Herpetological Conservation and Biology 10(3):839–849.
Submitted: 27 January 2015; Accepted: 16 September 2015; Published: 16 December 2015.

POPULATION STRUCTURE, SIZE, AND ACTIVITY PATTERNS OF *PHRYNOSOMA BLAINVILLII* IN THE SAN JOAQUIN DESERT OF CALIFORNIA

SUSAN M. HULT*[1,2] *AND DAVID J. GERMANO

Department of Biology, California State University, Bakersfield, California 93311, USA
[1]*Present address: 7356 394th Street, North Branch, Minnesota 55056, USA*
[2]*Corresponding author, email: incrediblehult@msn.com*

***Abstract*.—Blainville's Horned Lizard (*Phrynosoma blainvillii*) is in decline throughout much of its range including the San Joaquin Desert of California, USA, which has undergone significant habitat changes because of human activities. Knowledge of local distribution patterns and daily and seasonal activity levels is required for developing monitoring programs and successful habitat conservation and restoration programs. We performed a two-year baseline study beginning April 2009 in the San Joaquin Valley near Alpaugh, California. For adult *P. blainvillii,* we recorded a moderately skewed sex ratio of more males than females, but in young *P. blainvillii,* there were more females than males. Average snout-vent length (SVL) of adult females was 72.3 mm and average mass was 24.5 g, both of which were significantly larger than that of adult males (68.8 mm SVL and 20.3 g). Adult horned lizards were most active in April and May whereas we only found young horned lizards in August and September. The peak times of daily aboveground activity changed with the seasons. In the spring, activity hours of lizards peaked at 0900–1100, in summer, 0900–1000, and in fall, 0900–1300. All age classes of *P. blainvillii* were most often above ground and active at surface temperatures of 28–34 °C. These data further our knowledge of this declining species and can help land stewards manage this species in the San Joaquin Desert.**

Key Words.—Blainville's Horned Lizard; conservation; horned lizards; management; mass; snout-vent length

INTRODUCTION

Activity patterns and population structure are important biological characteristics for any animal species, and obtaining information on these characteristics is important to understanding the ecological role of the species. This type of information is lacking in many animal species due to their elusiveness, small population numbers, inaccessible habitats, or camouflage that make them difficult to observe. Thus, we know less about basic biological characteristics of cryptic species, such as horned lizards (*Phrynosoma* spp.), than we know about the same characteristics for more conspicuous species. Horned lizards rely on their superior ability to blend into their environment and have a tendency to remain motionless rather than flee (Pianka and Parker 1975; Wone and Beauchamp 1995; Sherbrooke 2003).

This lack of knowledge about basic biology is especially problematic for Blainville’s Horned Lizard (*P. blainvillii;* Fig. 1), formerly Coast Horned Lizard (*P. coronatum* or *P. coronatum frontale)*, because populations have experienced severe declines throughout their range leaving some locales of formerly abundant populations nearly or completely absent of lizards (Goldberg 1983; Jennings 1987; Jennings and Hayes 1994; Fisher et al. 2002; Stebbins 2003). The species is listed as a California Species of Special Concern (California Department of Fish and Game. 2011. Available from http:// www.dfg.gov./biogeodata/cnddb/pdfs/SPAnimals.pdf_[Accessed 2 July 2015]) and a Bureau of Land Management Sensitive Species (Bureau of Land Management. 2010. California-BLM Sensitive Animals. Available from http://www.blm.gov./ca/st/en/prog/wildlife.html. [Accessed 2 July 2015]). The historic range of *P. blainvillii* extends from as far north as the edges of the Sacramento Valley in Butte County, California, south to the northwestern tip of the Pacific coast of Baja California, west along the coast to the San Francisco Bay, and as far east as the western side of the Sierra Nevada mountains and deserts into southern California (Stebbins 2003; Montanucci 2004; Leaché et. al 2009). *Phrynosoma blainvillii* are found in a variety of habitats such as semiarid mountains, chaparral, oak woodland, coniferous forest, foothills, and valleys ranging in elevations from sea level to about 1800 m (Smith 1946; Sherbrooke 2003; Stebbins 2003; Leaché et al. 2009).

Despite their ability to reside in a variety of habitats, *P. blainvillii* face a number of factors that are contributing to their population declines. Habitat degradation and loss, human population growth and urbanization, and the introduction of exotic species into suitable lizard habitat have all had negative impacts on

FIGURE 1. Adult Blainville's Horned Lizards (*Phrynosoma blainvillii*; top) and hatchlings (bottom) from the San Joaquin Desert of California, USA. (Photographed by Susan Hult).

P. blainvillii populations (Goldberg 1983; Jennings 1987; Jennings and Hayes 1994; Stebbins 2003; Audsley et al. 2006). Also, pesticides and the introduction of the non-native Argentine Ant (*Linepithema humile*; Knight and Rust 1990; Jennings and Hayes 1994; Fisher et al. 2002; Suarez et al. 2000; Suarez and Case 2002) have limited the number of native harvester ants (*Pogonomyrmex* and *Messor* spp.; Erickson 1971; Pimentel 1995), the preferred prey of horned lizards (Sherbrooke 2003; Stebbins 2003).

Unlike the Texas Horned Lizard, *P. cornutum*, there have been few studies published on the general ecology of *P. blainvillii* (Smith 1946; Milne and Milne 1950; Jennings and Hayes 1994). Besides a few studies in the southern portion of their range (Goldberg 1983; Hager and Brattstrom 1997; Suarez et al. 1998; Fisher et al. 2002; Montanucci 2004), there has been only one behavioral (Tollestrup 1981) and one ecological (Gerson 2011) study in the San Joaquin Valley. Additional localized demographic and ecological data for *P. blainvillii* from the San Joaquin Valley likely will help clarify conservation needs for this species.

