

RESEARCH ARTICLE

**LONG-TERM POST-FIRE EFFECTS ON SPATIAL ECOLOGY AND  
REPRODUCTIVE OUTPUT OF FEMALE AGASSIZ'S DESERT TORTOISES  
(*GOPHERUS AGASSIZII*) AT A WIND ENERGY FACILITY NEAR  
PALM SPRINGS, CALIFORNIA, USA**

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**ABSTRACT**

We studied the long-term response of a cohort of eight female Agassiz's desert tortoises (*Gopherus agassizii*) during the first 15 years following a large fire at a wind energy generation facility near Palm Springs, California, USA. The fire burned a significant portion of the study site in 1995. Tortoise activity areas were mapped using minimum convex polygons for a proximate post-fire interval from 1997 to 2000, and a long-term post-fire interval from 2009 to 2010. In addition, we measured the annual reproductive output of eggs each year and monitored the body condition of tortoises over time. One adult female tortoise was killed by the fire and five tortoises bore exposure scars that were not fatal. Despite predictions that tortoises would make the short-distance movements from burned to nearby unburned habitats, most activity areas and their centroids remained in burned areas for the duration of the study. The percentage of activity area burned did not differ significantly between the two monitoring periods. Annual reproductive output and measures of body condition remained statistically similar throughout the monitoring period. Despite changes in plant composition, conditions at this site appeared to be suitable for survival of tortoises following a major fire. High productivity at the site may have buffered tortoises from the adverse impacts of fire if they were not killed outright. Tortoise populations at less productive desert sites may not have adequate resources to sustain normal activity areas, reproductive output, and body conditions following fire.

**Keywords:** Agassiz's desert tortoise, California, fire effects, *Gopherus agassizii*, movement, reproduction, Sonoran Desert, wind energy

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## INTRODUCTION

Ecosystems can be classified as either fire-dependent or non-fire-dependent based on their evolutionary history of exposure to fire (Mutch 1970). Fire-adapted habitats like the long-leaf pine ecosystem of the southeastern United States (Gilliam and Platt 1999) and the chaparral and coastal sage scrub ecosystems of California (Keeley 1987) are well known for their resilience to fire and even promote fire through their inherent flammable properties (Bond and Keeley 2005). Animals living in these ecosystems also have adaptations to recurring fire that allow them to persist under such a significant disturbance regime (Mushinsky 1985, Russell *et al.* 1999).

In contrast, some ecosystems are poorly adapted to fire, especially deserts where fuel density is low and woody plants evolved under widely spaced conditions (reviewed by Lovich and Bainbridge 1999). Fire was historically uncommon in the Mojave Desert of North America (Brooks 1999, 2002) but is increasing in both frequency and size as a result of the combination of increases in flammable invasive plants, mainly grasses (Brown and Minnich 1986), and anthropogenic ignitions (Brooks 1999, Brooks and Esque 2002, Brooks and Matchett 2006). Therefore, native species of this region are very sensitive to fire disturbances. For example, Agassiz's desert tortoise (*Gopherus agassizii*, hereafter referred to as desert tortoise) is a federally protected species in the Mojave Desert (Ernst and Lovich 2009) that can be negatively affected by fire (Brooks and Esque 2002, Esque *et al.* 2003, US Fish and Wildlife Service 2011).

