortoises and other species have not been quantified (Esque et al. 2003). Thus, the relative value of burned critical habitat for the sustainability and recovery of desert tortoise populations is currently unknown. At present, the fundamental questions remain: do burned desert shrublands function as habitat that can sustain populations of tortoises, and if not, what is required to sustain or promote tortoise populations in these areas? To quantify the indirect

effects of wildfire on desert tortoises, we studied wild desert tortoise ecology and habitat use in and around the SNC area during 2006–2012. In particular, we evaluated movement patterns, home-range size, microhabitat use, behavior, reproduction, and survival for desert tortoises located in, and adjacent to, burned habitat. We hypothesized that habitat changes due to wildfire may result in emigration of tortoises away from burned habitat and lower reproductive effort, ultimately having a more profound and lasting effect on the survival of tortoise populations than the direct impacts of the fires.

STUDY AREA

Hidden Valley study site encompasses approximately 12,719 ha (127.1 km²) of public lands in the northeast Mojave Desert, approximately 90 km north of Las Vegas in Clark County (Nevada, USA). Previous surveys of this area indicated patchy desert tortoise distribution with local density estimates ranging from 0.84 to 3.01 tortoises/km² (USFWS 2006). Elevation of the site ranged between 829 m and 958 m. The area was largely dominated by Mojave desert scrub vegetation (Turner 1982) consisting of a creosote bush-white bursage (*Larrea tridentata*–*Ambrosia dumosa*) plant association, with tree yuccas (*Yucca brevifolia* and *Y. schidigera*) that were visually dominant.

METHODS

Habitat Measures

To delineate the perimeter of burned habitat, we employed a generalized additive model (GAM) in R (R Development Core Team 2012, Vienna, Austria) using remotely sensed data. We used Landsat 5 imagery from 2 dates (Sep 2005 and May 2010) and derived normalized difference vegetation index (NDVI) layers for each date. We used 2 dates to improve discrimination of burned areas by contrasting the dates immediately following the fire (2005) with a spring of high production following high winter rainfall (2010), which resulted in increased production in burned areas that was visible in NDVI imagery. We used these NDVI layers with 6 Landsat bands (1–5 and 7) to train the GAM across recorded field observations ($n = 2,147$) in burned and unburned habitats at Hidden Valley. The model's predicted threshold score to maximize agreement with the greatest number of verified unburned and burned habitat points was 0.65.

We established 18 paired 400-m × 400-m (16 ha) monitoring plots at random to compare vegetation changes between burned and unburned areas during each year of the study. We measured winter to spring precipitation data (Oct–Mar) using rain gauges at each monitoring plot for comparison with production values. We estimated annual shoot biomass on each plot using 30 20-cm × 50-cm quadrats placed at random during peak production (Apr–May). We identified annual plants to species, clipped them at ground level, and sorted them as native or non-native. We dried samples in a convection oven at 50°C to a constant mass and weighed samples to the nearest 0.001 g. We averaged biomass of annual plants across the 30 quadrats to

obtain a representative value for each monitoring plot in each year and then compared biomass between burned and unburned habitats using a linear mixed effects model (R Package lme4 ver 2.13.2) with plot identification as the random effects structure.

We determined canopy cover of perennial vegetation along 3 100-m line-intercept transects within each unburned and burned plot (Canfield 1941). Each transect originated 10 m from the center of vegetation monitoring plots and was oriented at 60°, 180°, and 300° from north (Herrick et al. 2005). We identified perennial herbs, grasses, shrubs, and cacti to species and recorded them as live or dead. We summarized species that comprised ≥5% of canopy cover in any year and occurred within the top 90% of cumulative cover. We analyzed percent cover as a function of habitat status (unburned or burned) among years, and entered plot as a random factor in a linear mixed effects model to account for repeated measurements.

Habitat Use by Tortoises

Sign counts.—We conducted surveys of general tortoise sign (i.e., occurrence of live or dead animals, active burrows, tracks, or scat) on the vegetation monitoring plots during spring and fall when desert tortoises were most active from 2006 to 2008. Teams of 4–9 biologists spaced at 15 to 25-m intervals made successive passes until they surveyed 100% of the plots. Because scat accumulations may occur near winter dens, scat refers to the number of locations where we found fecal pellets rather than the total number of individual scats. We collected all scat each year during the surveys to avoid multiple counts in successive years. We analyzed tortoise sign with respect to habitat type (unburned and burned), plot, and year in which surveys were conducted using a generalized linear mixed effects model where plot was a random factor to account for repeated measurements among years.

Focal animals.—We studied 53 adult tortoises (22 M and 31 F) from 2006 to 2012. We initially located live tortoises within or adjacent to burned habitat during sign count surveys and fitted them with very high frequency (VHF) radio-transmitters (Model RI-2B [13.8–15.0 g]; Holohil Systems Ltd., Carp, Ontario, Canada). We tracked telemetered tortoises weekly during March–October and monthly during November–February each year. During peak tortoise activity (Apr and May), we intensively tracked each animal several times a day to obtain detailed habitat use information. On each tortoise encounter, we recorded the identification number (ID), date and time of encounter, geographic location (Universal Transverse Mercator, North American Datum 1983), and habitat status (unburned or unburned).

Behavior and microhabitat.—We analyzed behavior and microhabitat location for telemetered tortoises during peak activity (Apr and May) in 2007–2011 (Inman et al. 2009). We classified animal behavior into 4 categories (inactive, basking, moving, and foraging; sensu Ruby and Niblick 1994). We described behavior as inactive for tortoises that we found in underground burrows as well as those observed resting on the surface if we did not observe any other

behavior. We made distinctions for active behaviors (basking, moving, and foraging). We recorded basking for tortoises that were on the surface often near the burrow entrance with fully extended limbs and distinctive posturing to maximize thermal exposure. We identified moving when we observed tortoises walking across the landscape. We identified foraging when we observed tortoises eating.

We classified microhabitat into 1 of 3 categories (burrow, open, and vegetation). We defined burrows as shelters excavated in soil or in naturally occurring caliche caves that provided cover for the entire tortoise. We defined microhabitats as vegetation only when plants provided partial to full shelter and the tortoise was outside of a burrow. We defined open as the absence of cover or thermal shelter. We observed most tortoises using these microhabitats in both burned and unburned habitats.

We analyzed both behavior and microhabitat selection using separate multivariate analyses of variance (MANOVA) to compare the relative behavior and microhabitat use by telemetered tortoises in unburned and burned habitats using R (Version 3.0.1). Because the numbers of observations differed among animals, for each tortoise and for each habitat type, we calculated the proportion of observations for the behaviors (inactive, basking, moving, and foraging), and for the microhabitats (burrow, open, and vegetation). Because these were frequency data, we calculated log difference matrices to perform the MANOVA analysis as described in Aebischer et al. (1993). We substituted a value of 0.001 for 0 values in the matrices of both unburned and burned habitat types. Subsequent to MANOVA, we conducted univariate analyses of variance (ANOVA) on individual behaviors and microhabitats, and used Tukey's honestly significant differences (HSD) to evaluate pairwise differences in behavior and microhabitat selection among habitat types.

Movement, habitat use, and home range.—We analyzed animal movements by calculating the linear distances from the edge of the nearest burned area for all telemetered tortoise locations in burned habitat using the *v.distance* function in Geographic Resources Analysis Support System (GRASS) geographic information system (GIS) software (v 6.4.2; GRASS Development Team 2010). We analyzed distances using a Bayesian zero-inflated compound Poisson linear model with mixed effects (cplm package 0.6–4 for R; Zhang 2012), where tortoise ID was a random effect to account for repeated observations. We used Akaike's Information Criterion (AIC) rankings to select among models for movements into the burned habitat examining effects of sex, year, and month as factors and day of year and shell length (i.e., maximum carapace length) as covariates (Burnham and Anderson 2002). We conducted post hoc comparisons to analyze the differences in the Bayesian simulations for each comparison of interest (e.g., year; Y. Zhang, University of Southern California, personal communication).