Activity patterns are an important characteristic of horned lizard behavior and ecology that can reveal how the lizards relate to their surrounding environment (Adolph and Porter 1993). Because horned lizards are ectothermic, their body temperature is essentially determined by air and substrate temperatures. One of the principal means by which horned lizards thermoregulate is by modifying their daily and seasonal activity patterns (Smith 1946; Heath 1965; Sherbrooke 2003; Stebbins 2003). In this paper, we present

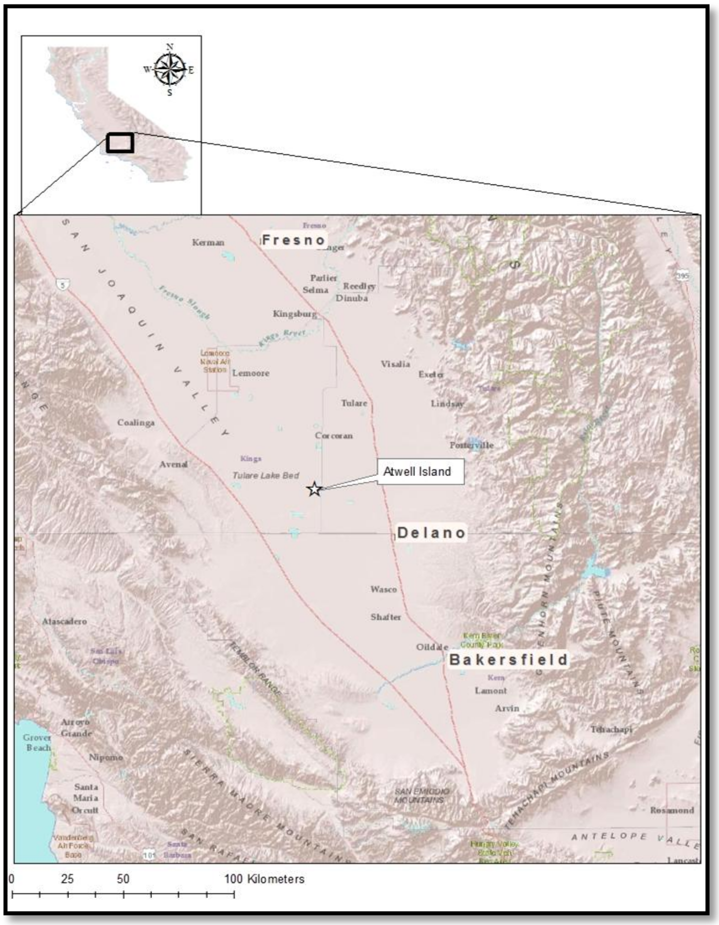

FIGURE 2. Map of the study site, Atwell Island, in Kings County in the San Joaquin Desert of California, USA. (Map created by Susan Hult).

information on activity patterns, thermal ecology, and population structure, which can be essential information to land managers for making decisions on land use and conservation practices within *P. blainvillii* habitat. In a companion paper, we present data on habitat use and home ranges (Hult and Germano 2015) that can help predict presence or absence of *P. blainvillii* in the San Joaquin Desert of the valley and aid land managers in acquiring, maintaining, or restoring critical habitat.

MATERIALS AND METHODS

Study sites.—We conducted research in the Tulare Basin of the San Joaquin Desert of California (Germano et al. 2011). The study site was specifically in southwestern Tulare County, 1.6 km south of the town of Alpaugh at Atwell Island on Bureau of Land Management (BLM) land (Fig. 2). The San Joaquin Desert covers about two thirds of the San Joaquin Valley and has a Mediterranean climate of hot, dry summers and cool, moist winters (Germano et al. 2011). July is the warmest and driest month with an average high temperature of 37.8° C, while January is the coolest month with an average high temperature of 13.8° C (Western Regional Climate Center. 2012. Cooperative climatological data summaries. NOAA cooperative stations-temperature and precipitations. C. California and S. California. Available from http://www.wrcc.dri.edu/climatedata/climsum [Accessed 2 July 2015]). Most of the average annual rainfall of 183 mm falls December through March (Western Regional Climate Center. 2012. *op. cit*.). We used two study locations on the Atwell Island Project, administered by the BLM, to study the natural history of *P. blainvillii*.

At Location 1 (pasture), we surveyed for lizards in a fenced 156 ha parcel that had been grazed seasonally by cattle for many years. The dominant shrubs within the pasture were Bush Seepweed (*Suaeda moquinii*), Alkali Heath (*Frankenia salina*), Goldenbush (*Isocoma acradenia*), and a few Valley Saltbush (*Atriplex polycarpa*). The forbs present included Spikeweed (*Centromadia pungens*), goldfields (*Lasthenia californica* and *L. minor*), Fiddleneck (*Amsinkia menziesii*), and Broadleaf Filaree (*Erodium botrys*), while Saltgrass (*Distichlis spicata*) and non-native annual grasses (*Bromus* spp.) were the dominant grasses present. Throughout the pasture, there were many large open spaces with little or no vegetative structure due to cattle grazing, the natural senescence of herbaceous vegetation as the season became hotter and drier, and an abundance of soil mounds created mostly by Heermann's Kangaroo Rats (*Dipodomys heermanni*). Sympatric lizards in the pasture included the California Whiptail (*Aspidoscelis tigris munda*) and Western Side-blotched Lizard (*Uta stansburiana elegans*). The overall topography was mostly level at an elevation range of 61–66 m above sea level. The land surrounding the pasture was formerly cultivated fields that were fallow or had undergone habitat restoration treatments in the years preceding our study. Unlike the immediately surrounding areas, the pasture had not undergone cultivation or significant substrate disturbance, such as canal or road development, deep disk plowing, or laser leveling; thus, this study site consists of exactly the type of habitat most in need of study and preservation for this species (Jennings and Hayes 1994). Based on visual estimates and aerial imagery, the overall habitat composition within the pasture was 30% dense herbaceous vegetation, 25% bare ground, 20% shrubs, 15% sparse herbaceous vegetation, and 10% medium dense herbaceous vegetation. The management practice at the time of our study was seasonal cattle grazing.