The effects of fire on desert tortoise populations (including Morafka's desert tortoise, *G. morafkai*) were reviewed by Esque *et al.* (2002) and Schwalbe *et al.* (2002) and included three possible outcomes. The first is direct mortality caused by exposure to flames or smoke, resulting in death of the individual during or sometime after the fire. Fire mortality may dramatically affect the size structure and survivorship of tortoise populations as shown by Stubbs *et al.* (1985) and Hailey (2000) for the tortoise *Testudo hermanni* in Greece, and Lambert *et al.* (1998) for the tortoise *Stigmochelys (Geochelone) pardalis* in Africa. The latter study suggests that the effects may persist for decades. Desert tortoises are particularly vulnerable to fire when they are active outside their burrows. Tortoise burrows provide low temperature refugia during fires (Gibson *et al.* 1990) that may prevent mortality. The second effect of fire on desert tortoises is the alteration of habitat through loss of vegetative cover that may change the aboveground thermal environment to the detriment of tortoises. As ectotherms, desert tortoises must resort to the shade of nearby plants or burrows when environmental temperatures exceed their tolerance (Zimmerman *et al.* 1994). If shade or burrows are not available, they will die when body temperature reaches 43.1 °C (Hutchison *et al.* 1966). Thirdly, fires may indirectly affect habitat quality by altering the future availability or nutritional value of desert tortoise food plants for years following the conflagration. This is especially true when native perennial plants and annual forbs are replaced by nutritionally inferior grasses (Nagy *et al.* 1998), such as the exotic species Medi-

terranean split grass (*Schismus* spp.), buffel-grass (*Pennisetum ciliare* L.), and red brome (*Bromus madritensis* ssp. *rubens* [L.] Duvin), that proliferate following fire (D'Antonio and Vitousek 1992, Brooks 1999, Schwalbe *et al.* 2002, Brooks *et al.* 2004).

Although Esque *et al.* (2002) quantified the effects of direct mortality on desert tortoise populations in the Sonoran Desert following wildfires, we are aware of no published studies assessing longer-term post-fire effects on the species. The objectives of this study were to examine the possible behavioral and reproductive effects of a wildfire on a group of female desert tortoises in a wind energy generation facility near Palm Springs, California, 15 years post fire. Although pre-fire data are not available for the desert tortoise population, we tested four hypotheses about the potential long-term post-fire effects on tortoises:

1. Desert tortoises would shift their activity areas (AA), as measured by directional movement of AA centroids, away from burned habitat toward unburned habitat, over time.
2. The percent of burned habitat within an individual desert tortoise AA was predicted to decrease over time due to concomitant decreases in habitat quality affecting their thermal environment and nutrition since the desert tortoise is an obligate herbivore.
3. Reproductive output measured as annual egg production would decrease over time due to a potential decline in habitat quality and nutritional quality of food plants that could negatively affect the amount of energy available for reproduction (Congdon 1989).
4. A measure of body condition (mass divided by length) would decrease over time, again due to a potential decline in habitat quality and nutrition.

In our analyses, sampling periods are divided into proximate post fire (PPF) for the pe-

riod from 1997 to 2000, and long-term post fire (LTPF) for the period from 2009 to 2010, when studies were reinitiated.

## METHODS

### Site Description and Fire History

The study site (locally known as the Mesa wind farm) is located in the foothills of the southeastern San Bernardino Mountains in Riverside County, California, approximately 13 km northwest of the city of Palm Springs. Vegetation in the area is a complex mixture of desert, coastal sage scrub, and chaparral species at the western edge of the Colorado Desert subdivision of the Sonoran Desert (Burk 1977). North-facing slopes are visually dominated by California sagebrush (*Artemisia californica* Less.), whereas southern exposures contain a mixture of desert (e.g., creosote bush [*Larrea tridentata* {DC.} Coville]) and chaparral (e.g., chamise [*Adenostoma fasciculatum* Hook. & Arn.]) plant species. The site was developed for utility-scale wind energy generation starting in 1983 on land administered by the Bureau of Land Management. This resulted in construction of an extensive network of dirt roads to provide access to each of 460 turbines. A matrix consisting of native vegetation remained within and around the footprint of construction, although the entire site was grazed by cattle until sometime around the year 2000 when grazing was eliminated. A more detailed description of the energy-generation infrastructure and vegetation at this site is given in Lovich and Daniels (2000).