We also used locations to estimate fixed kernel home ranges for each telemetered animal annually (Calenge 2006, R Package adehabitat v1.8.2). We calculated an individual-

based smoothing parameter (h) with reference validation, and home-range area based on a 95% isopleth. We imported home ranges into GRASS GIS and intersected home ranges with the layer delineating burned areas to calculate the area within each home range that consisted of burned and unburned habitat. We analyzed home ranges by sex and year using a linear mixed effects model with tortoise ID entered as a random factor to account for repeated measurements among years.

Tortoise Health, Survival, and Reproduction

We quantified health and survivorship by comparing the survivorship, health assessments, sex, and shell length of tortoises during each spring and fall as indications of potential impacts of burned habitat. Assessments included the animal's general posture, respiration, face (with specific attention to the eyes, periocular tissue, nares, mouth, tongue, and oral mucosa), skin, and shell for any clinical signs of disease, abnormalities, or damage (USFWS 2011a). We recorded shell length for each animal as the midline carapace length measured from the center tip of the nuchal and supracaudal scutes. No clinical signs of disease occurred in our study animals, and therefore, we did not conduct any additional analyses. We analyzed animal survivorship using a logistic-exposure model (Shaffer 2004) coded in R (package `nestsurvival` 0.5; Herzog 2010). We evaluated survivorship relative to sex, shell length, habitat, month, year, home range, percentage of home range in burned habitat, and distance of movement into the fire interior.

We assessed reproduction in 23 females occupying both burned ($n=14$) and unburned ($n=9$) habitats. Selected telemetered females in burned landscapes had access to both burned and unburned areas but were observed to extensively select burned habitat throughout the study (approx. 70% observations per individual). For comparison, we located and telemetered additional females ($n=9$) residing in unburned habitat approximately 4 km north of the primary study site (away from the burned landscape). These females exclusively used unburned habitat. We quantified egg production using X-radiography to understand the potential influence of the habitat alteration on reproduction. We assessed reproduction only in 2012. We evaluated females biweekly from May through July 2012 until eggs were no longer detected after 2 consecutive scans. We detected eggs using a portable X-ray machine (MinXray HF80, Northbrook, IL) with digital cassettes at 60 KVP for 0.02 s (Hinton et al. 1997). We digitized and electronically archived cassettes using a digital scanner (Model CR-2500, Diagnostic Imaging Systems, Rapid City, SD). Following X-rays, we released animals at the point of capture. We compared the number of clutches and total number of eggs between habitats at the unburned control site and burned study site, with covariates of shell length, and distance from burned habitat using a generalized linear model. We conducted all handling and experiments using animals according to Institutional Animal Care and Use Committee guidelines (U.S. Geological Survey WERC-2012-03 and University of California-Davis WERC-2007-02) and under the appropriate state (Nevada Division of

Wildlife Permit # S33762) and federal (U.S. Fish and Wildlife Service TE-030659) permits.

RESULTS

Habitat Change

Wildfires in the SNC burned a significant portion (34.5 km² or 27.1%) of Hidden Valley in 2005. Fire intensity was highly variable (Derasary et al. 2011), leaving small patchy islands of unburned habitat. Re-sprouting of dominant shrubs in the core burned areas was rare (<1% of total canopy cover during the study, L. A. DeFalco, U.S. Geological Survey, unpublished data).

Total shoot biomass of annual species varied among years ($F_{6, 192} = 12.39$, $P < 0.01$) with low production during springs 2007, 2008, and 2012. Shoot biomass coincided with trends in winter to spring precipitation averaged across plots (76 mm [2005–2006], 44 mm [2006–2007], 40 mm [2007–2008], 133 mm [2008–2009], 139 mm [2009–2010], 160 mm [2010–2011], and 42 mm [2011–2012]). Native shoot biomass did not vary between habitat types (unburned vs. burned; $F_{1, 16} = 3.24$, $P = 0.09$; Fig. 1A); however, non-native biomass was 10 times greater in burned than unburned areas ($F_{1, 16} = 18.73$, $P < 0.01$, Fig. 1B). Live perennial canopy cover, in contrast, was reduced by >90% in burned than unburned areas in the years following the fire ($F_{1, 16} = 198.88$, $P < 0.01$, Fig. 2) and remained lower in burned areas than unburned areas throughout the study. Unburned areas supported canopy cover of long-lived woody perennials

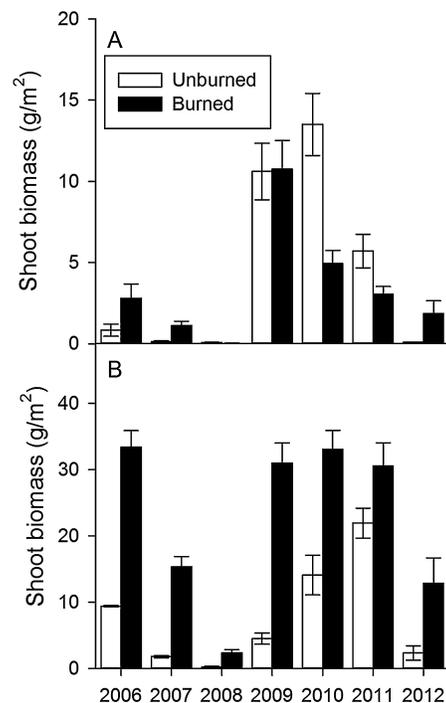


Figure 1. Mean (\pm SE) shoot biomass for native (A) and non-native (B) annual plant species during peak production in Hidden Valley (Nevada, USA) during 2006–2012. Note different scales for the y-axes.

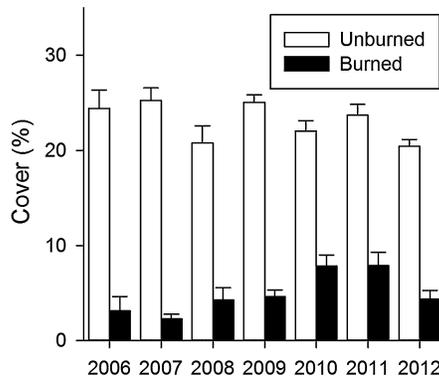


Figure 2. Mean (\pm SE) live perennial canopy cover at Hidden Valley (Nevada, USA) during 2006–2012.

such as creosote bush (*Larrea tridentata*), an evergreen shrub; *Ambrosia dumosa*, a drought deciduous shrub; and *Yucca schidigera*, a tall succulent (see also Behavior and Microhabitat Selection). In contrast, burned skeletons of these species predominated after the fire and rarely re-sprouted, and early colonizing herbaceous perennials including the subshrub desert globemallow (*Sphaeralcea ambigua*) and the sparse-canopied forb desert trumpet (*Eriogonum inflatum*) rapidly colonized the burn.

Habitat Use by Tortoises

Tortoise sign surveys on monitoring plots.—We used sign counts involving live tortoises, fresh scat, burrows, and tortoise carcasses on the monitoring plots as a conservative estimate of tortoise sign for each year. Near the fire perimeter, we found half the number of live tortoises in burned habitat relative to unburned areas (Table 1). Counts of tortoise sign were approximately 12% more numerous in unburned habitat; however, this metric was only marginally greater than sign in burned habitat ($Z=1.77$, $P=0.08$). Tortoise sign counts varied among years with more sign observed in 2008 in both habitat types than recorded in previous years ($Z=6.88$, $P<0.01$).

