

ORIGINAL ARTICLE

Mojave desert tortoise (*Gopherus agassizii*) thermal ecology and reproductive success along a rainfall cline

Annette E. SIEG,¹ Megan M. GAMBONE,² Bryan P. WALLACE,^{3,4} Susana CLUSELLA-TRULLAS,⁵ James R. SPOTILA⁶ and Harold W. AVERY⁷

¹Department of Natural Sciences, University of Michigan-Dearborn, Dearborn, Michigan, USA, ²HDR, Plymouth Meeting, Pennsylvania, USA, ³Nicholas School of the Environment, Duke University Marine Laboratory, Beaufort, North Carolina, USA, ⁴Stratus Consulting, Boulder, Colorado, USA, ⁵Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Private Bag X1, Matieland 7602, South Africa, ⁶Department of Biodiversity, Earth and Environmental Science, Drexel University, Philadelphia, Pennsylvania, USA and ⁷Department of Biology, The College of New Jersey, Ewing, New Jersey, USA

Abstract

Desert resource environments (e.g. microclimates, food) are tied to limited, highly localized rainfall regimes which generate microgeographic variation in the life histories of inhabitants. Typically, enhanced growth rates, reproduction and survivorship are observed in response to increased resource availability in a variety of desert plants and short-lived animals. We examined the thermal ecology and reproduction of US federally threatened Mojave desert tortoises (*Gopherus agassizii*), long-lived and large-bodied ectotherms, at opposite ends of a 250-m elevation-related rainfall cline within Ivanpah Valley in the eastern Mojave Desert, California, USA. Biophysical operative environments in both the upper-elevation, “Cima,” and the lower-elevation, “Pumphouse,” plots corresponded with daily and seasonal patterns of incident solar radiation. Cima received 22% more rainfall and contained greater perennial vegetative cover, which conferred 5°C-cooler daytime shaded temperatures. In a monitored average rainfall year, Cima tortoises had longer potential activity periods by up to several hours and greater ephemeral forage. Enhanced resource availability in Cima was associated with larger-bodied females producing larger eggs, while still producing the same number of eggs as Pumphouse females. However, reproductive success was lower in Cima because 90% of eggs were depredated versus 11% in Pumphouse, indicating that predatory interactions produced counter-gradient variation in reproductive success across the rainfall cline. Land-use impacts on deserts (e.g. solar energy generation) are increasing rapidly, and conservation strategies designed to protect and recover threatened desert inhabitants, such as desert tortoises, should incorporate these strong ecosystem-level responses to regional resource variation in assessments of habitat for prospective development and mitigation efforts.

Key words: *Gopherus agassizii*, operative environments, reproductive ecology, resource gradient

Correspondence: Annette E. Sieg, Department of Natural Sciences, University of Michigan-Dearborn, Dearborn, MI 48128, USA.
E-mail: aesieg@umich.edu

INTRODUCTION

Deserts are characterized by scant, unpredictable rainfall and resource environments (e.g. microclimates and food) that are closely tied to water (Ehleringer &

Mooney 1983; Sowell 2001). Regional variation in desert ecosystems arises from strong responses to modest changes in rainfall due to latitude, elevation and location relative to topographical land features (e.g. bajadas and washes; Beatley 1974a, 1974b; Sowell 2001). For example, relatively stable bajadas of the arid southwestern USA may experience seasonal rainfall, which supports high perennial shrub densities, while nearby washes, where rainfall scours the soil, lack both perennial and ephemeral vegetation, and other open areas in between shrubs typically support the highest densities of ephemeral vegetation.

Desert aridity is coupled with hot, highly variable environmental temperatures (Sowell 2001). For desert ectotherms, the thermal environment and thermoregulation are also strong influences on their ecology because environmental temperatures directly affect their body temperature. This, in turn, affects their habitat utilization, physiological processes and energy acquisition (Zimmerman *et al.* 1994). Studies of resulting life history variation in vertebrate desert ectotherms have tended to focus on the influences of elevation, rainfall and environmental temperatures on small, short-lived lizards (e.g. Dunham 1978; Grant & Dunham 1988, 1990; Adolph & Porter 1993; Sears 2005) as well as small snakes (e.g. Beaupre 1995). Generally, higher altitudes and/or wetter years are associated with increased rainfall, cooler temperatures, greater activity periods, increased food availability and intake, higher growth rates, larger mature females and greater size-specific fecundity (Dunham 1978; Grant & Dunham 1988, 1990; Beaupre 1995). However, greater activity periods can expose small lizards to greater depredation risk (Adolph & Porter 1993; Sears 2005) and cooler temperatures constrain digestion and limit energy accrual from ingested food (Grant & Dunham 1988, 1990).

We examined how the thermal ecology of the Mojave desert tortoise (*Gopherus agassizii* Cooper, 1863), a large-bodied, long-lived ectothermic herbivore, is tied to regional variation in the resource environments of the Mojave Desert. The Mojave desert tortoise is a federally threatened species in the USA (USFWS 1990). The results of this study have relevant conservation implications because desert areas are increasingly affected by myriad land use impacts (e.g. urban development [Field *et al.* 2007]; military facilities expansion [Heaton *et al.* 2008]; solar and wind energy generation [USFWS 2011]), and conservation strategies for threatened species, such as desert tortoises, include the transloca-

tion of affected individuals to alternative habitat (Field *et al.* 2007; USFWS 2011). Better understanding of the contributions of desert resource environments to population growth rates will enhance assessments of current habitat for prospective development, and potential alternative habitat for displaced organisms, by adding ecological considerations beyond those related to anthropogenic effects (Heaton *et al.* 2008).