The second location (Location 2) was a 120 ha area adjacent to and southwest of the pasture, but separated by an unlined irrigation (Poso) canal. This area was not fenced in and we delineated the boundary based on soil type, vegetative communities, roads, and reports of historical sightings of horned lizards from locals. This location had been cultivated with grain crops until the late 1980s and had been fallow since that time. Despite the agricultural activity, Location 2 had also never undergone laser leveling or deep disk plowing (U.S. Department of the Interior, unpubl. report). There was never a grazing regime at this location with the exception of an occasional trespass of grazing sheep. Because of the decades of inactivity, the vegetative community and structure in Location 2 were dominated by dense areas of non-native annual grasses (*Bromus* spp.) with fewer scattered patches of shrubs and forbs. An unpaved and rarely used road bisected Location 2 and this was the main source of open space and bare ground. Aside from the road, a few rodent burrows scattered throughout the location provided areas of bare ground and promoted sparse herbaceous vegetation. There were narrow trails formed by Desert Cottontails (*Sylvilagus auduboni*), Black-tailed Jackrabbits (*Lepus californicus*), and Heermann's Kangaroo Rats in the dense grass. The Western Side-blotched Lizard and the California Whiptail were the only other lizard species we observed at this location. Based on visual estimates and aerial imagery, the overall habitat in this location as 75% dense grassland, 10% bare ground, 5% shrubs, 5% medium dense herbaceous vegetation, and < 5% sparse herbaceous vegetation.

Field data collection.—We conducted our research over two seasons beginning 20 April 2009 and continuing through 15 November 2010. In the first season, we focused our search times between 0800 and 1500 to coincide with the peak activity period of most diurnal lizards (Heath 1965; Pianka and Parker 1975; Hager and Brattstrom 1997). In the second season, 2010, we increased our search times to include more afternoon and evening encounters to determine if *P. blainvillii* uses additional times for activity.

We located lizards using meandering transects and chance encounters 5–6 d a week. Meandering transects were accomplished by walking linear pathways within the entire boundary of both locations using various landmarks arbitrarily chosen as end points, such as a utility pole or fence posts. We made searches during all weather conditions except for rainfall, which made the dirt roads leading to our study site impassible. We captured lizards by hand and recorded the date, time of day, and the capture location using Global Positioning System (GPS) in the WGS 1984 coordinate system obtained by a Magellan MobileMapper CX GPS Unit (Magellan, Santa Clara, California, USA). We recorded the ambient air temperature at chest height and wind speed using a Kestrel 3000 series pocket weather meter (Nielsen-Kellerman, Boothwyn, Pennsylvania, USA). At the location we caught a lizard, we measured surface temperature by propping a Max/Min digital thermometer (Stock # 89102, Forestry Suppliers, Inc., Jackson, Mississippi, USA) approximately 2 cm off the surface and shading it from direct sunlight with our bodies. Once we finished data collection, we returned each lizard to its exact capture location. We designated spring as the months of April and May, summer as June, July, and August, and fall as September, October, and November.

Demography and morphometrics.—We recorded snout-vent length (SVL) to the nearest 1 mm using a clear plastic metric ruler and mass to nearest 1 g using a 10 g or 60 g spring scale. We determined the sex of the lizard based on the presence of enlarged post-anal scales that are indicative of males (Tinkham 1951; Powell and Russell 1985; Sherbrooke 2003). To permanently mark lizards > 55 g, we injected a 12 mm Passive Integrated Transponder (PIT) tag (Biomark Inc., Boise, Idaho, USA) subcutaneously on the left margin of the ventral side using a 12-gauge needle. We closed the small hole left by the needle by gently pinching the margin of the hole together and then applying a drop of cyanoacrylate glue.

TABLE 1. Sex, age class, and descriptive statistics of snout-vent length (SVL) and body mass of *Phrynosoma blainvillii* captured April-November in 2009 and 2010 in the San Joaquin Desert in Tulare and Kings counties, California, USA. Recaptures (Recap.) not included in descriptive statistics.

					SVL (mm)			Body Mass (g)		
Year	Age	Sex	n	No. Recap.	Mean	SE	Range	Mean	SE	Range
2009	Adult	F	19	1	72.3	1.3	63–85	24.2	1.3	14.5–32.0
	Adult	M	26	4	68.6	0.74	63–75	19.9	0.77	15.0–26.5
	Young	F	62	6	46.5	1.5	29–62	7.5	0.6	1.5–15.0
	Young	M	39	4	47.7	1.44	31–62	7.7	0.72	2.5–18.5
2010	Adult	F	12	1	72.2	1.8	63–81	25.0	2.2	14.0–38.0
	Adult	M	17	3	69.1	1.4	63–82	21.0	0.93	16.5–28.0
	Young	F	39	0	39.7	1.5	26–61	4.9	0.56	1.4–13.5
	Young	M	40	1	42.1	1.3	26–57	5.7	0.5	1.0–13.5

We recorded the age class for each lizard as either adult or young. Previous studies have used a broad range of minimum SVL (61–75 mm) to classify *P. blainvillii* as adults (Howard 1974; Pianka and Parker 1975; Goldberg 1983; Hager and Brattstrom 1997; Gerson 2011). A dissected specimen from southern California was sexually mature at 61 mm SVL (Howard 1974) and a female closer to our study site had eggs at 65 mm SVL (Gerson 2011). We classified male and female lizards ≥ 63 mm SVL as adults. Unlike minimum adult SVL size, there is more consensus as to the size of hatchlings: 24–31 mm (Shaw 1952; Howard 1974; Goldberg 1983; Hager 1992).

Activity.—In 2009, we based activity levels on the frequency of chance encounters during our meandering transect surveys. Because this type of sampling done on an extremely cryptic species such as *P. blainvillii* inherently involves observer bias based on visibility and our ability to spot them, we categorized only two activity levels: Active, meaning fully exposed and eating, mating, or sunning, and Seeking Shade, meaning we detected the lizard under shrubs or in patches of herbaceous vegetation. In addition to the data collected in 2009, we used activity data gathered in 2010 from a home range study using radio-telemetry (Hult and Germano 2015). We used the activity data from the 155 observations we recorded from seven lizards, which provided us with a comparative data set of activity of lizards unaffected by problems of visibility when finding lizards by sight only, thus eliminating observer bias (See Hult and Germano 2015 for radio telemetry information).