The human-ignited Verbenia Fire, unrelated to wind-energy generation operations, started on 4 August 1995, about 2.65 km from the core of our study site (Figures 1 and 2). This time of year is near the end of the spring-summer active season for desert tortoises at the study site, with aboveground activity usually confined to early morning and late afternoon due to high air temperatures in August. The fire spread rapidly to encompass 71 % (4.44



**Figure 1.** A view near the middle of our study site taken sometime shortly before the 1995 Verbenia Fire. Note the dense creosote bush (*Larrea tridentata*) community. Photograph by Jeff Lovich.



**Figure 2.** The same perspective of our study site as shown in Figure 1 photographed in 1995 shortly after the Verbenia Fire. Note the almost complete mortality of creosote bush (*Larrea tridentata*) in comparison to Figure 1. Photograph by Jeff Lovich.

km<sup>2</sup>) of the total area occupied by desert tortoises (Figure 3) at the study site. To generate the estimate of area occupied by tortoises, we used 1771 capture locations and circumscribed the cloud of points with a minimum convex polygon (MCP) buffered at the edges to 12 m based on the Global Positioning System (GPS) accuracy values (Figure 3). Three-dimensional surface area of the MCP was estimated at 6.25 km<sup>2</sup>. Fire intensity was rated as low to moderate by the responding fire crew: hot enough to kill a large percentage of the creosote bush, all of the teddybear cholla (*Cylind-*

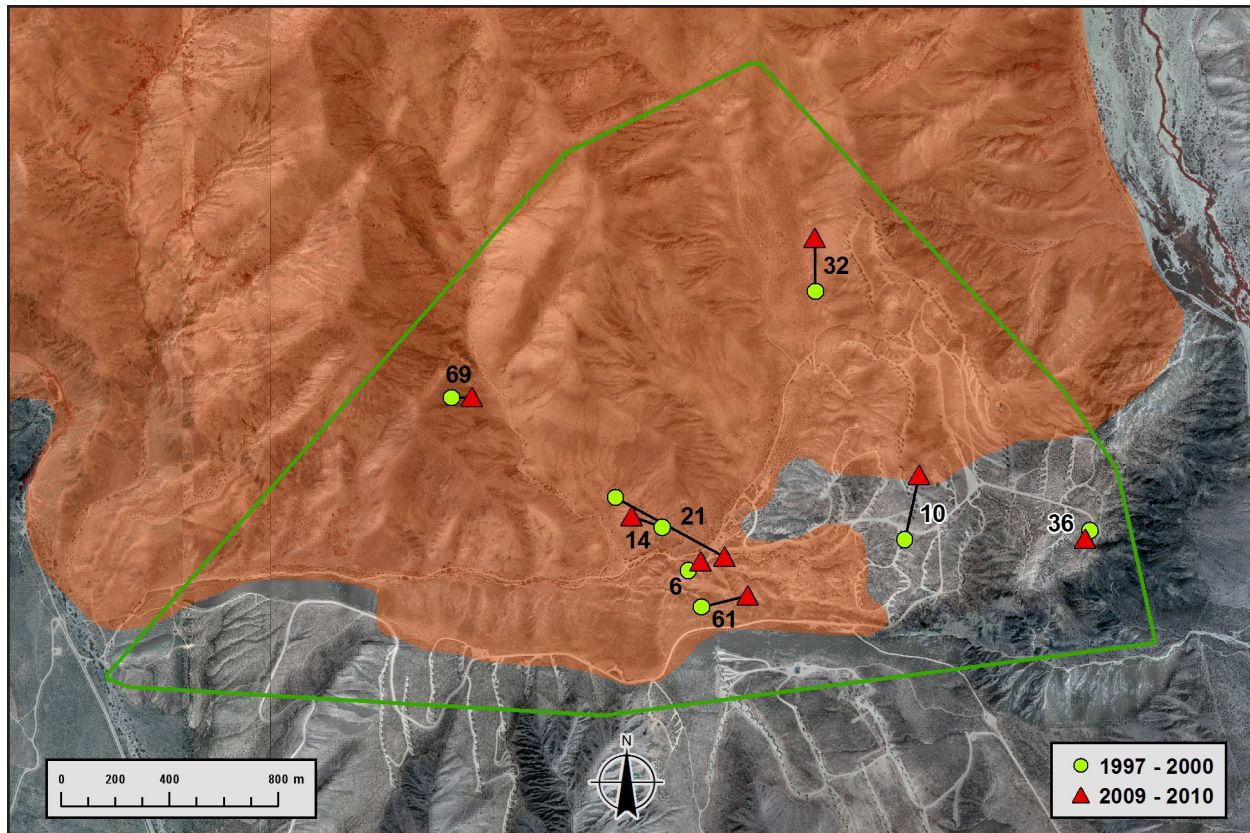
*ropuntia bigelovii* [Engelm.] F.M. Knuth), and many of the other desert perennial plants at the site. Areas with low fire intensity resulted in spotty mortality of individual creosote bushes, while moderate fire intensity areas sustained complete mortality. Random transects were walked through a portion of the burn within the area occupied by wind energy turbines on 7 August 1995, looking for evidence of desert tortoise mortality by visiting known tortoise burrows. Additional surveys of the burned area occurred on 25, 28, and 31 August 1995.