Long-term annual rainfall differences have been monitored at opposite elevation extremes of Mojave desert tortoise habitat within Ivanpah Valley in the eastern Mojave Desert, California, USA since 1997 (Lovich *et al.* 1998, 1999; Avery 2001). Annual rainfall increases the density and aboveground productivity of shrubs (Beatley 1974a; Ehleringer & Mooney 1983; Thomas *et al.* 2004) that provide wind shadows and shade for desert tortoises on the surface (Shreve 1931; O'Connor *et al.* 2000). Rainfall also increases the biomass of herbaceous forage (Beatley 1974b), temporarily cools surface operative temperatures (Gates 1980), and increases water intake by tortoises, allowing them to flush accumulated waste and to digest senescent plant material (Peterson 1996; Henen 1997).

We established study plots in which the higher altitude plot (1116 m, "Cima") receives on average 22% greater annual rainfall (see Table 1) than the lower (879

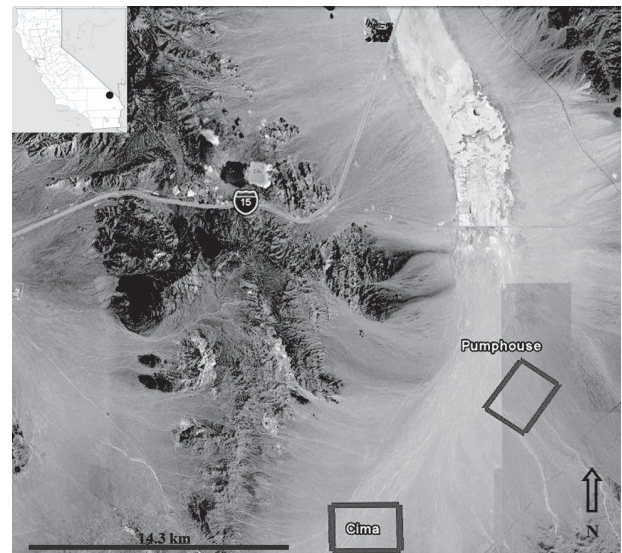


Figure 1 Map of Ivanpah Valley, eastern Mojave Desert, California, USA.

m, ‘‘Pumphouse’’; Fig. 1). We hypothesized that lower rainfall in Pumphouse creates a relatively resource-poor environment in which lower food availability and increased biophysical constraints on activity (e.g. fewer shade plants and lower shade quality) limit energy accrual and reproductive output. While increased rainfall has clear benefits for desert tortoises, it is unknown whether desert tortoise depredation incidence increases in response to greater rainfall because of predator population increases due to enhanced small mammal prey availability (e.g. increased *Vulpes macrotis* population due to rainfall [Dennis & Otten 2000]). *Vulpes macrotis* are common desert tortoise egg and occasional adult predators (Peterson 1994; Bjurlin & Bissonette 2004). Alternatively, desert tortoise depredation incidence could increase in response to lower rainfall due to prey switching, as observed previously in Ivanpah Valley with increased desert tortoise adult depredation primarily by *Canis latrans* during a drought period (Peterson 1994). We assessed depredation on tortoise eggs as well as on monitored adult females to determine whether depredation enhanced or counteracted the effects of the biophysical and resource environments on reproductive success and survivorship in these neighboring plots with long-term annual rainfall differences.

MATERIALS AND METHODS

The two Ivanpah Valley (35°29'60", 115°20'3") rectangular, equivalently-sized study plots are separated by 7-km straight line distance from Pumphouse (north-east) to Cima (south-west). The 60-km² total study site contains creosote bush mixed scrub vegetation that transitions into mid-elevation, mixed desert scrub (see Thomas *et al.* 2004). Mojave desert tortoises inhabit sites between the two plots and some of the surrounding area in Ivanpah Valley not incorporated in this study. Focal females in this study had been monitored for over five years without observation of movement between plots (Avery 1998; Franks *et al.* 2011), but some adult male tortoises had home ranges that spanned both plots (Franks *et al.* 2011). Hatchling and juvenile movements are unknown.

Rainfall and vegetation

We recorded rainfall from 11 plastic rain gauges (8 in Pumphouse, 3 in Cima; Avery 1998). Precipitation from October–March and June–September was considered winter and summer rainfall, respectively (Beatley 1974b; Wallis *et al.* 1999). Winter rainfall is the necessary precursor for spring vegetative forage for desert tortoises (Beatley 1969, 1974b). We recorded rainfall

Table 1 Habitat characteristics of the 2 *Gopherus agassizii* study plots in Ivanpah Valley

	Cima	Pumphouse
Elevation (m)	1116	879
Precipitation (mm)		
Annual mean 1997–2003	139.9 ± 22.3	105.7 ± 15.7
(Range)	(57.2–237.7)	(38.5–175.4)
Summer 2002	21.2 ± 1.3*	12.6 ± 0.6
Winter 2002–2003	102.7 ± 1.8*	80.8 ± 4.5
Summer 2003	51.4 ± 5.7*	23.5 ± 3.1
Herbaceous plant biomass 2003 (g m ²) [†]	45.6 ± 9.7	13.5 ± 6.4
Shrub species richness 2001–2003 [†]	7.8 ± 0.5	2.6 ± 0.2
Perennial plant species richness 1997	8.1 ± 0.6	4.3 ± 0.4
Total perennial plant cover 1997 (%)	25.5 ± 1.8*	16.3 ± 1.9
Canopy cover 1997 (m ²)		
<i>Larrea tridentate</i>	37.9 ± 1.2*	24.1 ± 1.3
<i>Ambrosia dumosa</i>	1.5 ± 1.1	2.8 ± 0.9
<i>Hilaria rigida</i>	0.9 ± 0.9	2.4 ± 2.2

Data are means ± 1 SEM; ranges are in parentheses. *Significantly greater $P < 0.05$. [†]Beever and Pyke (2005) and Beever *et al.* (2006).

from Summer 2002, Winter 2002–2003 and Summer 2003 for this study, and rainfall has previously been monitored in the same plots since 1997 (Avery 2001).