Statistical analysis.—We compared average SVL of males to females using one-way ANOVA. Because the data on mass did not have equal variances, we compared the mass of males to females using the Mann-Whitney test. We used Chi-square with Yates correction to compare sex ratios of adults and young. To determine if adult and young lizards had significantly different sex ratios between years or in both years combined, we used the Chi-square goodness of fit test for observed counts. We compared size distributions from 2009 to 2010 using the Kolmogorov-Smirnov test by categorizing lizards by 5 mm SVL increments from 25–90 mm SVL.

To determine if lizards shifted their peak times of aboveground activity in the first part of the day according to season, we compared hourly activity times from 0800 to 1300 in spring, summer, and fall using a 6 x 3 Fisher exact contingency table test. To elucidate significant differences in peak times of aboveground activity between seasons, we used a 6 x 2 Fisher exact contingency table. To determine if young lizards are active at different surface temperatures compared to adults, we compared the activity periods of young and adult lizards against surface temperatures using a Kolmogorov-Smirnov test. We performed the same tests separately on the data from our telemetered lizards to provide an unbiased test of the results from our observations on non-telemetered lizards. For all tests, $\alpha = 0.05$.

RESULTS

Demography and morphometrics.—In 2009 we made 146 observations of 131 unique individual *P. blainvillii* (Table 1). Of those unique individuals, 30.3% (n = 40) were adults. The ratio of females to males was 1:1.2, which was not significantly different from 1:1 ($\chi^2 = 0.225$, df = 1, $P = 0.635$). The young lizards found in 2009 exhibited a significantly skewed sex ratio of 1:0.57, females (n = 56) to males (n = 35; $\chi^2 = 4.396$, df = 1, $P = 0.036$). In 2010, we made 112 observations with 107 of those being unique individuals (Table 1). Adults comprised 23.4% (n = 25) of the total individual lizards with a female (n = 11) to male (n = 14) sex ratio of 1:1.3, which was not significantly different from 1:1 ($\chi^2 = 0.160$, df = 1, $P = 0.689$). In 2010 the sex ratio of young lizards was not skewed to either sex as we found

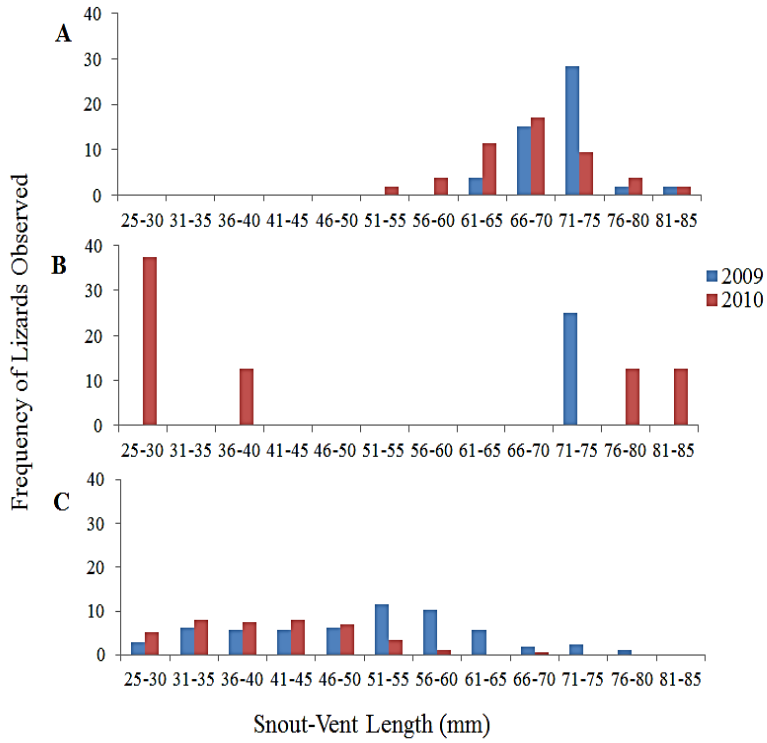

FIGURE 3. Frequency distributions of snout-vent lengths of individual *Phrynosoma blainvillii* captured April to November 2009 and 2010 at the Atwell Island study sites in the San Joaquin Desert of California, USA. A) April and May, B) June through August, and C) September through November. Data from recaptured lizards was not included in this analysis.

equal numbers of females and males (n = 39 each sex). We found four young lizards for which we could not determine sex. The average adult female SVL was 72.3 mm (± 5.6 SD) with an average mass of 24.5 g (± 6.14 SD), while the average adult male SVL was 68.8 mm (± 4.1 SD) with an average mass of 20.3 g (± 3.5 SD). Average adult female SVL was larger than that of adult males ($F_{1,63}$ = 8.50, P = 0.005), as was mass (W = 1186.5, P = 0.001). The smallest SVL of all lizards encountered was 26 mm and the largest SVL was a female at 85 mm (Table 1).

Activity.—We encountered *P. blainvillii* at our study site 5 April to 11 November across the two years. The highest level of aboveground activity exhibited by adults occurred in late April and May, with a sharp decrease in activity beginning in June and lasting throughout the remainder of the season (Fig. 3). Juveniles and hatchlings were most active in August and September (Fig. 3). Hatchlings (25–31 mm SVL) began to appear in July, and we continued to find them into early November, suggesting lizards laid eggs from April until early September based upon a 60-d incubation period (Howard 1974; Zeiner et al. 1988; Jennings and Hayes 1994). By the middle of November, we no longer encountered lizards of any age class.

Peak activity periods differed significantly among the seasons (Fisher Exact Test, P < 0.001; Fig. 4). In the spring, aboveground activity peaked for two hours from 0900–1100. This was significantly different from summer (Fisher Exact Test, P = 0.026) in which peak activity was reduced to one hour from 0900–1000. In the fall, *P. blainvillii*'s activity peaked for a 4-h period between 0900–1300 and was significantly different from that of summer (Fisher Exact Test, P < 0.001) and spring (Fisher Exact Test, P < 0.001).