Other smaller fires affected different parts of the study area from 1979 to 2010 (all started by industrial operations on site) ranging in size from 0.02 ha to 58.71 ha. Prior to the 1970s, wildland fire was almost unknown in the immediate vicinity of our study site according to Brown and Minnich (1986). The Verbenia Fire may have been the first major wildland fire to affect our study site in modern history (R. Minnich; University of California, Riverside; personal communication).

### Methodology

We studied desert tortoise habitat use at the site starting in 1995 (Lovich and Daniels 2000) and continued with studies of demography, movements, reproductive ecology, nesting ecology, and hatchling behavior at various times during six field seasons from 1997 to 2000 and 2009 to 2010 (Lovich *et al.* 1999, 2011; J. Lovich, US Geological Survey, unpublished data). During that time, 145 individual tortoises (including 74 hatchlings emerging from monitored nests in 2000) were captured, marked, and monitored in the area. Individuals were marked both by notching unique combinations of codes into their marginal scutes with a file (Cagle 1939) and by gluing correspondingly numbered tags onto their carapaces with clear epoxy. Female tortoises were outfitted with radio transmitters during the study (7 to 17 females each year).





**Figure 3.** Close-up map of study site. The green boundary represents the minimum convex polygon of the outermost tortoise observations (buffered 12 m). The area shaded in orange denotes the local extent of the 1995 Verbenia Fire (unburned area to the southeast). Centroids of female tortoise activity areas for the proximate post-fire period from 1997 to 2000 are shown with green circles and the same for the long-term post-fire period from 2009 to 2010 are shown with red triangles. Individual tortoise identification numbers are shown next to each centroid pair. Wind turbine access roads and individual turbines are visible in the lower and right half of the image. The Whitewater River channel is visible in the upper right corner.

Radios were attached using the procedure recommended by Boarman *et al.* (1998). For the purpose of our study, we used data from a cohort of eight females that were monitored over the entire period from 1997 to 2010. All females were relatively large adults in 1997, and thus likely were adults during the fire in 1995, based on known growth and maturity patterns for the species (Ernst and Lovich 2009).

Our protocol varied over the years, but typically we relocated radio-tagged female desert tortoises at 7- to 10-day intervals, starting in late March or early April, through late July. Relocations generally continued at monthly intervals thereafter as stipulated by our permit. All tortoises were measured (carapace length, CL) when captured and weighed.

Mature females (greater than about 200 mm) were x-rayed to determine annual egg production (AEP), calculated by summing clutch sizes for each clutch produced by a female in a given year. Clutch size was determined using field X-radiography at dosages considered safe for turtles (Hinton *et al.* 1997), so that eggs still in the female could be counted. We included all adult females in every year, regardless of whether they produced a clutch of eggs or not. Thus, our analysis of AEP reflects output for both reproductive and non-reproductive (but sexually mature) individuals.