A vegetation study conducted by the United States Geological Survey included measures of rooted herbaceous biomass and shrub species richness in April/May from 2001 to 2003 (Beever & Pyke 2005; Beever *et al.* 2006). We analyzed vegetation data from Beever and others (2005, 2006) from 6 sites within 500 m of the meteorological station (see next section) in each plot. Twenty transects of line-intercept measurements from June 1997 provided additional measures of individual perennial plant canopy cover within each plot (following Ludwig *et al.* 1975). *Ambrosia dumosa*, *Hilaria rigida* and *Larrea tridentata* occurred in Cima and Pumphouse in great enough densities to permit comparisons between plots. With the exception of *H. rigida*, each of these species exhibits slow population turnover (>15 years; Cody 2000) and little response to interannual variation in rainfall (Beatley 1974a). Because the major canopy species are long-lived and differences in annual rainfall have been consistent since 1997 (Table 1), these 1997 canopy measurements add to our understanding of relative shade availability in Cima versus Pumphouse.

Thermal habitat and thermoregulation

From May–July 2003, we set up an automated meteorological and tortoise operative temperature model array in Cima and Pumphouse. A datalogger (Campbell Scientific CR-10X, Logan, Utah, USA) and multiplexer (AM32, Logan, Utah, USA) recorded environmental data every 15 min from a cup anemometer (R.M. Young Wind Sentry, Traverse City, Michigan, USA) at a height of 50 cm, a pyranometer (Li-Cor LI200X, Lincoln, Nebraska, USA) on the ground surface, and an air temperature profile with shielded thermocouples (Christian and Tracy 1985) at –2, 0, 2, 5, 10, 25 and 50-cm height. The –2 cm thermocouple corresponded to the depth of a typical pallet, or ground depression, used by tortoises as a refugium. We recorded temperature measurements from thermocouples placed within a burrow in each plot, positioned 1 m from the entrance (approximate tortoise retreat distance). A live tortoise displaced the thermocouple in the Cima burrow several times during the study period. Hereafter, we present burrow temperature measurements solely from the Pumphouse burrow (<1 °C difference between burrow temperatures during unoccupied periods in the Cima burrow). All thermocou-

ples (Omega Engineering, Stamford, Connecticut, USA) were accurate to ± 0.1 °C.

We placed 40 thick-walled solid aluminum tortoise models (200-mm, midline carapace length [MCL]), painted teal blue (Krylon enamel 1904) to match the integrated spectral absorptivity of Mojave desert tortoises, in 25 × 25-m arrays at each plot (following Zimmerman *et al.* 1994). Models were positioned on vertices 5-m apart within the array so that 3–4 were in full-sun (i.e. not shaded during daytime), 3 in full-shade (placed at base of a creosote bush), and 13–14 in partial-shade at different cardinal directions relative to a shrub. There were insufficient models to place on each 5-m vertex in both plots, so our representative sample focused on placing models in as many different types of partial-shade along vertices as possible and spreading the full shade and full sun models throughout the plot. Each model contained a thermocouple inserted into a central body cavity (following Zimmerman *et al.* 1994), and temperature measurements were recorded by the meteorological station datalogger every 15 min.

Using tortoise biotelemetry (see Reproduction methods below), at each capture we recorded the date, time, behavior of the tortoise (e.g. inactive in burrow, foraging), body temperature (by pressing a thermocouple into the inguinal area) and shaded air temperature (10-cm above the ground). Due to logistical constraints, we only captured tortoises during morning hours and we did not measure body temperatures at every capture.

Reproduction

From April–July 2003, we maintained a mark–recapture study using focal adult female tortoises equipped with 50-g radio transmitters (Advanced Telemetry Systems [following Boarman *et al.* 1998]) and incidental captures of other females in the plots. Tortoises were initially measured with calipers (MCL; ± 0.5 mm). We then repeatedly recaptured 19 focal females, 8 in Pumphouse and 11 in Cima. A combination of X-rays (every 2 weeks) and frequent weighing (every second day) was used to monitor reproduction. A drop in mass of approximately 100 g indicated the timing of egg clutch deposition (Turner *et al.* 1984). We measured weight with an Ohaus Scout Pro Digital Portable Balance (Parsippany, New Jersey, USA). X-rays, with safe radiation exposure levels (portable x-ray machine [Minxray-HF100, Northbrook, Illinois, USA] with settings of 60 kVP for 0.02 s [Hinton *et al.* 1997]), measured egg clutch characteristics (egg quantity and size). To obtain mean egg volume for each clutch, egg size (maximum length and breadth)

was determined using digital calipers (± 0.02 mm) on x-ray images. Egg volume was then calculated based on the assumption that the eggs were ellipsoids (Rose *et al.* 1996). We corrected for image magnification of the true egg size following Graham and Petokas (1989). We also X-rayed untransmitted adult females. We returned all tortoises to the point of capture within 30 min.