We recorded P. *blainvillii* at surface temperatures ranging from 19–41° C, but they were most often active at surface temperatures between 28–34° C throughout the year (Fig. 5). The corresponding range of ambient air temperature at chest height during their peak surface temperature activity was 26–30° C. We did not find a significant differences in surface temperatures at which adults and juveniles were active (D = 0.122, P = 0.682). The data from the seven lizards we radio tracked in 2010 gave the same pattern for above-ground activity (D = 0.273, P = 0.736; Fig. 4) and for surface temperature when active (D = 0.385, P = 0.226; Fig. 5) as found for non-telemetered lizards. Additionally, the data from the telemetered lizards revealed that when surface temperatures reached approximately 33° C, lizards began

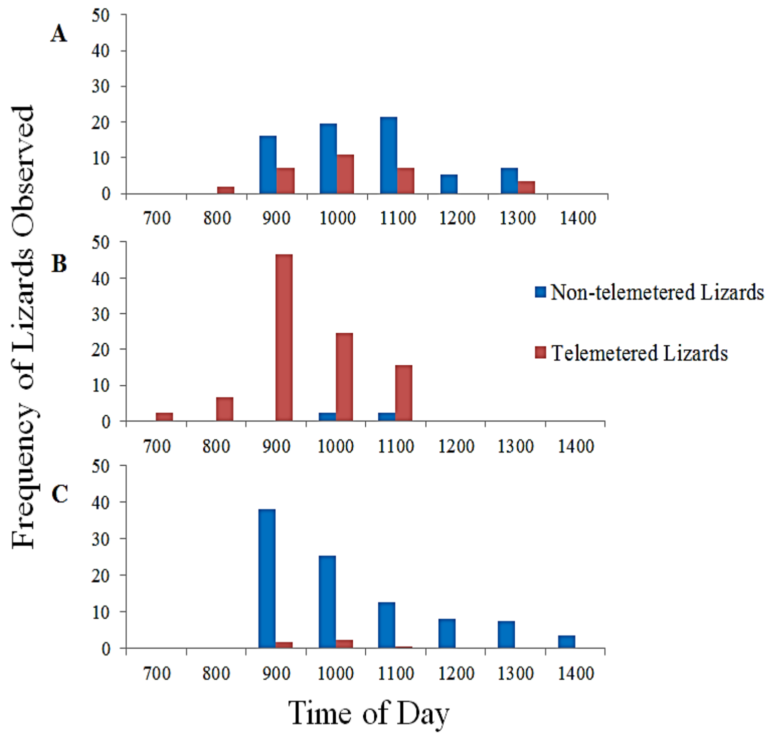

FIGURE 4. Frequency of sightings of *Phrynosoma blainvillii* when above ground by time of day at the Atwell Island study site in the San Joaquin Desert of California, USA: A) April and May, B) June and July, and C) September and November. In 2010, we fitted several lizards with radio-transmitters, which allowed us to use telemetry to locate lizards in an unbiased fashion and served as a comparison to lizards found without telemetry.

to seek cover in burrows. When surface temperatures were < 24° C, lizards tended to bury themselves in sand.

DISCUSSION

Horned lizards are atypical among most vertebrates in that for nearly all *Phrynosoma* species, females are significantly larger than males (Pianka and Parker 1975; Montgomery et al. 2003; Sherbrooke 2003; Lahti et al. 2010; Gerson 2011). This is what we found for *P. blainvillii* on our study site in the San Joaquin Desert. Our average adult female SVL of 72.3 mm and average adult male SVL of 68.8 mm appeared to be comparable to the average adult female SVL of 75.1 mm (n = 29) and average adult male SVL of 69.8 mm (n = 28) to another population of *P. blainvillii* in the northern San Joaquin Valley in Merced County (Gerson 2011), approximately 241 km northwest of our study site. However, the differences were significant for females (one-sample t-test, $t = 2.69$, df = 28, $P = 0.012$) but not for males ($t = 1.46$, df = 35, $P = 0.154$). Despite the significant differences in female size, the adult lizards from the San Joaquin Desert populations were more similar in size to each other than either was to a population of adult lizards in southern California, near Moreno Valley, 362 km southwest of our study site (Hager 1992). In this southern California population, Hager (1992) reported an average SVL of adult females of 103.0 mm (n = 5) and an adult male SVL of 91.6 mm (n = 8). Average SVL of adult males and females at our site were significantly smaller than those in southern California (one-sample t-tests, males: $t = 33.4$, df = 35, $P < 0.001$; females: $t = 29.6$, df = 28, P <, 0.001). When the lizards of the San Joaquin Valley and the lizards of southern California were considered separate subspecies, this geographic difference in SVL length had been reported in previous studies as one of the morphological characteristics that were used to differentiate the populations: *P. c. blainvillii* in the south and *P. c. coronatum* in the north (Smith 1946; Jennings and Hayes 1994). Similar latitudinal differences in adult SVL size have been noted in other *Phrynosoma* species as well (Montgomery et al. 2003; Endriss et al. 2007). The tendency for smaller SVL to be in higher latitudes may be the consequence of shorter seasonal activity periods and a reduction in available energy to produce primary productivity resulting in less resource availability, or some other unrecognized factor or combination of factors (Montgomery et al. 2003). Whereas adult SVL sizes at our site differed from other populations of *P. blainvillii* on a spatial scale, the range of hatchling size of 25–31 mm SVL (Shaw 1952; Howard 1974; Hager

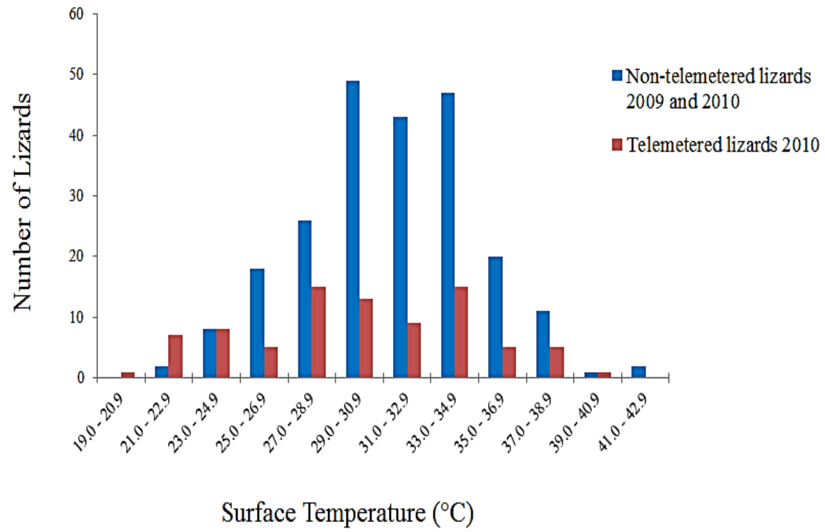

FIGURE 5. Number of lizards observed and the substrate surface temperatures at which *Phrynosoma blainvillii* were active at the Atwell Island site in the San Joaquin Desert of California, USA. In 2010, we fitted several lizards with radio-transmitters, which allowed us to use telemetry to locate lizards in an unbiased fashion and served as a comparison to lizards found without telemetry.