Relocation points at each capture were recorded with a GPS unit, and activity areas (AA) were constructed using minimum convex polygons around the cluster of location points

for each tortoise and time interval. Since home ranges of animals are known to be linearly dependent upon the number of captures, a minimum of 20 captures has been recommended for accurate estimation of this parameter (Mares *et al.* 1980). Despite the fact that several of the tortoises we monitored had slightly less than 20 relocations in the LTPF interval (Table 1), linear regressions between the log of the number of relocations and the log of AA were not significantly different from zero for PPF ( $F_{1,6} = 1.65$ ,  $P = 0.25$ ) or LTPF intervals ( $F_{1,6} = 0.05$ ,  $P = 0.84$ ), suggesting that our estimates of AA are not adversely affected by having less than 20 relocations for some of the tortoises.

We acquired Landsat 5 imagery for 10 September 1995 from the US Geological Survey for the study area to delineate the boundary of the Verbenia Fire. We followed procedures outlined in the fire effects monitoring protocol (Lutes *et al.* 2006) for calculating the Normalized Burn Ratio. These procedures calculate burn severity of the study area with additional adjustments made to smooth the polygon boundary of the fire footprint for the region encompassing the Verbenia Fire. We overlaid the MCP with the fire polygon to de-

termine the amount of burned area within the study area.

We used ArcGIS (ArcGIS 10) to develop and analyze all spatial data. Tortoise GPS locations were converted into point layers, which formed the basis for all subsequent spatial analyses. All spatial data layers were in the Universal Transverse Mercator projection, Zone 11, North American Datum of 1983. Digital elevation models (DEM) acquired from the US Geological Survey were used in the analyses for calculating path distances and activity areas in three-dimensional space. Calculating distances between centroids or areas of polygons using the elevation values from the DEM provide more representational values that incorporate the three-dimensional properties of the land surface. Recognizing that animals do not utilize all of an occupied area with equal intensity (Dixon and Chapman 1980), we calculated centroids for each three-dimensional estimate of AA as another metric of habitat use by individual tortoises.

### Analyses

We tested all data for normality using the Shapiro-Wilk W Test and conducted the appro-

**Table 1.** The number of female desert tortoise locations and relocations occurring in both time periods of our analysis. Pre-2001 relocations are considered as proximate post-fire, and 2009 to 2010 relocations are considered long-term post-fire.

Tortoise identification number	Pre-2001 locations (n)	2009 to 2010 locations (n)	Locations for all years (n)
6	85	36	121
10	83	13	96
14	38	37	75
21	25	17	42
32	75	35	110
36	66	18	84
61	23	19	42
69	20	16	36
Totals	415	191	606



appropriate statistical and post-hoc tests (i.e., Tukey Honestly Significant Difference Test). Activity area data did not meet the assumption of normality ( $W = 0.77$ ,  $P = 0.01$ ); therefore, we conducted a matched pairs Wilcoxon Sign-Ranked Test to determine differences between PPF and LTPF. Percentage of AA area burned and elevation of AA centroids met the assumption of normality ( $W = 0.86$  to  $0.89$ ,  $P = 0.11$  to  $0.23$ ); therefore, we conducted matched pairs  $t$ -tests to determine differences between PPF and LTPF. Annual egg production data met the assumption of normality ( $W = 0.91$  to  $0.97$ ,  $P = 0.14$  to  $0.20$ ). For all of the between-group comparisons (i.e., AEP and CL), we conducted incomplete block design one-way analysis of variance (ANOVA) using individual tortoise nested within category (i.e., PPF and LTPF) as a random effect, and category as a fixed effect. Means are followed with standard deviations and ranges. All statistical analyses were conducted in JMP version 8 (SAS Institute Inc., Cary, North Carolina, USA) and Systat (Systat Software, Inc., Chicago, Illinois, USA) with alpha of 0.05.