We located nest sites based on tortoise capture locations around the time of egg deposition and by using slight excavation and palpation of the soil in burrow interiors. We prevented researcher scent transfer to the area by using gloves and a ground cloth (following Bjurlin & Bissonette 2004). During the incubation period, we regularly observed nest locations from a distance in order to determine the timing of depredation events, if they occurred. After at least 100 days of incubation, we excavated nests to determine hatching and emergence success.

Analyses

Data are presented as mean \pm 1 SEM. Repeated measures analysis of variance (rmANOVA) tested rainfall variation between plots in Summer 2002, Winter 2002–2003 and Summer 2003. ANOVAs compared plot herbaceous plant biomasses and canopy areas (m^2).

Thick-walled aluminum operative temperature models exhibit thermal inertia and their longer thermal time constants result in integrated, as opposed to instantaneous, operative temperatures (O'Connor 2000). An iterative deconvolution routine estimated instantaneous operative temperatures by reducing the difference between measured model temperatures and calculated operative temperatures based on the wind speed at each time step (O'Connor 2000). Spearman's ρ tested for a significant 2-tailed correlation between time of capture and the difference between body temperature and shaded air temperature. A Mann–Whitney *U* test is performed to determine significant differences in body temperatures between plots.

Two-tailed Student *t*-tests compared MCLs and total annual egg production between plots. Generalized estimating equations tested whether egg volumes or clutch sizes were significantly affected by plot and clutch number (fixed factors) with MCL as a covariate. We specified the correlation matrix structure in both models as exchangeable (Zuur *et al.* 2009). A Poisson distribution with a log link was specified for clutch size analysis. A Mann–Whitney *U* test is performed to determine differences in frequency of second clutch production and depredation between plots. We carried out all statisti-

cal analyses using SPSS 15.0. The estimated marginal means for significant fixed effects were compared using the least significant difference. The significance level for all analyses was $P < 0.05$.

RESULTS

Rainfall and vegetation

There was a significant effect of plot on precipitation from 2002 to 2003 ($F_{1,9} = 30.3$, $P < 0.001$), with significantly more rain in Cima (Table 1; $P < 0.001$). There was also a significant effect of plot on herbaceous biomass in 2003 ($F_{1,28} = 7.7$, $P = 0.01$), with significantly greater Cima biomass ($P = 0.01$). Perennial species richness was 2 to 3 times greater in Cima from 2001 to 2003, and in 1997. Cima total perennial cover was significantly greater ($t_{18} = 3.5$, $P = 0.003$). The most frequently encountered perennial species in both plots were *H. rigida* (Cima 44.9%, Pumphouse 9.5%), *A. dumosa* (Cima 16.5%, Pumphouse 41.8%) and *L. tridentata* (Cima 13.0%, Pumphouse 22.6%). *H. rigida* is a bunch grass and *A. dumosa* is a sub-shrub. Therefore, canopy cover in both plots was dominated by *L. tridentata*, and was significantly greater in Cima ($P < 0.001$). Cima also contained several larger canopy plants not found in Pumphouse, including *Yucca schidigera* (1.7%), *Lycium andersonii* (1.7%) and *Ephedra nevadensis* (1.2%).

Thermal habitat and thermoregulation

Incident solar radiation levels were generally greater in Cima (Fig. 2a), and levels increased from May to July in both plots (Table 2). Wind speeds were similar between plots during the day, but they were lower in Pumphouse at night (Fig. 2b). Morning ground surface temperatures increased more rapidly in Pumphouse, but they were higher at midday and into the afternoon in Cima (Fig. 2c). In both plots, ground surface temperatures increased almost 40 °C during daytime hours. Daytime air temperatures were up to 15 °C cooler than the ground. Pallet temperatures (–2 cm) remained below 40 °C until almost midday, were similar to burrow temperatures in the evening up until midnight, and remained warmer than ground surface temperatures throughout nighttime hours.

In both plots, operative temperatures in full-shade were generally depressed throughout daytime hours by 10 to 15°C compared to those in full-sun (Fig. 3), with the greatest difference observed in Cima at midday and into the afternoon hours. Daytime (07.00 to 21.00 hours)