Home-range size and movements for telemetered tortoises.—Between 2006 and 2012, we found 35 adult tortoises in unburned habitat and 18 in burned habitat. Of the 12,223 observations of telemetered tortoises, 6,328 (52%) occurred in unburned habitat and 5,895 (48%) in burned habitat. Home-range size did not vary between sexes ($F_{1, 89}=1.65$, $P=0.20$); however, a marginally significant year effect reflected smaller home-range size in females during 2006 than other years ($F_{6, 84}=2.18$, $P=0.05$; Table 2). The estimated home range (57.7 ± 4.2 ha, $n=48$; Table 2) varied from 3.4 ha to 314.6 ha among individuals. Approximately 45% of the estimated home ranges for study animals at this site were located in burned habitat.

Tortoises monitored with telemetry moved farther into the burned area each year following the fire in 2005 up until 2010 on average, and retreated from the burn during 2011 and 2012. The best model describing the distance that tortoises moved into the burn (with an Akaike weight of 1) indicated a strong month \times year interaction (Fig. 3) with no support for models that included sex or shell length. During the early years, animals generally moved deeper into burned areas from April to July during the spring activity season, retreated during the hot summer months until September, and then increased again in October during the peak of the fall activity season. In 2010, however, tortoises prolonged movement farther into the burn during summer, and retreating in fall, a pattern that in 2012 reverted to that of the initial years (Fig. 3).

Behavioral and microhabitat selection.—We found significant behavioral differences in telemetered tortoises between burned and unburned habitats (MANOVA Pillai = 0.22, $F_{3, 101}=9.3$, $P<0.01$) with a year \times habitat type interaction (MANOVA Pillai = 0.34, $F_{12, 309}=3.3$, $P<0.01$). We observed most tortoises as inactive (mean proportion of observations = 0.65–0.85, ANOVA $F_{1, 103}=14.7$, $P=0.01$; Fig. 4A). Basking, moving, and foraging behaviors ranged from 0.01 to 0.12 depending on year and habitat type (Fig. 4B–D, respectively). Basking behavior was greater in burned habitat during 2 of the 5 years ($F_{1, 103}=14.1$, $P=0.01$, Fig. 4B). Tortoises were observed foraging

Table 1. Desert tortoise (*Gopherus agassizii*) sign recorded for unburned ($n=9$) and burned ($n=9$) monitoring plots from 2006 to 2008 in Hidden Valley (Nevada, USA).

| Year | Sign | Unburned | Burned | Total |
|------|---------------|----------|--------|-------|
| 2006 | Tortoise | 4 | 3 | 7 |
| | Fresh scat | 14 | 0 | 14 |
| | Active burrow | 39 | 24 | 63 |
| | Carcass | 14 | 5 | 19 |
| | Total | 71 | 32 | 103 |
| 2007 | Tortoise | 9 | 2 | 11 |
| | Fresh scat | 21 | 2 | 23 |
| | Active burrow | 44 | 33 | 77 |
| | Carcass | 17 | 13 | 30 |
| | Total | 91 | 50 | 141 |
| 2008 | Tortoise | 2 | 1 | 3 |
| | Fresh scat | 16 | 2 | 18 |
| | Active burrow | 124 | 94 | 218 |
| | Carcass | 24 | 15 | 39 |
| | Total | 166 | 112 | 278 |

Table 2. Mean (± 1 SE) home-range size and percent home range burned for adult telemetered desert tortoises (*Gopherus agassizii*) in Hidden Valley (Nevada, USA) from 2006 to 2012.

| Year | <i>n</i> | Home range (ha) | SE | % Burned | SE |
|------|----------|-----------------|------|----------|-----|
| 2006 | 12 | 48.7 | 21.4 | 29.5 | 9.2 |
| 2007 | 24 | 41.4 | 9.4 | 47.5 | 6.7 |
| 2008 | 22 | 35.2 | 4.3 | 51.7 | 6.5 |
| 2009 | 23 | 53.1 | 12.4 | 50.7 | 8.3 |
| 2010 | 21 | 78.8 | 15.5 | 41.3 | 7.3 |
| 2011 | 24 | 72.4 | 7.6 | 41.5 | 6.4 |
| 2012 | 30 | 68.0 | 8.8 | 43.0 | 6.3 |

proportionately more in burned habitat than in unburned habitat ($F_{1, 103} = 49.6, P < 0.01$; Fig. 4D). Moving behavior was also greater in burned than in unburned habitat ($F_{1, 103} = 18.5, P = 0.01$, Fig. 4C).

The proportion of microhabitats used by telemetered tortoises also differed between unburned and burned habitats (MANOVA Pillai = 0.08, $F_{2, 101} = 4.5, P = 0.01$) and among years (MANOVA Pillai = 0.14, $F_{8, 202} = 1.97, P = 0.05$; Fig. 5), but we found only marginal evidence of a year \times habitat interaction (MANOVA Pillai = 0.14, $F_{8, 202} = 1.8, P = 0.07$). The difference in use between habitats was largely due to the variable use of open ($F_{1, 101} = 8.3, P < 0.01$) and vegetated ($F_{1, 101} = 4.5, P = 0.01$) microhabitats, whereas burrow use was similar between burned and unburned areas ($F_{1, 101} = 1.2, P = 0.27$). In the burned habitat, use of the vegetation microhabitat was predictably lower (Tukey's HSD, $P = 0.01$) and open areas higher ($P < 0.01$) than in the unburned habitat.

Tortoises in unburned habitat were predominantly associated with live canopy cover and subtly shifted use among 3 woody species throughout the study that comprised the majority of cover in unburned habitat (Table 3). Immediately following the fire, tortoises used bursage (*A. dumosa*) and creosote bush (*L. tridentata*) even though canopy cover was largely dead but then shifted a portion of

use to live canopy of desert globemallow (*S. ambigua*; Table 3). After live cover of globemallow peaked in 2009 and 2010 and tortoise use peaked in 2010, mortality and canopy reduction of globemallow corresponded with a shift in tortoise use back to dead canopy cover (e.g., *A. dumosa*, *L. tridentata*, *Y. schidigera*, *Y. brevifolia*, and *H. salsola*) again in 2011 and 2012 (Table 3).

Health, Survival, and Reproduction

We did not observe clinical signs of disease within the study group. Only 1 male tortoise had fire-related burn injuries as a result of the SNC wildfires (Drake et al. 2012). We observed tortoise mortalities each year between 2008 and 2011. During this period, we discovered 16 animals (7 M and 9 F) with signs of predation, presumably by coyotes (*Canis latrans*). Annual survival was not influenced by sex ($Z = 0.75, P = 0.45$), shell length ($Z = 0.33, P = 0.74$), habitat type (unburned or burned; $Z = -1.33, P = 0.18$), home-range size ($Z = 1.21, P = 0.23$), percentage of home range burned ($Z = 0.99, P = 0.34$), or distance moved into the fire interior ($Z = 1.16, P = 0.25$).

Reproductive effort in 2012 reflected an average of 6.5 ± 0.6 eggs per female (range 3–12 eggs per female, $n = 21$). Approximately 95% ($n = 21$) of the females scanned were gravid, and 30% ($n = 7$) laid 2 clutches within the season. The number of eggs was reduced slightly between

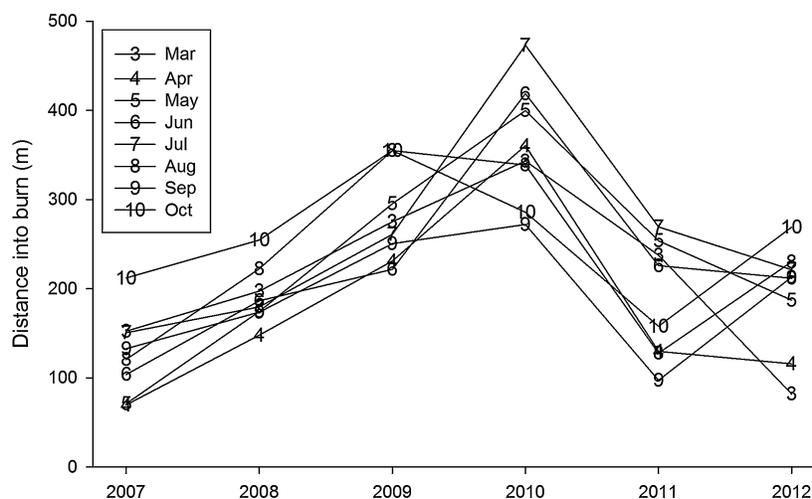


Figure 3. Mean linear distance from the edge of unburned and burned habitats during months of expected activity (Mar–Oct) for telemetered desert tortoises (*Gopherus agassizii*) located within burned habitat at Hidden Valley (Nevada, USA) following the 2005 wildfires.