## RESULTS

Surveys conducted shortly after the fire confirmed that one adult female tortoise died of severe burns sustained while in a shallow burrow under a spiny hopsage bush (*Grayia spinosa* [Hook.] Moq.). In addition, three adult males and two adult females (CL = 21.4 cm to 28.1 cm) were found between 1998 and 2010 that exhibited fire scarring on the scutes covering their carapaces (Figure 4), possibly caused by the Verbenia Fire. We captured 28 adult tortoises (11 females and 17 males) in 2009 and 2010, 22 of which were recaptures (79%) from earlier studies (1997 to 2001), including the 8 females used in this analysis. Some of the tortoises had extensive relocation histories. For example, tortoises numbered 6 and 32 in our group had been relocated over 100 times during the course of our research (Table 1).



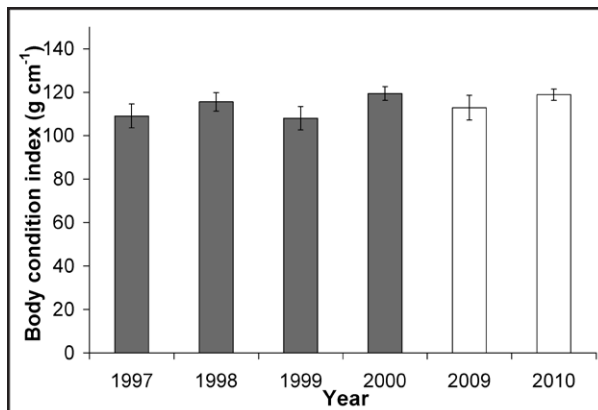
**Figure 4.** Male desert tortoise from our study site showing extensive fire scars on posterior and lateral scutes of the carapace. Photograph by Jeff Lovich, April 2010.

Activity areas estimated from minimum convex polygons ranged from 2.85 ha to 42.63 ha (mean = 14.67 ha) in PPF, and 3.34 ha to 30.75 ha (mean = 10.60 ha) in LTPF, and did not differ between the time intervals ( $Z = -6.00$ ,  $P = 0.46$ ). The AA centroids for only two tortoises were outside the area burned in PPF (148.0 m and 355.0 m from the edge of the burn, respectively). In the LTPF interval, one tortoise AA centroid shifted from unburned to burned areas, and only one tortoise AA centroid remained in the unburned area (381.4 m from the edge of the burn). The mean distance between the AA centroids of each tortoise in PPF and LTPF time periods was 173.0 m (range 34.7 m to 244.7 m). The mean vector of direction between PPF and LTPF AA centroids was  $52.3^\circ$ , or almost northeast, with a circular standard deviation of  $79.7^\circ$ . Rayleigh's test did not reject the null hypothesis that the vectors of movement between the PPF and LTPF centroids were distributed in a uniform manner ( $Z = 1.15$ ,  $P = 0.33$ ). The mean elevation of AA centroids did not differ between PPF ( $746.7 \pm 40.7$  m) and LTPF ( $745.1 \pm 43.2$  m;  $t = -0.23$ ,  $P = 0.82$ ).

During the PPF interval, six of eight (75%) tortoise AAs were entirely within the burned area. The mean percent AA burned for the

other two tortoises was 11 % (range of 10 % to 12 %). During LTPF, four of eight (50 %) tortoise AAs were entirely within the burned area, one was entirely in the unburned area, and the mean percent AA burned for the other three tortoises was 71.3 % (range of 25 % to 98 %). The percent AA burned did not differ between the time intervals ( $t = -0.35$ ,  $P = 0.73$ ). In addition, the proportion of tortoises with AAs entirely within the burned area did not differ between PPF and LTPF (Fisher's exact test,  $P = 0.61$ ).

The AEP was not significantly different ( $F = 0.69$ ,  $df = 1$ ,  $P = 0.42$ ) between PPF ( $6.7 \pm 3.9$ ) and LTPF ( $5.4 \pm 3.7$ ). Similarly, body condition did not differ (Figure 5) between PPF ( $115.6 \pm 8.8 \text{ g cm}^{-1}$ ) and LTPE ( $118.1 \pm 8.0 \text{ g cm}^{-1}$ ) ( $F = 0.33$ ,  $df = 2$ ,  $P = 0.58$ ).