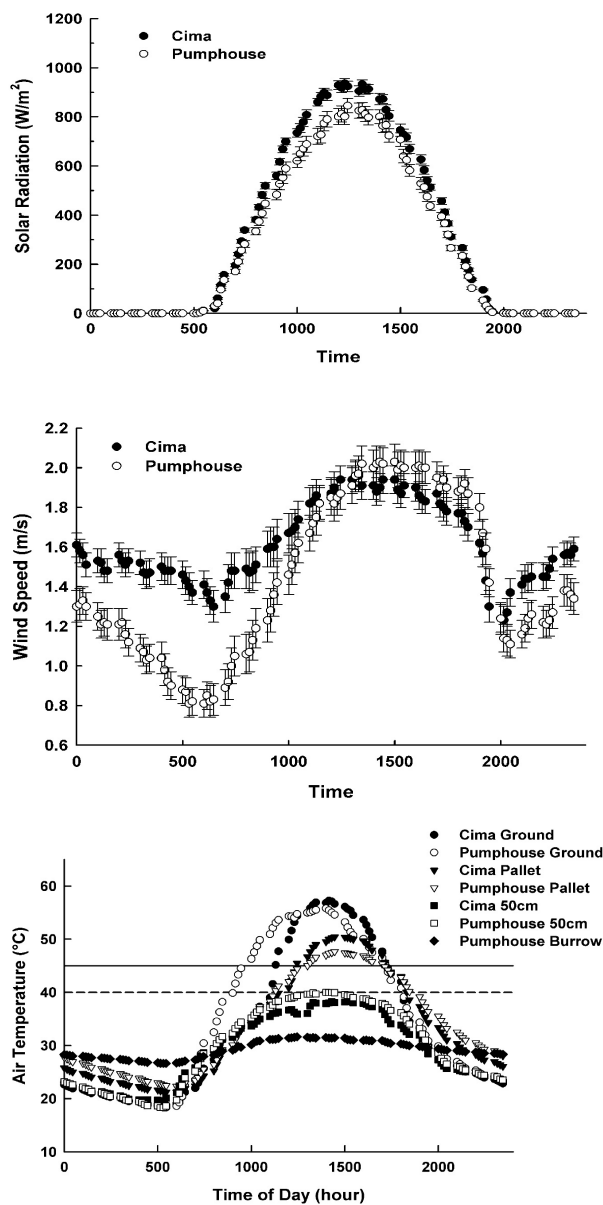


Figure 2 Microhabitat characteristics for Mojave desert tortoises in Ivanpah Valley from May to July 2003 measured by meteorological stations in Cima ($N = 1$) and Pumphouse ($N = 1$): (a) incident solar radiation; (b) wind speeds at 50 cm height off the ground; and (c) air temperatures at the ground surface, in pallets, in a burrow, and at 50 cm height off the ground. The solid reference line is the mean critical thermal maximum for desert tortoises (45 °C, Naegle 1976) and the dashed line is the temperature at which desert tortoises enter burrows (40°C, Zimmerman *et al.* 1994). All points correspond to mean values ± 1 SEM.

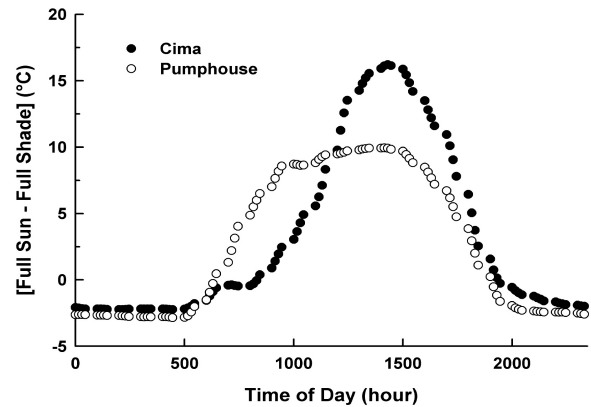


Figure 3 Shade quality in the Cima and Pumphouse plots as assessed by calculating the relative difference between operative temperature in full-sun and in full-shade for each plot (from May to July 2003).

partially-shaded operative temperatures were only moderately different from full-sun operative temperatures (within approximately 5 °C, App. A.1). Summer monsoonal rains occasionally drastically cooled all operative temperatures (e.g. Julian Day = 157, App. A.1–3), and yet, in general, daily and even weekly operative temperature variation was fairly modest in comparison with the monthly incremental increase in peak midday operative temperatures (App. A.1–3). Based on differences in full-shade operative temperatures, and a mean critical thermal maximum of 45 °C (Naegle 1976), we estimated that the morning active period for Pumphouse tortoises was 1–1.5 h greater than in Cima (Table 2), and the afternoon Cima active period was 3–3.75 h greater than the Pumphouse active period (Table 2). Partial-shade in both plots resulted in estimated morning and afternoon active periods differing by up to 0.5 h. Seasonal progression increased mandatory periods of inactivity (full-shade operative temperatures above 45 °C) throughout Ivanpah Valley from the early spring, when activity was possible throughout daytime hours, to mid-summer, when desert tortoises were inactive at least 4 to 6 h during the day (Table 2).

The extended window for potential morning activity in Pumphouse corresponded with our increased observations of morning (0700 to 1200 hours) tortoise activity outside of burrows in Pumphouse as compared to in Cima (Fig. 4). Regardless of plot, tortoise activity outside their burrows decreased as the season progressed

Table 2 Monthly maximum incident solar radiation levels, maximum ground surface temperatures, and estimated inactivity periods for *Gopherus agassizii* in Ivanpah Valley based on when operative temperatures exceeded the mean critical thermal maximum (45°C, Naegle 1976)

	Cima	Pumphouse
Maximum incident solar radiation ($W\ m^{-2}$)		
May	981.0 ± 16.3	911.5 ± 40.2
June	990.6 ± 6.2	857.8 ± 49.2
July	994.0 ± 27.7	973.5 ± 15.7
Maximum ground surface temperature (°C)		
May	55.7 ± 1.5	53.9 ± 1.2
June	58.8 ± 0.8	57.5 ± 0.7
July	60.9 ± 1.5	60.8 ± 0.7
Inactivity period (hours)		
Full-sun		
May	6.5 (1030–1700)	6 (1045–1645)
June	7.75 (0945–1730)	8.25 (0930–1745)
July	8.75 (0930–1815)	9.25 (0915–1830)
Full-shade		
May	—	—
June	1.25 (1045–1200)	3 (1200–1500)
July	4 (0945–1345)	6.75 (1045–1730)

Means ± 1 SEM. Range of recorded hours when operative temperatures exceeded 45 °C are in parentheses. — Indicates that operative temperatures never exceeded 45 °C.

from spring into summer (Fig. 4). There was no significant correlation between time of capture and the difference between body temperature and shaded air temperature in either plot (Fig. 5a, $P > 0.05$), and this pattern did not change with seasonal progression (Fig. 5b). There were also no significant differences overall between plots in tortoise body temperatures (Fig. 5; Mann–Whitney $U = 228.0$, $P > 0.05$).