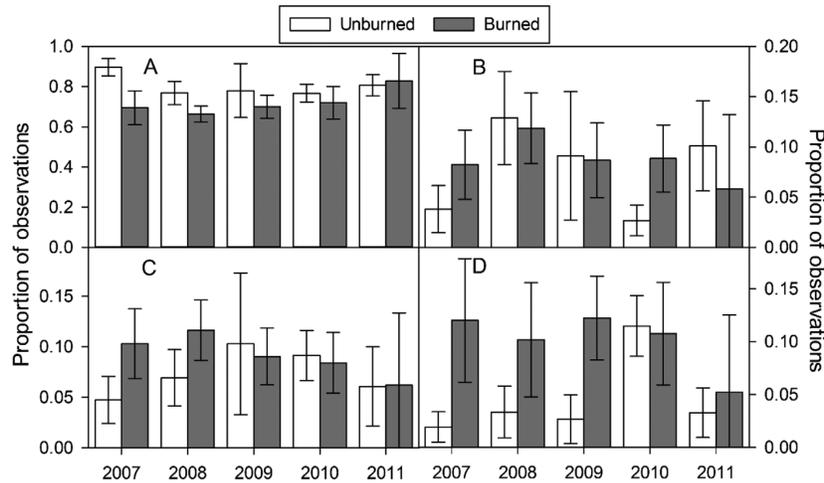


Figure 4. Proportion of behavioral observations (\pm SE) recorded in April and May each year (2006–2011) for telemetered desert tortoises in unburned and burned habitats at Hidden Valley (Nevada, USA). Behaviors included inactive (A), basking (B), moving (C), and foraging (D). Please note the scales differ among panels.

clutches; we observed an average of 5.0 ± 0.3 eggs and 4.6 ± 0.4 eggs in first and second clutch, respectively. Shell length (243.7 ± 3.3 mm) was related to the number of eggs and the number of clutches ($Z = 2.27$, $P = 0.02$), with larger females producing more eggs. Egg production for tortoises occupying unburned habitat was not different than those in burned habitats ($Z = 1.32$, $P = 0.19$).

DISCUSSION

Our study demonstrates that a single wildfire can dramatically alter tortoise habitat, but counter to our hypothesis, wildfire impacts to vegetation did not deter tortoises from using burned habitat. Similar to the western Mojave and Colorado deserts, wildfire diminished live perennial canopy cover in our study by as much as 90% (Brown and Minnich 1986, Brooks 1999, Esque 2004) leaving only persistent dead skeletons of the dominant shrub *L. tridentata* for cover immediately following this 1-time burn. Production of annual plants that tortoises depend on for their diet was 10 times greater in the burned area but was dominated by non-natives that rapidly re-colonize desert shrublands and capture soil resources more effectively than native species (Esque 1994, Brooks 1999, Esque and Schwalbe 2003, DeFalco et al. 2010, Esque et al. 2010b). We did not have the opportunity to observe tortoise behavior during or immediately after the fire; thus, we cannot confirm that tortoises emigrated from the burned area. However, our results suggest that with increased annual biomass of abundant forage plant species in burned habitats, and as perennial canopy cover becomes sufficient, adult tortoises can immigrate into once-burned areas for important aspects of their life history in parallel with gradual vegetation recovery.

Desert tortoises spend the majority of their lives inactive, and during peak periods of spring activity (Apr and May; Inman et al. 2009) devote minimal time to moving, foraging, and basking to meet their energetic needs before food plants senesce (proportion of observations that tortoises were active ≤ 0.12 in our study). Seasonal movements of tortoises deeper into burned habitat and more frequent foraging compared with unburned areas corresponded with greater production of annual plants and herbaceous perennials that make up the majority of their diets (Esque 1994, DeFalco 1995, Jennings 2002). Alternatively, more frequent basking behavior may

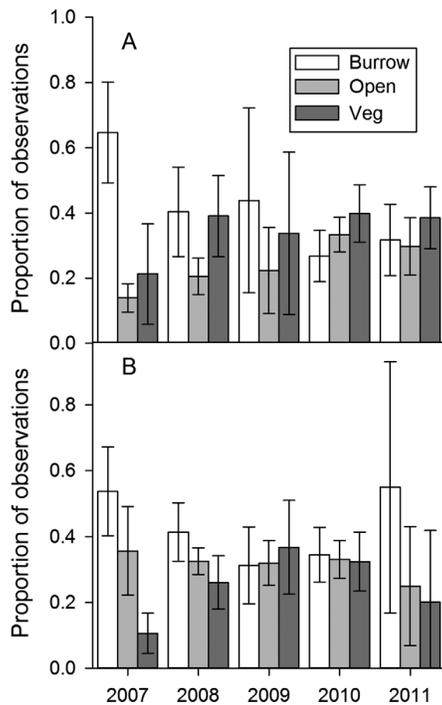


Figure 5. Proportion of microhabitat (\pm SE) selected by telemetered desert tortoises in April and May each year (2006–2011) for unburned (A) and burned (B) habitats at Hidden Valley (Nevada, USA).

Table 3. Percentages of total occurrences for telemetered desert tortoises observed beneath vegetation cover (i.e., shrub canopies or pallets) and relative canopy cover measured along vegetation transects by species in burned and unburned monitoring plots at Hidden Valley (Nevada, USA) from 2007 to 2012. Numbers of observations of tortoises under vegetation for burned (B) and unburned (U) habitats were 6 B/11 U (2007), 110 B/287 U (2008), 214 B/232 U (2009), 240 B/425 U (2010), 44 B/85 U (2011), and 39 B/59 U (2012). We included perennial species if they were important cover or shade resources (i.e., $\geq 10\%$ of tortoise occurrences or if they were prevalent in unburned or recovering burned vegetation (i.e., $\geq 5\%$ of vegetation cover in any year).