**Figure 5.** Mean body condition indices ( $\text{g cm}^{-1}$ ) and standard errors of female desert tortoises for the years indicated. Bars shaded in gray are for the proximate post-fire interval, while those in white show data for the long-term post-fire interval.

## DISCUSSION

Fire has been identified as a significant threat to the recovery of the federally protected Agassiz's desert tortoise (US Fish and Wildlife Service 2011). We confirmed the negative effects of fire through observations of direct mortality and fire scarring of surviving tortoises at our study site following a massive wildland fire. However, despite predictions to the

contrary, we did not observe statistically significant changes in the spatial ecology, reproductive output, or body condition of a cohort of female desert tortoises 2 yr to 14 yr post fire. Surprisingly, AA centroids for six out of eight tortoises remained inside the burned area during PPF, and one centroid shifted from outside to inside the burned area during LTPF. Little evidence of burned area avoidance was observed despite the fact that distance from burned to unburned centroids were within the range of tortoise movements observed throughout the study.

Activity areas and AA centroids might be expected to change over time from burned to unburned areas if fire caused habitat degradation in the form of a decrease in thermal cover or availability of nutritious forage for the ectothermic and herbivorous desert tortoise (Esque *et al.* 2003). In addition, percent AA burned was hypothesized to decrease over time. Although none of these hypotheses were supported by our data, we do not have detailed measurements on plant species composition or distribution needed for a thorough analysis of microhabitat conditions within an AA.

Desert fires can cause a decrease in the number of plant species as time since fire increases (Alford *et al.* 2005), but the response varies among plant species and is complicated by other factors like seed bank size, rainfall (Abella *et al.* 2009), competition, disturbance history, and nutrient availability (Rew and Johnson 2010). For example, fire can temporarily reduce the seed bank of less nutritious grasses like the exotic species red brome, but the exotic Mediterranean split grasses can quickly increase above pre-fire levels (Brooks 2002). The latter plant species, when eaten by tortoises, do not contain enough digestible nitrogen to compensate for nitrogen lost through excretion (Meienberger *et al.* 1993). If there was a decrease in the number of plant species with increasing time since fire, as suggested by Alford *et al.* (2005), and a decrease in native annual forbs as shown by others (Brooks 1999,



Brooks and Esque 2002), tortoises might be expected to forage more widely (Ofstedal *et al.* 2002) in search of preferred food plants (Henen 2002) over time. Again, this is not reflected in our data. Sanz-Aguilar *et al.* (2011) compared minimum convex polygons for the Mediterranean tortoise *Testudo graeca*, a species that lives in a fire-prone ecosystem, in burned and unburned areas and found no difference. They concluded that individuals living in burned areas did not have to increase their territories to feed. None of their tortoises moved from burned to unburned areas despite the small size of their study site (70 ha).

Another negative impact of the fire on food plant abundance for tortoises was the creation of conditions that allowed the exotic annual forb Sahara mustard (*Brassica tournefortii* Gouan) to proliferate at the site. The seeds can reestablish high stem densities quickly following fire (Brooks 2000). Although established in the region surrounding our study site for over 80 years, Sahara mustard achieves high abundance mainly during years of above-average precipitation, with associated negative effects on native annual plants, including 80% to 90% reductions in flower and seed production (Barrows *et al.* 2009). Stands of Sahara mustard do not typically reach biomass levels in the Mojave and Sonoran deserts at which they can readily carry fire on their own. Where fires have been observed spreading through Sahara mustard stands, they are typically carried by a combination of an invasive annual grass (Mediterranean spelt grass and red brome) understory and a Sahara mustard overstory (M. Brooks, US Geological Survey, personal communication). These conditions may have contributed to the large size and rapid spread of the Verbenia Fire at our study site because the years 1994 to 1995 experienced an explosive abundance of Sahara mustard (Barrows *et al.* 2009).