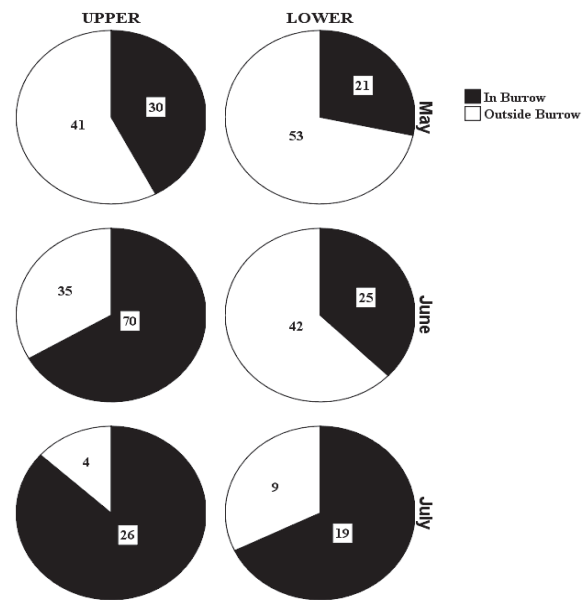


Figure 4 Mojave desert tortoise activity during morning hours (0700–1200 hours) in the Cima and Pumphouse plots. Sizes of pie slices correspond to percent of total captures with individuals found outside versus inside a burrow at the time of capture. Numbers within pie slices are sample sizes (N).

Reproduction

During 2003, 18 of 19 transmitted adult female tortoises deposited at least 1 clutch of eggs, with first clutches deposited between 26 May and 9 June and second clutches between 12 June and 3 July. We detected egg clutches in eight untransmitted female tortoises. Because these untransmitted tortoises were not captured regularly, we could not determine with confidence whether detected clutches were first or second clutches (Unknown Clutch, Table 3). Three transmitted tortoises also had incomplete X-ray records due to the tortoise eluding capture (Unknown Clutch, Table 3). There was no significant difference between plots in the proportion of transmitted tortoises depositing a second clutch, with 6 out of 10 in Cima depositing 2 clutches and 2 out of 5 in Pumphouse (Mann–Whitney $U = 20.0$, $P > 0.05$). There was also no significant difference between plots in the total annual number of eggs deposited per tortoise with 4.6 ± 1.2 ($N = 5$) in Pumphouse and 5.5 ± 0.62 ($N = 10$) in Cima ($t_{13} = 0.74$, $P = 0.47$).

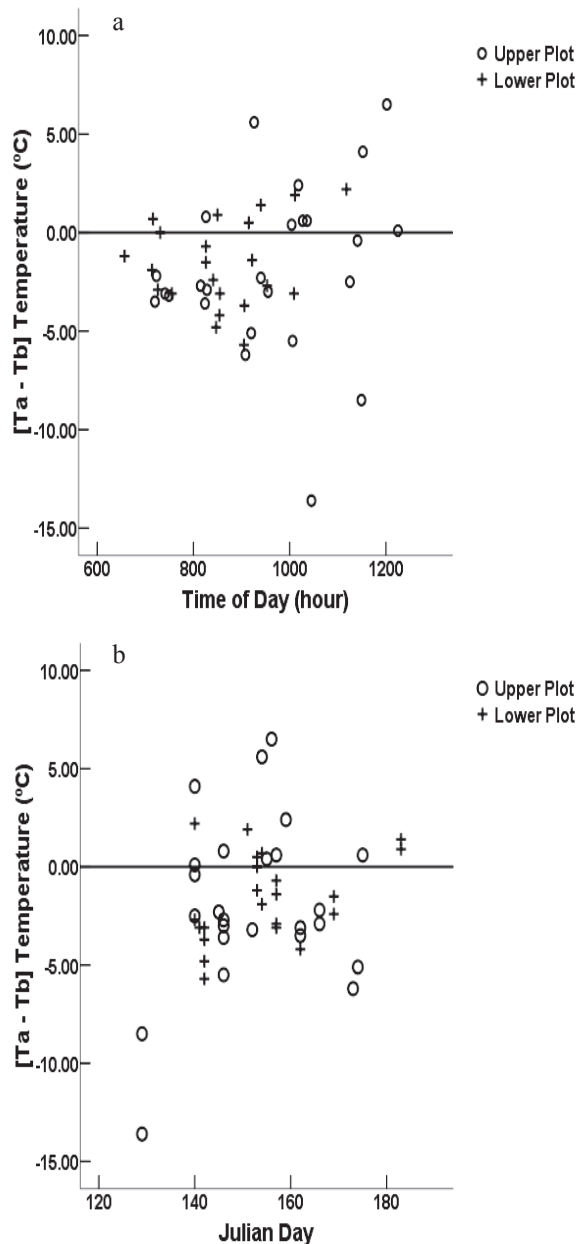


Figure 5 Difference between shaded air temperature and body temperature at the: (a) time and (b) date of capture in the Cima and Pumphouse plots. The reference line at 0°C indicates no difference between ambient and body temperature.