1992; Gerson 2011) is relatively consistent across latitudes and the smallest lizards we found fell within that range.

Sex ratios in adult horned lizards do not appear to be consistent. The 1:1.2 female to male adult sex ratio from the *P. blainvillii* population at our site was not significantly skewed. Other authors have reported similar findings (Pianka and Parker 1975; Turner and Medica 1982; Henke 2003; Montgomery and Mackessy 2003; Gerson 2011) but others have reported a skewed adult sex ratio (Tollestrup 1981; Moeller et. al 2005). Sex ratios in non-adult lizards from our study were skewed in 2009 (toward females) but not in 2010. A certain amount of circumspection should be employed when interpreting sex ratio data. Certain factors such as sample size, collecting bias, or seasonally different social behaviors of males and females can affect results (Sherbrooke 2002; Montgomery and Mackessy 2003). In our study, we had a small sample size of adults (40 in 2009 and 25 in 2010).

Phrynosoma blainvillii at our study sites had seasonal activity patterns that closely approximated the seasonal activity patterns reported for other *P. blainvillii* populations. The emergence from winter dormancy in mid-April and continued activity into November is characteristic of this species (Jennings and Hayes 1994; Hager and Brattstrom 1997; Burrow et al. 2001), although the beginning and end of seasonal activity can vary by individual, geography, and yearly climate variables (Jennings and Hayes 1994; Hager and Brattstrom 1997). The differences in the seasonal activity by age-class that we observed are congruent with other populations of *P. blainvillii* as well. Hager and Brattstrom (1997) found that adults were active from April-July with peak activity in June and mostly not found after July. Hatchlings and young were found from July-October. This age-class activity pattern was also reported in a closely related species, *P. platyrhinos,* in Utah (Pianka and Parker 1975) and in *P. solare* from Arizona (Parker 1971). We found the same pattern for *P. blainvillii* at our site, with the exception of seeing young lizards into early November.

Horned lizards modify their daily surface activity in response to thermal variations (Smith 1946; Heath 1965; Pianka and Parker 1975; Hager and Brattstrom 1997; Sherbrooke 2003). Many species, including *P. blainvillii*, have been reported to have a daily unimodal activity pattern in the cooler months of spring and fall. That is, once they begin their daily activity, they remain steadily active throughout the day (Heath 1965; Pianka and Parker 1975; Hager and Brattstrom 1997; Montgomery and Mackessy 2003). In contrast, *P. blainvillii* at our site did not remain steadily active throughout the morning in the spring and fall; rather, they had periods where activity was noticeably higher for a few hours then dropped off considerably by midday. Furthermore, their specific hours of activity shifted with the seasons. In the spring, the lizards were out earlier in the morning and for a shorter period than in the fall. During the hot summer months, surface activity mirrored that of other desert-dwelling species in that *P. blainvillii* were rarely active (Pianka and Parker 1975; Zimmerman et al. 1994; Hager and Brattstrom 1997; Montgomery and Mackessy 2003). While the apparently limited daily activity is atypical of *P. blainvillii*, the shift in seasonal activity patterns is consistent with previous studies (Smith 1946; Heath 1965; Pianka and Parker 1975; Hager and Brattstrom 1997). The reason our *P. blainvillii* maintained peak periods of daily activity even in the cooler months is unclear, but it is not likely due to observer bias given that the data collected from the telemetered lizards revealed the same limited hours of daily activity throughout the year, regardless of season.

Because horned lizards are ectotherms, they rely on their external environment to regulate their internal body temperature. They thermoregulate by basking, burrowing, seeking the shade of vertical objects, or retreating into rodent burrows (Heath 1965; Adolph and Porter 1993; Burrow et al. 2001). We found that surface temperatures significantly affected the behavioral thermoregulatory pattern of *P. blainvillii* at our study sites in the San Joaquin Valley. At surface temperatures of 28–34° C, lizards of all age classes were most active. Additionally, the data from the telemetered lizards revealed that at surface temperatures approximately 35° C and above, lizards tended to seek cover in a burrow and at surface temperatures 24° C and below, they tended to bury themselves in sand. The use of burrows to escape midday heat was also observed in *P. mcallii* in southern California near the Mexican border (Wone and Beauchamp 2003). At substrate temperatures that exceeded 49° C, all telemetered *P. mcallii* sought refuge in burrows (Wone and Beauchamp 2003).

Although some quantitative studies of demography, morphometrics, and activity patterns of *P. blainvillii* exist (Goldberg 1983; Hager and Brattstrom 1997; Suarez et al. 1998; Fisher et al. 2002; Montanucci 2004), only a few papers have discussed variations of these natural history aspects of *P. blainvillii* in the San Joaquin Valley (Tollestrup 1981; Gerson 2011). Because *P. blainvillii* occurs in a variety of habitat types, being knowledgeable of these life-history traits as they pertain to the particular locale of the population of concern is critical. For example, our study revealed differences between peak daily activity times, dates when active, and morphometrics of *P. blainvillii* in the San Joaquin Valley and those of *P. blainvillii* in southern California. Land managers can use this information to conduct presence/absence surveys and schedule maintenance and other activities to minimize the impacts on *P. blainvillii*, and to educate recreationists such as bikers and off-road vehicle users to the times that *P. blainvillii* are above ground and vulnerable in areas of open habitat such as roads and trails.