| | Tortoise occurrence (%) | | | | | | Vegetation cover (%live/%dead) | | | | | |
|-----------------------------------|-------------------------|------|------|------|------|------|--------------------------------|-------|-------|-------|-------|-------|
| | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 |
| Burned | | | | | | | | | | | | |
| <i>L. tridentata</i> ^a | 17 | 82 | 72 | 28 | 14 | 28 | 8/62 | 1/64 | <1/49 | <1/39 | 1/37 | 1/32 |
| <i>A. dumosa</i> ^a | 50 | 2 | 2 | 13 | 25 | 18 | 2/5 | 2/4 | 3/2 | 3/<1 | 3/<1 | 3/1 |
| <i>L. andersoni</i> ^a | 0 | 0 | 0 | 0 | 5 | 5 | 2/<1 | 1/<1 | <1/<1 | <1/<1 | <1/<1 | <1/0 |
| <i>P. fremontii</i> ^a | 17 | 0 | 0 | 2 | 0 | 0 | 3/3 | 4/3 | 2/4 | 1/2 | 1/1 | 1/3 |
| <i>K. grayi</i> ^a | 0 | 0 | 0 | 0 | 0 | 0 | 0/<1 | 0/<1 | 0/0 | 0/0 | 0/<1 | 0/0 |
| <i>Y. schidigera</i> ^a | 17 | 0 | 2 | 8 | 7 | 5 | <1/3 | <1/3 | <1/2 | <1/1 | 1/<1 | 2/1 |
| <i>H. salsola</i> ^a | 0 | 0 | 0 | 0 | 7 | 15 | <1/<1 | 1/<1 | <1/0 | 0/0 | <1/0 | <1/<1 |
| <i>S. ambigua</i> ^b | 0 | 3 | 10 | 36 | 23 | 10 | 3/<1 | 8/<1 | 24/<1 | 22/3 | 9/11 | 2/18 |
| <i>E. inflatum</i> ^b | 0 | 0 | 1 | 1 | 0 | 0 | <1/0 | 1/0 | 5/<1 | 18/<1 | 23/2 | 18/8 |
| <i>Y. brevifolia</i> ^a | 0 | 0 | 0 | 0 | 9 | 0 | 0/<1 | 0/<1 | 0/<1 | <1/2 | <1/<1 | <1/<1 |
| Unburned | | | | | | | | | | | | |
| <i>L. tridentata</i> ^a | 45 | 80 | 67 | 28 | 25 | 24 | 36/2 | 35/2 | 35/6 | 34/6 | 35/6 | 36/5 |
| <i>A. dumosa</i> ^a | 18 | 5 | 15 | 26 | 24 | 37 | 27/6 | 27/9 | 23/11 | 28/5 | 24/8 | 21/11 |
| <i>L. andersoni</i> ^a | 6 | 6 | 5 | 5 | 14 | 2 | 3/3 | 3/3 | 3/2 | 3/1 | 3/1 | 2/1 |
| <i>P. fremontii</i> ^a | 0 | 0 | 0 | 3 | 0 | 0 | 2/<1 | 1/<1 | 2/<1 | 2/<1 | 2/0 | 2/0 |
| <i>K. grayi</i> ^a | 0 | 0 | 0 | 0 | 1 | 7 | 3/<1 | 2/<1 | 2/<1 | 3/0 | 3/0 | 3/0 |
| <i>Y. schidigera</i> ^a | 27 | 1 | 4 | 21 | 15 | 14 | 2/<1 | 1/<1 | 2/<1 | 1/1 | 2/1 | 1/1 |
| <i>H. salsola</i> ^a | 0 | 0 | 0 | 0 | 2 | 2 | <1/<1 | <1/<1 | <1/<1 | 1/<1 | 1/0 | 1/0 |
| <i>S. ambigua</i> ^b | 0 | 0 | 0 | 0 | 0 | 0 | 0/0 | 0/0 | 0/0 | <1/0 | <1/<1 | <1/<1 |
| <i>E. inflatum</i> ^b | 0 | 0 | 0 | 0 | 0 | 0 | <1/0 | <1/<1 | <1/0 | <1/<1 | <1/<1 | <1/<1 |
| <i>Y. brevifolia</i> ^a | 0 | 0 | 0 | 0 | 6 | 2 | <1/<1 | 2/<1 | <1/<1 | 1/<1 | 1/<1 | <1/<1 |

^a Shrub or arboreal leaf succulent.

^b Herbaceous perennial forb or subshrub.

reflect reduced canopy cover in burned habitat. However, non-native annual brome grasses that dominated burned habitat typically have lower digestibility than annual forbs (DeFalco 1995, Tracy et al. 2006), and greater basking times in burned habitats may have been due to digestion requirements. Coincident with senescing vegetation as temperatures warmed, tortoises retreated closer to unburned areas by summer and used shrub canopy to escape from extreme surface temperatures characteristic of open burned areas.

In addition to seasonal movements, a yearly trend of adult tortoises moving into burned areas reached its peak in 2010 and coincided with the developing canopy cover of the fast-growing perennial *S. ambigua*, an herbaceous subshrub that often colonizes quickly during post-fire recovery in the Mojave Desert (Webb et al. 2003, Abella et al. 2009, Engel and Abella 2011). Interestingly, tortoises retreated from burned areas later in the season during 2010 and did not return in October as in other years, possibly because tortoises met their annual energetic requirements earlier with abundant spring forage in that year. As adult, *S. ambigua* reached the end of its life span (L. A. DeFalco, unpublished data), cover for this short-lived perennial declined, and movements contracted from the burned interior during 2011 and 2012. We found no differences in health or survivorship for tortoises occupying either habitat (burned or unburned) during this study or in reproduction during 2012. Production of food plants in the burned area does not appear to be a constraint for adult female egg formation (Lovich et al. 2011, Sanz-Aguilar et al. 2011). However, non-native annual

grasses, particularly red brome (*Bromus madritensis* ssp. *rubens*), dominated the burned areas, and the sharp-pointed florets of this species are known to cause extended mechanical injury to the mouth and jaw of desert tortoises, especially in younger animals (Medica and Eckert 2007). Whether sustained consumption of red brome, particularly in burned areas where it dominates, could have long-term impacts to health and survival of this long-lived tortoise is currently unknown and deserves further study.

Whereas herbaceous subshrubs, such as *S. ambigua*, appear to be effective cover for tortoises immediately following wildfires, their typically short life span brings into question their reliability for long-term habitat recovery, particularly through drought periods when short-lived species and perennial grasses experience high mortality (Webb et al. 2003, Miriti et al. 2007). Long-lived perennial species that provide vertical structure such as Nevada jointfir (*Ephedra nevadensis*) and creosote bush (*L. tridentata*) are preferred by desert tortoises for thermal cover from environmental extremes (Burge 1977, Berry and Turner 1986, Nussear et al. 2012). These species take decades to centuries to re-establish naturally across broad landscapes disturbed by wildfire (Webb et al. 2003). Re-sprouting of Mojave desert perennials following wildfire is typically low (Abella 2009) and varies depending on individual species' responses, as well as the environmental conditions during recovery (DeFalco et al. 2010). Surprisingly, the canopy of dead stems and branches of *L. tridentata* following the fire was still used by tortoises in higher proportion than that of any other

perennial species, as *L. tridentata* was more abundant in burned landscapes. Tortoise use of this dead vertical structure emphasizes that once-burned *L. tridentata*–*A. dumosa* vegetation communities can still provide some habitat value. Mojave shrublands that burn multiple times lose live and dead shrub structure (Brooks 2012) and are less likely to support dense tortoise populations. Empirical work on tortoise responses to repeatedly burned habitat has not been conducted but is nevertheless important for conservation of this unique tortoise and its habitat.

Comparisons of species' responses to wildfire can highlight important differences among tortoises faced with changing habitats (Mushinsky and Gibson 1991). Some tortoise species occupy productive, fire-adapted communities that benefit from regular fire return intervals (e.g., *Gopherus polyphemus*, McCoy et al. 2006, *Testudo hermanni*, Popgeorgiev 2008), whereas other species occupy desert habitats that are not fire adapted (e.g., *G. agassizii* and *G. morafkai*; Esque et al. 2003). Despite the SNC wildfire killing many individual desert tortoises, others survived the fire and may have been temporarily displaced outside of the burned area (Esque et al. 2003). Similarly, Hermann's tortoise (*T. hermanni*) and spur-thighed tortoise (*T. graeca*) experienced high fire-related mortality near the center of burned areas and less mortality near the edges of the fires (Popgeorgiev 2008). Spur-thighed tortoises in the Mediterranean region of Spain had similar home ranges between unburned and burned habitats, but contrary to our study, tortoises did not move between habitat types (Sanz-Aguilar et al. 2011). In contrast to the open shrublands occupied by Mojave desert tortoises, gopher tortoises (*G. polyphemus*) in the southeastern United States occupy heavily vegetated habitats with multiple structural layers that when left undisturbed, shade out important diet species in the understory as maturing forest increases canopy closure (Yager et al. 2007). Similarly, spur-thighed tortoises in Spain occupy habitats in early and middle seral stages of vegetative growth that develop into woodlands and forests when left undisturbed and thus are not optimal habitat for that species (Sanz-Aguilar et al. 2011). Although work reported here and elsewhere indicates that tortoises such as gopher tortoises and spur-thighed tortoises live in fire-dependent plant communities where burning maintains favorable foraging habitat, Mojave desert tortoises and Morafka's tortoise (*G. morafkai*) mostly occupy habitats that are optimal when undisturbed by fire.