The MCL of all captured gravid female tortoises in Cima was 235.0 ± 4.9 mm ($N = 13$), and this was significantly greater than in Pumphouse (222.2 ± 3.8 mm; $N = 13$, $t_{24} = 2.1$, $P = 0.048$). Using just the observations for known clutch numbers, we found that Mojave desert

Table 3 Reproductive characteristics of *Gopherus agassizii* in Ivanpah Valley, 2003. Clutch sizes and egg volumes were determined from X-rays, and the percent depredated was determined from nest excavation

	Cima	Pumphouse
First clutch		
N	10	5
Clutch size (# eggs) [†]	3.5 ± 0.2	3.7 ± 0.4
Egg volume (mL) [‡]	71.7 ± 1.8	62.5 ± 3.0
Depredated (%)	100	0
Second clutch		
N	6	2
Clutch size (# eggs) [†]	3.1 ± 0.3	3.2 ± 0.6
Egg volume (mL) [‡]	61.3 ± 1.8	64.8 ± 2.7
Depredated (%)	100	0
Unknown clutch [†]		
N	3	8
Clutch size (# eggs)	3.3 ± 0.3	3.5 ± 0.3
Egg volume (mL)	67.8 ± 2.2	56.6 ± 2.0
Depredated (%)	0	25
Overall clutch size [‡]	3.3 ± 0.2	3.4 ± 0.2
Overall egg volume [‡]	$67.7 \pm 1.7^*$	60.3 ± 2.2
Overall Depredation level	$90.0 \pm 9.5^*$	11.0 ± 1.1

Data are means \pm 1 SEM; N = sample size (# clutches). [†]Could not determine clutch number (see Results). [‡]Estimated marginal means \pm 1 SEM. *Significantly greater $P < 0.05$.

tortoise MCL was not a significant covariate with clutch size (Wald $\chi_1^2 = 1.6$, $P > 0.05$) and there was no significant effect of plot (Table 3; Wald $\chi_1^2 = 0.2$, $P > 0.05$) or clutch number (Wald $\chi_1^2 = 1.0$, $P > 0.05$) on clutch size. There was, however, a significant interactive effect of plot and clutch number on egg volume (Wald $\chi_1^2 = 10.3$, $P = 0.001$), with the largest egg volumes in Cima first clutches (Table 3). MCL was positively correlated with egg volume ($+0.2$ mL, CI: 0.02–0.3; Wald $\chi_1^2 = 5.0$, $P = 0.025$).

We monitored 20 nests (11 nests in Cima and 9 in Pumphouse) from 17 different females. All nests were within burrows dug into coppice mounds either directly underneath or near *L. tridentata* or *A. dumosa*. Depredation levels were significantly higher in Cima where 9 out of 10 nests (1 unknown) were depredated as compared to 1 out of 9 nests (11%) in Pumphouse (Mann–Whitney $U = 9.5$, $P = 0.001$). In the former, depredation events were evenly distributed over 10 weeks of monitored incubation with approximately 1 observation of

nest depredation per week. The most common nest predators in Ivanpah Valley were *V. macrotis* as determined either by scat deposition, tracks, a lack of burrow opening enlargement, or some combination of these characteristics at the site of depredation. At least 1 nest in this study was probably depredated by either *Canis latrans* or *Taxidea taxus* because the burrow opening was greatly enlarged and there was substantial excavation of the burrow near the nest site. The hatching success in Cima was 40% for the only non-depredated nest, and $67.5 \pm 13.3\%$ in Pumphouse, where 7 out of 8 nests produced at least 1 hatchling and 1 nest was depredated.

DISCUSSION

Elevation differences in Mojave desert tortoise habitat within Ivanpah Valley corresponded to environmental differences in rainfall, perennial and ephemeral vegetation, and opportunities for surface activity. Pumphouse was more resource-poor in every respect, which corresponded to smaller-sized mature female desert tortoises, and smaller eggs (i.e. volume). However, the differences in thermal and food resources at the 2 plots did not create a divergence in the number of eggs produced or the number of clutches laid. Instead, depredation had the greatest effect on hatchling production in these tortoises.

Rainfall-based resource environments

Ivanpah Valley differences in rainfall were positively correlated with higher elevation, and this result has also previously been observed elsewhere in the Mojave (Beatley 1974b). Strong temporal variation in rainfall occurs in the Mojave because the El Niño-Southern Oscillation greatly increases winter rainfall in El Niño years (e.g. Henen *et al.* 1998).

Ephemeral vegetation generally tracks differences in rainfall. Herbaceous plant biomass: (i) is greatest at higher elevations in pluvial years (Beatley 1974b); (ii) increases in response to higher winter rainfall (Beatley 1969; Henen *et al.* 1998), but this is dependent on the timing of the rainfall (Beatley 1974b); and (iii) is extremely patchy with standard deviations often greater than the means in quadrat measurements (Nussear 2004). Perennial canopy cover and the density of perennial shrubs are generally greater in higher-elevation desert tortoise habitat (Beatley 1974a; Ehleringer & Mooney 1983), and active desert tortoises tend to se-

lect larger than average shrub species for shade (Nussear 2004). Shade quality of perennial vegetation was key to the microgeographic variation in surface activity and food resource acquisition of Ivanpah Valley Mojave desert tortoises.