Considering that human population growth in the Central Valley is predicted to occur at one of the fastest rates of any region in California (California Department of Finance. 2012. Interim population projections for California and its counties 2010-2050. Available from http://www.dof.ca.gov/research/demographic/reports/projections/P-1/. [Accessed 2 July 2015]), habitat destruction, degradation, and fragmentation can reasonably be expected to continue. The present study provides baseline field data on demographics and activity patterns that can help create local land management strategies and help land managers to evaluate the impacts of continued surface disturbances, as well as contribute to the larger effort to monitor *P. blainvillii* populations throughout its range.

Acknowledgments.—We would like to thank Dana Gasper and Teresa O'Keefe for the many hours of field assistance they provided, resulting in large amounts of valuable data for this study. We would also like to acknowledge Sue Lynch, DVM, who provided advice on the use of adhesive when repairing the hole left by the PIT tag needle to ensure minimal risk of toxicity to the lizards. We are grateful to Jack Mitchell and Steve Laymon who provided valuable information on all things Atwell and to Denis Kearns for giving terminology advice on all things botany. This study would not have been possible without the Bureau of Land Management's (BLM) Student Career Experience Program and without the support of BLM supervisors Steve Larson and John Skibinski as well as many BLM colleagues. We thank Steve Laymon and Brandon Pratt for reading an earlier version of this manuscript. All work was carried out under the California Fish and Wildlife Scientific Permit SC-10049 and with the approval of the Institutional Animal Care and Use Committee of California State University, Bakersfield.

LITERATURE CITED

Adolph, S.C., and W.P. Porter. 1993. Temperature, activity, and lizard life histories. The American Naturalist 142:273–295.

Audsley, B.W., C.E. Bock, Z.F. Jones, J.H. Bock, and H.M. Smith. 2006. Lizard abundance in an exurban southwestern savanna, and the possible importance of roadrunner predation. American Midland Naturalist 155:395–401.

Burrow, A.L., R.T. Kazmaier, E.C. Hellgren, and D.C. Ruthven, III. 2001. Microhabitat selection by Texas Horned Lizards in southern Texas. The Journal of Wildlife Management 65:645–652.

Endriss, D.A., E.C. Hellgren, S.F. Fox, and R.W. Moody. 2007. Demography of an urban population of the Texas Horned Lizard (*Phrynosoma cornutum*) in central Oklahoma. Herpetologica 63:320–331.

Erickson, J.M. 1971. The displacement of native ant species by the introduced Argentine Ant *Iridomyrmex humilis mayr*. Psyche 78:257–266.

Fisher, R.N., A.W. Suarez, and T.J. Case. 2002. Spatial patterns in the abundance of the Coastal Horned Lizard. Conservation Biology 16:205–215.

Germano, D.J., G.B. Rathbun, L.R. Saslaw, B.L. Cypher, E.A. Cypher, and L.M. Vredenburgh. 2011. The San Joaquin Desert of California: ecologically misunderstood and overlooked. Natural Areas Journal 31:138–147.

Gerson, M.M. 2011. Population status and habitat affinities of the Blainville's Horned Lizard (*Phrynosoma blainvillii*) at a site in the northern San Joaquin Valley, California, USA. Herpetological Conservation and Biology 6:228–236.

Goldberg, S.R. 1983. Reproduction of the Coast Horned Lizard, *Phrynosoma coronatum*, in southern California. The Southwestern Naturalist 28:478–479.

Hager, S.B. 1992. Surface activity, movement, and home range of the San Diego Horned Lizard, *Phrynosoma coronatum blainvillii*. M.S. Thesis, California State University Fullerton, Fullerton, California, USA. 126 p.

Hager, S.B., and B.H. Brattstrom. 1997. Surface activity of the San Diego Horned Lizard *Phrynosoma coronatum blainvillii*. The Southwestern Naturalist 42:339–344.

Heath, J.E. 1965. Temperature regulation and diurnal activity in horned lizards. University of California Publications in Zoology 64:97–136.

Henke, S.E. 2003. Baseline survey of Texas Horned Lizards, *Phrynosoma cornutum*, in Texas. The Southwestern Naturalist 48:278–282.

Howard, C.W. 1974. Comparative reproductive ecology of horned lizards (Genus *Phrynosoma*) in Southwestern United States and Mexico. Journal of the Arizona Academy of Science 9:108–116.

Hult, S.M., and D.J. Germano. 2015. Habitat use and home range of *Phrynosoma blainvillii* in the southern San Joaquin Desert of California. Herpetological Conservation and Biology 10:850–863.

Jennings, M.R. 1987. Impact of the curio trade for San Diego Horned Lizards (*Phrynosoma coronatum blainvillii*) in the Los Angeles basin, California: 1885–1930. Journal of Herpetology 21:356–358.

Jennings, M.R., and M.P. Hayes. 1994. Amphibian and Reptile Species of Special Concern in California. Final Report. Contract Number 8023. California Department of Fish and Game Inland Fisheries Division, Rancho Cordova, California, USA.

Knight, R.L., and M.K. Rust. 1990. The urban ants of California with distribution notes of imported species. Southwestern Entomologist 15:167–178.

Lahti, M.E., D.D. Beck, and T.R. Cottrell. 2010. Ecology of the Pygmy Short-Horned Lizard (*Phrynosoma [Tapaja] douglasii*) in Washington. Northwestern Naturalist 91:134–144.

Leaché, A.D., M.S. Koo, C.L. Spencer, T.J. Papenfuss, R.N. Fisher, and J.A. McGuire. 2009. Quantifying ecological, morphological, and genetic variation to delimit species in the Coast Horned Lizard species complex (*Phrynosoma*). Proceedings of the National Academy of Sciences 106:12418–12423.

Milne, L.J., and M.J. Milne. 1950. Notes on the behavior of horned toads. American Midland Naturalist 44:720–741.

Moeller, B.A., and E.C. Hellegren, D.C. Ruthven III, R.T. Kazmaier, and D.R. Synatzske. 2005. Temporal differences in activity patterns of male and female Texas Horned Lizards (*Phrynosoma cornutum*) in southern Texas. Journal of Herpetology 39:336-339.