Although the impact to adult desert tortoises is less severe than we initially hypothesized, demographic considerations of population persistence demand that we consider the influence of fire-induced habitat change on smaller subadult and juvenile Mojave desert tortoises. Juvenile tortoises have different requirements for feeding, thermoregulation, and cover from predators than adults (Berry and Turner 1986, Morafka 1994, Morafka et al. 2000, Esque et al. 2014), and further study is necessary to determine if landscape changes in perennial vegetation cover and forage composition and abundance following wildfire affect the growth and survival of younger age classes. The reduction of perennial vegetation associated with burning is expected to persist for many

decades (Turner et al. 2010, Vamstad and Rotenberry 2010, Webb et al. 2003); although our results are encouraging, burned habitat may take years to recover sufficiently to fully support tortoise populations.

Although tortoises appear to be acclimating and slowly re-colonizing the burned areas, other wildlife may take longer to occupy burned habitat. Many songbirds rely on desert shrubs and trees to provide cover and structure for nesting (Engels 1940, Crampton 2004), and long-lived desert plants may take decades to re-establish. Likewise, fire has long-term effects on native seed availability and species composition, and can reduce densities of granivorous birds and other species (Marone 1990, Wirtz 1995), especially small-mammal communities in desert environments, with immediate shifts toward open-dwelling species (Ojeda 1989, Vamstad and Rotenberry 2010). Predators of small mammals are in turn affected because changes in prey abundance and protective cover can have measurable effects on their survivorship at least in the short term (Cunningham et al. 2006, Nelson et al. 2007). Most of our knowledge of the responses of wildlife to wildland fire occurs for either forest or grassland systems, which have fast recovery rates for many perennial species. It remains to be seen whether long-term effects of fire on wildlife in arid deserts has deeper and longer lasting effects for a variety of species.

MANAGEMENT IMPLICATIONS

Our 7-year study on adult Mojave desert tortoise responses to once-burned critical habitat determined that adult tortoises can adjust their behavior immediately following wildfires without impact to reproduction and short-term survival. Whether we can accelerate re-vegetation of burned habitat, particularly by restoring persistent thermal cover provided by long-lived perennial shrubs and reducing non-native annual species, remains to be determined for the critical management and recovery of Mojave desert tortoises. Preventing once-burned habitats from burning multiple times by reducing fine fuels produced by non-native annual grasses is essential for protecting habitat for the recovery of the species. Our findings are not only relevant for tortoises and related desert species as habitat continues to be transformed by wildfire but also for habitat that is altered by other disturbances such as renewable energy development, military operations, and urbanization (USFWS 1994, USFWS 2011b). Similar to wildfire, these disturbances increase the propensity for non-native species, denude landscapes of important vegetation cover, and change quality of food needed by tortoises and related species. Re-establishing long-lived perennial species by re-seeding and transplanting greenhouse-raised seedlings (Abella and Newton 2009, Scoles-Sciulla et al. 2015) are also important for rehabilitating desert tortoise habitat affected by wildfires and other large-scale disturbances in the future because desert tortoises may not be able to cope with denuded landscapes over long time scales.

ACKNOWLEDGMENTS

We would like to thank many people for their field assistance in vegetation and tortoise monitoring during this study, especially R. Inman, K. Vittum, C. Phillips, S. Snyder, B. Jacobs, M. Walden, F. Chen, 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, P. Van Linn, K. Huxster, M. Poelman, B. Waitman, and many Student Conservation Association interns. Additionally, we thank M. Bunyon, C. Lund, A. Styles, K. Field, L. Allison, and R. Averill-Murray for providing technical, economical, and logistical support for this research. We appreciate constructive comments made by B. Halstead and 2 anonymous reviewers that significantly improved the manuscript. Funding was provided by the BLM Emergency Stabilization and Rehabilitation Program, Clark County Desert Conservation Program (Project # 2009-USGS-808A), USGS Priority Ecosystem Science Program, and Coyote Springs Investment Corporation. Any use of trade, product or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