Thermal ecology

Shade availability from perennial shrubs and succulents in Cima extended periods of daily potential surface activity for desert tortoises during afternoon hours. Otherwise, strict thermal constraints (e.g. lethal surface operative temperatures at midday) on desert tortoise microhabitat utilization necessitated the use of burrows (observed in this study; Nagy & Medica 1986; Zimmerman *et al.* 1994). Daily and seasonal patterns of operative temperatures and activity periods tracked temporal changes in incident solar radiation, which is also observed elsewhere in the desert tortoise range (Zimmerman *et al.* 1994; Averill-Murray *et al.* 2002), although monsoonal rainfall occasionally relaxes these constraints on desert tortoise surface activity in the summer (Nagy & Medica 1986; Henen *et al.* 1998).

Biotelemetry measurements supported operative temperature modeling-based estimates of surface activity in each plot during morning hours. Pumphouse tortoises had greater potential and actual morning surface activity, and this was likely due to the aspect and slope of the Pumphouse plot. Afternoon activity was not assessed directly in this study, but estimates of extended surface activity in Cima are supported by observations of desert tortoises active in the late afternoon and evening (Zimmerman *et al.* 1994), although activity in these periods may be curtailed relative to morning activity (Moulherat *et al.* 2014). Relative differences between plots in microhabitat utilization do not appear to be counteracted by differing thermoregulatory strategies. Desert tortoises generally do not defend precise body temperatures during surface activity (observed in this study; Zimmerman *et al.* 1994; Nussear 2004), nor do they appear to drastically alter their behavioral or thermoregulatory tactics in response to relative opportunities for surface activity in a particular habitat. Instead, large-bodied desert tortoises rely on thermal inertia to dampen heating rates, and this may be energetically favorable due to the patchy distribution of resources in their habitat and the energetic expense of moving their large mass (Zimmerman *et al.* 1994; Nussear 2004).

Reproductive success

With its resource-poor environment, Pumphouse mature female Mojave desert tortoises are among the smallest across their range (Mueller *et al.* 1998; Wallis *et al.* 1999), although these results should be viewed cautiously given the small sample sizes in this study that are common in desert tortoise demography studies (reviewed in Sieg 2010). Mature female desert tortoise body size tends to be positively correlated with reproductive output parameters such as clutch frequency, clutch size and total annual egg production (Averill-Murray & Klug 2000). Because female pelvic width is positively correlated with body size, variation in egg size, particularly egg width, may also be correlated with body size if upper-limit constraints on egg size are imposed by pelvic width (Congdon & Gibbons 1987). In Ivanpah Valley, mature female pelvic apertures were positively correlated with MCL (Cima: 51.6 ± 0.8 mm vs Pumphouse: 47.4 ± 1.1 mm), and we found a positive correlation between female size and egg size. However, Ivanpah Valley plot-related egg size differences only occurred in first clutches, and it is possible that the size differences were actually due to differential allocations of yolk and/or albumen regardless of adult female size. Greater accumulation of energetic and/or hydric resources in Cima females may have permitted larger allocations to reproductive output, and larger first-clutch eggs in Cima could confer an advantage in terms of neonate size, water and/or energy reserves (Wallace *et al.* 2006).

In an average rainfall year, we found desert tortoise egg clutch depredation to be positively correlated with rainfall. To our knowledge, only 1 other study has measured desert tortoise hatching success in relation to depredation. Bjurlin and Bissonette (2004) observed depredation levels of 47% in 1998 ($N = 17$) and 12% in 1999 ($N = 25$; Bjurlin & Bissonette 2004), but it remains unclear whether this result is tied primarily to environmental effects or researcher influence due to scent transfer in the first year of study (Bjurlin & Bissonette 2004). The population density of the primary desert tortoise egg predator, *V. macrotis*, positively covaries with rainfall (Dennis & Otten 2000), and this may be related to the influence of rain on small mammal prey species (Beatley 1969; Arjo *et al.* 2007) as well as the availability of water for the kit foxes themselves. Future study of

how variation in egg size and predator density relates to hatchling survivorship will be an important contribution to understanding exactly how finely tuned desert tortoise reproduction is to regional resource differences.

CONCLUSIONS

Regional ecosystem responses to enhanced resource availability are commonly observed in studies of life history variation in small desert ectothermic vertebrates (Dunham 1978; Grant & Dunham 1990), plants (Beatley 1974a; Cody 2000) and mammals (Beatley 1969; Dennis & Otten 2000). Typically, growth, survivorship and reproductive output are positively correlated with enhanced resource availability (Beatley 1969, 1974a; Dunham 1978; Grant & Dunham 1988, 1990), but increased juvenile and adult depredation risk can counteract these positive effects (Sears 2005). Our results for the large-bodied desert tortoise are consistent with these previous studies in indicating that differences in desert tortoise reproduction are tied to regional environmental heterogeneity. However, the role of adult phenotypic plasticity versus developmental plasticity in desert tortoise reproduction is still unknown. Conservation strategies designed to protect and recover desert organisms, such as Mojave desert tortoises, should: (i) utilize ecological information at appropriate scales; (ii) monitor reproductive success, which includes egg depredation; and (iii) carefully consider potential tradeoffs for population growth rates in both resource-rich and resource-poor habitat. These are important considerations, for example, in estimating vital rates for demographic analyses and in the assessment of new habitat for the translocation of desert tortoises, a mitigation technique for land-use impacts on desert tortoise native habitat.

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