We do know that a significant number of the creosote bush plants at the site were killed by the fire (Figures 1 and 2). As the largest

and most abundant perennial shrub through much of the range of the desert tortoise, creosote bush is an important source of thermal cover for tortoises when they are above ground. Based on a visual assessment of the site over time, it is obvious to us that brittlebush (*Encelia farinosa* A. gray ex Torr.) replaced creosote bush as one of the dominant perennial plant species, a common response to fire in this part of the Sonoran Desert, where brittlebush accounts for most of the seedlings observed in the year following fire, and most of the total plant cover 3 yr to 5 yr following fire (Brown and Minnich 1986). Perennial plant cover in the Mojave and Sonoran deserts is known to reestablish faster than plant composition following fire (Abella 2009). Tortoises at our site frequently shelter under brittlebush during the day; therefore, the loss of shade associated with creosote bush mortality appears to be compensated for by increases in brittlebush cover and abundance.

Our reproductive output data do not support the hypothesis that annual egg production would decrease over time. This suggests that resource availability for energy allocation to reproduction did not change greatly over the period of study. A similar conclusion was reached by Sanz-Aguilar *et al.* (2011) for the tortoise *T. graeca* living in burned and unburned areas in Spain. Neither clutch frequency nor clutch size differed between the two groups one year after fire. Since the effects of fire on the desert landscape and availability of forage plants for tortoises are dramatic and long-lasting, including slow regeneration of long-lived shrub species and proliferation of less nutritious non-native grass species that foster recurring fires, the reproductive output of desert tortoises at the Mesa study site may be more resilient to unnatural disturbances like fire than hypothesized. We are quick to point out that there are no pre-fire reproductive data to compare to our post-fire data. However, Mesa's post-fire reproductive characteristics were within the ranges reported for other pop-

ulations of desert tortoises (reviewed by Ernst and Lovich 2009), with the exception that clutch frequency was higher due to the high primary productivity at the site relative to other tortoise habitats (Lovich *et al.* 1999). The fact that body condition of tortoises did not vary significantly over time supports the idea that forage conditions following the fire support consistent reproductive output.

It is perplexing that tortoises did not move the short distance from burned to unburned habitats over time, and that one even shifted its AA centroid into a burned area. However, it is important to emphasize that the results we observed at Mesa might be very different from other desert tortoise habitats. By virtue of its proximity to coastally influenced climate, Mesa is a wetter site than those typically occupied by tortoises elsewhere in California, and this promotes high production of winter annual food plants for tortoises (Lovich *et al.* 2011). As a result, even during drought years in the rest of the desert, there is some plant germination at Mesa (Lovich and Daniels 2000). The favorable conditions at Mesa may allow tortoises to compensate for the negative effects of fire. In contrast, in habitats farther into the desert where rainfall is greatly diminished and

more unpredictable in comparison to Mesa, tortoises are already stressed beyond the ability to compensate for resource limitations in some years (Peterson 1994, Longshore *et al.* 2003). At those sites, fire may have far more catastrophic long-term impacts on tortoises.

The actual long-term effects of the fire on the tortoise population that we studied will never be fully understood due to the fact that data are not available for our study site under pre-fire conditions. As such, it is possible that the effects we hypothesized may have occurred in the short interval between the fire and the beginning of our study, less than two years later. Carefully designed before-and-after studies are needed on the effects of fire on the desert tortoise, but these will be difficult or impossible to conduct outside of serendipity due to the threatened status of tortoises. Until then, post hoc long-term studies like ours and others (Sanz-Aguilar *et al.* 2011) provide the best opportunity to understand how tortoises respond to the effects of fire over time. While awaiting additional studies, it is prudent to vigorously prevent and suppress wildland fires in tortoise habitat due to the known potential for direct mortality as noted previously by the US Fish and Wildlife Service (2011).

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