LITERATURE CITED

- Abella, S. R. 2009. Post-fire plant recovery in the Mojave and Sonoran Deserts of western North America. *Journal of Arid Environments* 73:699–707.
- Abella, S. R. 2010. Disturbance and plant succession in the Mojave and Sonoran Deserts of the American Southwest. *International Journal of Environmental Research and Public Health* 7:1248–1284.
- Abella, S. R., E. C. Engel, C. L. Lund, and J. E. Spencer. 2009. Early post-fire plant establishment on a Mojave Desert burn. *Madroño* 56:137–148.
- Abella, S. R., and A. C. Newton. 2009. A systematic review of species performance and treatment effectiveness for revegetation in the Mojave Desert, USA. Pages 45–74 in A. Fernandez-Bernal and M. A. De La Rosa, editors. *Arid environments and wind erosion*. Nova Science Publishers, Inc., Hauppauge, New York, USA.
- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.
- Berry, K. H., and F. B. Turner. 1986. Spring activities and habits of juvenile desert tortoises, *Gopherus agassizii*, in California. *Copeia* 4:1010–1012.
- Billings, W. D. 1990. *Bromus tectorum*, a biotic cause of ecosystem impoverishment in the Great Basin. Pages 301–322 in G. W. Woodwell, editor. *The Earth in transition: patterns and processes of biotic impoverishment*. Cambridge University Press, New York, New York, USA.
- Brooks, M. L. 1999. Alien annual grasses and fire in the Mojave Desert. *Madroño* 46:13–19.
- Brooks, M. L. 2012. Effects of high fire frequency in creosote bush scrub vegetation of the Mojave Desert. *International Journal of Wildland Fire* 21:61–68.
- Brooks, M. L., and T. C. Esque. 2002. Alien plants and fire in desert tortoise (*Gopherus agassizii*) habitat of the Mojave and Colorado Deserts. *Chelonian Conservation Biology* 4:330–340.
- Brooks, M. L., and J. R. Matchett. 2006. Spatial and temporal patterns of wildfires in the Mojave Desert, 1980–2004. *Journal of Arid Environments* 67:148–164.
- Brown, D. E., and R. A. Minnich. 1986. Fire and changes in creosote bush scrub of the Western Sonoran Desert, California. *American Midland Naturalist* 116:411–422.
- Burge, B. L. 1977. Movements and behavior of the desert tortoise (*Gopherus agassizii*). Thesis, University of Nevada, Las Vegas, USA.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.
- Calenge, C. 2006. The package “adehabitat” for the r software: a tool for the analysis of space and habitat use by animals. *Ecological Modeling* 197:516–519.
- Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. *Journal of Forestry* 39:388–394.
- Crampton, L. H. 2004. Ecological determinants of the distribution, abundance and breeding success of Phainopepla (*Phainopepla nitens*, CL. Aves) at the northern edge of their range. Dissertation, University of Nevada, Reno, USA.
- Cunningham, S. C., L. Kirkendall, and W. Ballard. 2006. Gray fox and coyote abundance and diet responses after a wildfire in central Arizona. *Western North American Naturalist* 66:169–180.
- D’Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic process, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- DeFalco, L. A. 1995. Influence of cryptobiotic crusts on winter annuals and foraging movements of the desert tortoise. Thesis, Colorado State University, Fort Collins, USA.
- DeFalco, L. A., T. C. Esque, S. J. Scoles-Sciulla, and J. Rodgers. 2010. Desert wildfire and severe drought diminish survivorship of the long-lived Joshua tree (*Yucca brevifolia*; Agavaceae). *American Journal of Botany* 97:243–250.
- Derasary, L., N. Frakes, D. Gentilcore, T. Lenard, and K. Prentice. 2011. Southern Nevada complex emergency stabilization and rehabilitation final report. U.S. Department of the Interior, Bureau of Land Management. Ely, Nevada, USA.
- Drake, K. K., P. A. Medica, T. C. Esque, and K. E. Nussear. 2012. *Gopherus agassizii* (Agassiz’s Desert Tortoise) Scute dysecsis/sloughing. *Herpetological Review* 43:473.
- Engel, E. C., and S. R. Abella. 2011. Vegetation recovery in a desert landscape after wildfires: influences of community type, time since fire and contingency effects. *Journal of Applied Ecology* 48:1401–1410.
- Engels, W. L. 1940. Structural adaptations in thrashers (Mimidae: genus *Toxostoma*) with comments on interspecific relationships. University of California Publications in Zoology 42:341–400.
- Esque, T. C. 1994. Diet and diet selection of the desert tortoise in the northeast Mojave Desert. Thesis, Colorado State University, Fort Collins, USA.
- Esque, T. C. 2004. The role of fire, rodents and ants in changing plant communities in the Mojave Desert. Dissertation, University of Nevada, Reno, USA.
- Esque, T. C., K. K. Drake, and K. E. Nussear. 2014. Water and food acquisition and their consequences on life history and metabolism of North American tortoises. Chapter 10 in D. Rostal, H. Mushinsky, and E. D. McCoy, editors. *Biology and conservation of North American tortoises*. Johns Hopkins Press, Baltimore, Maryland, USA.
- Esque, T. C., J. P. Kaye, S. E. Eckert, L. A. DeFalco, and C. R. Tracy. 2010a. Short-term soil inorganic N pulse after experimental fire alters invasive and native annual plant production in a Mojave Desert shrubland. *Oecologia* 164:253–263.
- Esque, T. C., and C. R. Schwalbe. 2002. Alien annual grasses and their relationships to fire and biotic change in Sonoran deserts scrub. Pages 165–194 in B. Tellman, editor. *Invasive organisms in the Sonoran Desert*. University of Arizona Press, Tucson, USA.
- Esque, T. C., C. R. Schwalbe, L. A. DeFalco, T. J. Hughes, and R. B. Duncan. 2003. Effects of wildfire on small desert vertebrates, especially desert tortoises (*Gopherus agassizii*). *Southwestern Naturalist* 48:103–110.
- Esque, T. C., J. A. Young, and C. R. Tracy. 2010b. Short-term effects of experimental fires on a Mojave Desert seed bank. *Journal of Arid Environments* 74:1302–1308.
- Fox, B. J. 1982. Fire and mammalian secondary succession in an Australian coastal heath. *Ecology* 63:1332–1341.
- GRASS Development Team. 2010. Geographic Resources Analysis Support System (GRASS), GNU General Public License. <<http://grass.osgeo.org>>. Accessed 12 May 2010.
- Herrick, J. E., J. W. Van Zee, K. M. Havstad, L. M. Burkett, and W. G. Whitford. 2005. Monitoring manual for grassland, shrubland and savanna ecosystems. University of Arizona Press, Tucson, USA.