Montanucci, R.R. 2004. Geographic variation in *Phrynosoma coronatum* (Lacertilia, Phrynosomatidae): further evidence for a peninsular archipelago. Herpetologica 60:117–139.

Montgomery, C.E., and S.P. Mackessy. 2003. Natural history of the Texas Horned Lizard, *Phrynosoma cornutum* (Phrynosomatidae), in southeastern Colorado. The Southwestern Naturalist 48:111–118.

Montgomery, C.E., S.P. Mackessy, and J.C. Moore. 2003. Body size variation in the Texas Horned Lizard, *Phrynosoma cornutum*, from Central Mexico to Colorado. Journal of Herpetology 37:550–553.

Parker, W.S. 1971. Ecological observations on the Regal Horned Lizard (*Phrynosoma solare*) in Arizona. Herpetologica 27:333–338.

Pianka, E.R., and W.S. Parker. 1975. Ecology of horned lizards: a review with special reference to *Phrynosoma platyrhinos*. Copeia 1975:141–162.

Pimentel, D. 1995. Amounts of pesticides reaching target pests: environmental impacts and ethics. Journal of Agricultural and Environmental Ethics 8:17–29.

Powell, G.L., and A.P. Russell. 1985. Growth and sexual size dimorphism in Alberta populations of the Eastern Short-horned Lizard, *Phrynosoma douglassi brevirostre.* Canadian Journal of Zoology 63:139–154.

Shaw, C.E. 1952. Notes on the eggs and young of some United States and Mexican lizards. Herpetologica 8:71–79.

Sherbrooke, W.C. 2002. Seasonally skewed sex-ratios of road-collected Texas Horned Lizards (*Phrynosoma cornutum*). Herpetological Review 33:21–24.

Sherbrooke, W.C. 2003. Introduction to Horned Lizards of North America. California Natural History Guides No. 64. University of California Press, Berkeley, California, USA.

Smith, H.M. 1946. Handbook of Lizards: Lizards of the United States and of Canada. Cornell University Press, Ithaca, New York, USA.

Stebbins, R.C. 2003. Western Reptiles and Amphibians. 3rd Edition. Houghton Mifflin Co., Boston, Massachusetts, USA.

Suarez, A.V., and T.J. Case. 2002. Bottom-up effects on persistence of a specialist predator: ant invasions and horned lizards. Ecological Applications 12:291–298.

Suarez, A.V., D.T. Bolger, and T.J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology 79:2041–2056.

Suarez, A.V., J.Q. Richmond, and T.J. Case. 2000. Prey selection in horned lizards following the invasion of Argentine Ants in southern California. Ecological Applications 10:711–725.

Tinkham, E.R. 1951. On the recognition of two lower California horned lizards. Herpetologica 7:169–172.

Tollestrup, K. 1981. The social behavior and displays of two species of horned lizards, *Phrynosoma platyrhinos* and *Phrynosoma coronatum*. Herpetologica 37:30–141.

Turner, F.B., and P.A. Medica. 1982. The distribution and abundance of the Flat-tailed Horned Lizard (*Phrynosoma mcallii*). Copeia 1982:815–823.

Wone, B., and B. Beauchamp. 1995. Observations on the escape behavior of the horned lizard *Phrynosoma mcallii*. Herpetological Review 26:132–132.

Wone, B., and B. Beauchamp. 2003. Movement, home range, and activity patterns of the horned lizard, *Phrynosoma mcallii*. Journal of Herpetology 37:679–686.

Zeiner, D.C., W.F. Laudenslayer, Jr., and K.E. Mayer. 1988. California's Wildlife, Volume I. Amphibians and Reptiles. California Department of Fish and Game, Sacramento, California, USA.

Zimmerman, L.C., M.P. O'Connor, S.J. Bulova, J.R. Spotila, S.J. Kemp, and C.J. Salice. 1994. Ecology of Desert Tortoises in the Eastern Mojave Desert: seasonal patterns of operative and body temperatures, and microhabitat. Herpetological Monographs 8:45–59.

SUSAN HULT studied the ecology and demography of Blainville's Horned Lizard (*Phrynosoma blainvillii*) in the San Joaquin Desert of California for her M.S. degree in Biology, which she completed in June 2014 at California State University, Bakersfield, USA. She received her B.S. in Fisheries, Wildlife, and Conservation Biology from the University of Minnesota, Twin Cities. She has worked for the Bureau of Land Management in California's San Joaquin Valley at the Atwell Island Restoration Project, and in northeast Montana working on habitat analysis of Greater Sage Grouse (*Centrocercus urophasianus*), Black-tailed Prairie Dogs (*Cynomys ludovicianus*), and Burrowing Owls (*Athene cunicularia hypogea*). In Minnesota, she has worked in Gopher Snake (*Pituophis catenifer*) conservation and Tall-grass Prairie and Oak Savanna conservation and restoration for the Minnesota Department of Natural Resources. Susan is shown obtaining the mass of a hatchling Blainville's Horned Lizard. (Photographed by Amy Kuritsubo).

DAVID J. GERMANO is a Professor of Biology at California State University, Bakersfield, and is on the Board of Directors and is a Section Editor of *Herpetological Conservation and Biology*. He received his B.A. in Biology from California State University, Northridge, a M.S. in Wildlife Ecology from the University of Arizona, and his Ph.D. in Biology from the University of New Mexico, where he studied the growth and life history of North American tortoises (*Gopherus* spp.), including the Desert Tortoise (*G. agassizii*). His research interests involve population ecology and life-history analysis of small mammals, reptiles, and amphibians, as well as the effects of cattle grazing on small vertebrates. He has conducted long-term studies of Blunt-nosed Leopard Lizards (*Gambelia sila*), Western Pond Turtles (*Emys marmorata*), North American tortoises, Desert Box Turtles (*Terrapene ornata luteola*), and various species of kangaroo rats (*Dipodomys* spp.), including a 23-y study of Giant Kangaroo Rats (*D. ingens*). (Photographed by Larry Saslaw).