- Herzog, M. 2010. Nest survival analysis. R package version 1.8.0 or higher. <<http://www.npwrc.usgs.gov/resource/birds/nestsurv/>>. Accessed 8 Aug 2011.
- Hillard, S. 1996. The importance of the thermal environment to juvenile desert tortoises. Thesis, Colorado State University, Ft. Collins, USA.
- Hinton, T. G., P. Fledderman, J. Lovich, J. Congdon, and J.W. Gibbons. 1997. Radiographic determination of fecundity: Is the technique safe for developing turtle embryos? *Chelonian Conservation and Biology* 2:409–414.
- Huff, M. H., and J. Kapler Smith. 2000. Fire effects on animal communities in wildland fire in ecosystems: effects of fire on fauna. U.S. Department of Agriculture, Forest Service General Technical Report RMRS-GTR-42 (volume 1), Rocky Mountain Research Station, Ogden, Utah, USA.
- Inman, R. D., K. E. Nussear, and C. R. Tracy. 2009. Detecting trends in desert tortoise population growth: elusive behavior inflates variance in estimates of population density. *Endangered Species Research* 10:295–304.
- Jennings, W. B. 2002. Diet selection by the desert tortoise in relation to the flowering phenology of ephemeral plants. *Chelonian Conservation and Biology* 4:353–358.
- Lovich, J. E., J. R. Ennen, S. V. Madrak, C. L. Loughran, K. P. Meyer, T. R. Arundel, and C. D. Bjurlin. 2011. Long-term post-fire effects on spatial ecology and reproductive output of female Agassiz's desert tortoises (*Gopherus agassizii*) at a wind facility near Palm Springs, California, USA. *Fire Ecology* 7:75–87.
- Lowe, C. H., and D. S. Hinds. 1971. Effect of paloverde (*Cercidium*) trees on the radiation flux at ground level in the Sonoran Desert in winter. *Ecology* 52:916–922.
- Luckenbach, R. A. 1982. Ecology and management of the desert tortoise (*Gopherus agassizii*) in California. North American Tortoises: Conservation and Ecology. U.S. Fish and Wildlife Service, Wildlife Research Report 12:1–37.
- Lyon, L. J., H. S. Crawford, E. Czuhai, R. L. Fredriksen, R. F. Harlow, L. J. Metz, and H. A. Pearson. 1978. Effects of fire on fauna: state of knowledge review. U.S. Department of Agriculture, Ogden, Utah, USA.
- Lyon, L. J., E. S. Telfer, and D. S. Schreiner. 2000. Direct effects of fire and animal responses in wildland fire in ecosystems. U.S. Department of Agriculture, Forest Service General Technical Report WO-6, Rocky Mountain Research Station, Ogden, Utah, USA.
- Marone, L. 1990. Modifications of local and regional bird diversity after a fire in the Monte Desert, Argentina. *Revista Chilena de Historia Natural* 63:187–195.
- McCoy, E. D., H. R. Mushinsky, and J. Lindzey. 2006. Declines of the gopher tortoise on protected lands. *Biological Conservation* 128:120–127.
- Medica, P. A., and S. E. Eckert. 2007. *Gopherus agassizii* (desert tortoise). Food/mechanical injury. *Herpetological Review* 38:446–448.
- Miriti, M. N., S. Rodríguez-Burticá, S. J. Wright, and H. F. Howe. 2007. Episodic death across species of desert shrubs. *Ecology* 88:32–36.
- Morafka, D. J. 1994. Neonates: missing links in the life histories of North American tortoises. Pages 161–173 in R. B. Bury and D. J. Germano, editors. *Biology of North American tortoises*. U.S. Department of the Interior, National Biological Survey, Fish and Wildlife Research Report 13, Washington, D. C., USA.
- Morafka, D. J., E. K. Spangenberg, and V. A. Lance. 2000. Neontology of reptiles. *Herpetological Monographs* 14:353–370.
- Mushinsky, H. R., and D. J. Gibson. 1991. The influence of fire periodicity on habitat structure. Pages 237–259 in S. S. Bell, E. D. McCoy, and H. R. E. Mushinsky, editors. *Habitat structure: the physical arrangement of objects in space*. Chapman and Hall, London, England.
- Nelson, J. L., B. L. Cypher, C. D. Bjurlin, and S. Creel. 2007. Effects of habitat on competition between kit foxes and coyotes. *Journal of Wildlife Management* 71:1467–1475.
- Nussear, K. E., T. C. Esque, R. D. Inman, K. A. Thomas, L. Gass, C. S. A. Wallace, J. B. Blainey, D. M. Miller, and R. H. Webb. 2009. Modeling habitat of desert tortoise (*Gopherus agassizii*) in the Mojave and parts of the Sonoran deserts, California, Nevada, Utah, and Arizona. U.S. Geological Survey Open-file Report 2009-1102, Washington, D.C., USA.
- Nussear, K. E., C. R. Tracy, P. A. Medica, D. S. Wilson, R. W. Marlow, and P. S. Corn. 2012. Translocation as a conservation tool for Agassiz's desert tortoises: survivorship, reproduction, and movements. *Journal of Wildlife Management* 76:1341–1353.
- Ojeda, R. A. 1989. Small-mammal responses to fire in the Monte Desert, Argentina. *Journal of Mammalogy* 70:416–420.
- O'Leary, J. F., and R. A. Minnich. 1981. Post fire recovery of creosote bush scrub vegetation in the western Colorado Desert. *Madroño* 28:61–66.
- Popgeorgiev, G. 2008. The effects of a large-scale fire on the demographic structure of a population of Hermann's (*Testudo hermanni boettgeri* Mojsisovics, 1889) and spur-thighed (*Testudo graeca iberica* Pallas, 1814) tortoises in Eastern Rhodopes Mountains, Bulgaria. *Historia naturalis bulgarica* 19:115–127.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ruby, D. E., and H. A. Niblick. 1994. A behavioral inventory of the desert tortoise: Development of an ethogram. *Herpetological Monograph* 8:88–102.
- Sanz-Aguilar, A., J. D. Anadón, A. Giménez, R. Ballestar, E. Graciá, and D. Oro. 2011. Coexisting with fire: the case of the terrestrial tortoise *Testudo graeca* in Mediterranean shrublands. *Biological Conservation* 144:1040–1049.
- Scoles-Sciulla, S. J., L. A. DeFalco, and T. C. Esque. 2015. Contrasting long-term survival of two outplanted Mojave Desert perennials for post-fire re-vegetation. *Arid Land Research and Management* 29:110–124.
- Shaffer, T. L. 2004. A unified approach to analyzing nest success. *Auk* 121:526–540.
- Shryock, D. F., L. A. DeFalco, and T. C. Esque. 2014. Life history traits predict perennial species response to fire in a desert ecosystem. *Ecology and Evolution* 4(15):3046–3059.
- Soulard, C. E., T. C. Esque, D. R. Bedford, and S. Bond. 2013. The role of fire on soil mounds and surface roughness in the Mojave Desert. *Earth Surface Processes and Landforms* 38:111–121.
- Soulard, C. E., and B. M. Sleeter. 2012. Late twentieth century land-cover change in the basin and range ecoregions of the United States. *Regional Environmental Change* 12:813–823.
- Suazo, A. A., D. J. Craig, C. H. Vanier, and S. R. Abella. 2013. Seed removal patterns in burned and unburned desert habitats: Implications for ecological restoration. *Journal of Arid Environments* 88:165–174.
- Swantek, P. J., W. L. Halvorson, and C. R. Schwalbe. 1999. GIS database development to analyze fire history in southern Arizona and beyond: an example from Saguaro National Park. U.S. Geological Survey-Cooperative Studies Unit Technical Report #61, School of Renewable Natural Resources, University of Arizona Tucson, USA.
- Tracy, C. R., R. Averill-Murray, W. I. Boarman, D. Delehanty, J. Heaton, E. McCoy, D. Morafka, K. Nussear, B. Hagerty, and P. Medica. 2005. Desert Tortoise Recovery Plan Assessment. <http://www.fws.gov/nevada/desert_tortoise/documents/dtrpac/dtrpac_report.pdf>. Accessed 8 Feb 2013.
- Tracy, C. R., K. E. Nussear, T. C. Esque, K. Dean-Bradley, C. R. Tracy, L. A. DeFalco, K. T. Castle, L. C. Zimmerman, R. E. Esponiza, and A. M. Barber. 2006. The importance of physiological ecology in conservation biology. *Integrative and Comparative Biology* 46:1191–1205.
- Turner, R. M. 1982. Mohave desertscrub. Pages 157–168 in D. E. Brown, editor. *Biotic communities of the American southwest-United States and Mexico*. Desert Plants 4. Arizona University for Boyce Thompson Southwestern Arboretum, Superior, Arizona, USA.
- Turner, R. M., R. H. Webb, T. C. Esque, and G. F. Rogers. 2010. Repeat photography and low-elevation fire responses in the southwestern United States. Pages 223–244 in R. M. Turner and R. H. Webb, editors. *Repeat photography: methods and applications in the natural sciences*, Island Press, Washington, D.C., USA.
- U.S. Fish and Wildlife Service [USFWS]. 1994. Desert tortoise (Mojave population) recovery plan. U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2006. Range-wide monitoring of the Mojave population of the desert tortoise: 2001–2005 summary report. U.S. Fish and Wildlife Service, Desert Tortoise Recovery Office, Reno, Nevada, USA.
- U.S. Fish and Wildlife Service [USFWS]. 2011a. Health assessment procedures for the desert tortoise (*Gopherus agassizii*): a handbook pertinent to translocation. U.S. Fish and Wildlife Service, Desert Tortoise Recovery Office, Reno, Nevada, USA.

- U.S. Fish and Wildlife Service [USFWS]. 2011*b*. U.S. Fish and Wildlife Service [USFWS]. 2011*b* Revised recovery plan for the Mojave population of the desert tortoise (*Gopherus agassizii*). U.S. Fish and Wildlife Service, California and Nevada Region, Sacramento, California, USA.
- Vamstad, M. S., and J. T. Rotenberry. 2010. Effects of fire on vegetation and small mammal communities in a Mojave Desert Joshua tree woodland. *Journal of Arid Environments* 74:1309–1318.
- Webb, J. K., and R. Shine. 2008. Differential effects of an intense wildfire on survival of sympatric snakes. *Journal of Wildlife Management* 72:1394–1398.
- Webb, R. H., M. B. Murov, T. C. Esque, D. E. Boyer, L. A. DeFalco, D. F. Haines, D. Oldershaw, S. J. Scoles, K. A. Thomas, J. B. Blainey, and P. A. Medica. 2003. Perennial vegetation data from permanent plots on the Nevada Test Site, Nye County, Nevada. U.S. Geological Survey Open-File Report 03-336, Tucson, Arizona, USA.
- Webb, R. H., H. G. Wilshire, and M. A. Henry. 1983. Natural recovery of soils and vegetation following human disturbance. Pages 279–302 in R. H. Webb and H. G. Wilshire, editors. *Environmental effects of off-road vehicles: impacts and management in arid regions*. Springer-Verlag, New York, New York, USA.
- Wirtz, W. O. 1995. Responses of rodent populations to wildfire and prescribed fire in southern California chaparral. *Brushfires in California wildlands: ecology and resource management*. International Association of Wildland Fire, Fairfield, Washington, USA.
- Yager, L. Y., M. G. Hinderliter, C. D. Heise, and D. M. Epperson. 2007. Gopher tortoise response to habitat management by prescribed burning. *Journal of Wildlife Management* 71:428–434.
- Zhang, Y. 2012. Likelihood-based and Bayesian methods for Tweedie compound Poisson linear mixed models. *Statistics and Computing* 23:743–757.

Associate Editor: John Maerz.