

SPACE USE BY FREE-RANGING, JUVENILE SONORAN DESERT TORTOISES (*GOPHERUS MORAFKAI*) IN CENTRAL ARIZONA, USA

BRIAN K. SULLIVAN^{1,3} AND CHAD A. RUBKE²

¹*School of Mathematical and Natural Sciences, Post Office Box 37100, Arizona State University,
Phoenix, Arizona 85069, USA*

²*Terrestrial Branch, Arizona Game and Fish Department, 5000 West Carefree Highway, Phoenix, Arizona 85086, USA*

³*Corresponding author, e-mail: bsullivan@asu.edu*

Abstract.—Spatial ecology of very young (≤ 3 y of age) desert tortoises in the American Southwest remains little known, especially for Sonoran Desert Tortoises (*Gopherus morafkai*). From 2013–2021 at a field site in upland Sonoran Desert in central Arizona, USA, we observed 13 juvenile *G. morafkai* for an average of 9 mo each. Based on size and carapace characteristics, we estimated that most of our subjects were in their first- or second-year post-hatching (median straight line carapace length = 50 mm; range, 44–62 mm; $n = 13$). Relative to adults, these very young tortoises occupied extremely small home ranges: as estimated by Minimum Convex Polygons, they ranged from 0.002 to 0.055 ha, but the median was only 0.007 ha (= 70 m²). Young tortoises were active in every month of the year, but especially February, March, and April (75% of all sightings) and 88% of feeding events occurred during March and April. Mean daily speed, an estimate of movement within months, was significantly higher in late winter and early spring relative to the remainder of the year. There was no relationship between home range size and either tortoise size or duration of observation (months), or number of resightings. Rainfall stimulated activity, but we observed many individuals basking during the winter, even in cold, dry weather. Like adults, some individuals switched back and forth between refuges, which were typically small burrows at the bases of shrubs either self-made or co-opted from rodents.

Key Words.—Cave Buttes; hatchling; home range; Union Hills; winter activity; mean daily speed

INTRODUCTION

Over the past four decades researchers using radio-telemetry have greatly increased our understanding of the spatial ecology of Mohave Desert Tortoises (= MDT; *Gopherus agassizii*), and to some extent, Sonoran Desert Tortoises (= SDT; *Gopherus morafkai*). Space use by hatchlings and very young tortoises up to 80 mm in size (straight-line carapace length, = SLCL) of these two species, however, remains understudied (Averill-Murray et al. 2002; van Devender 2002). Consequently, the first 5 y of life for desert tortoises are largely a mystery to those attempting to evaluate their population biology and plan for their conservation (e.g., Campbell et al. 2015; Bridges et al. 2016). This is troubling because hatchling and young juvenile (1–5 y of age) tortoises are thought to represent especially vulnerable age classes of these typically long-lived reptiles (Lovich et al. 2017).

Data on space use by hatchling tortoises worldwide have been difficult to obtain given their cryptic nature and small size, but some observations have been gathered for free-ranging Gopher Tortoises (*G. polyphemus*; Pike 2006) and Texas Tortoises (*G. berlandieri*; Hellgren et al. 2000), and for MDTs in semi-natural enclosures (e.g., Tuberville et al. 2019). Keller et al. (1997) used radio-telemetry to document that Spur-thighed Tortoises

(*Testudo graeca*) have very small home ranges for up to 8 mo following hatching. Pike (2006) documented that Gopher Tortoises move little in their first fall season and begin moving increasingly the following spring. Together, these studies suggest that by relying on yolk reserves, hatchling tortoises may remain relatively inactive after they emerge from the nest in the summer or early fall and become more active the following spring.

The majority of prior work on activity of desert tortoises in the American Southwest has focused on the MDT in the Mojave Desert of California. Far fewer reports exist on activity in the more recently described SDT (Murphy et al. 2011). Variation in rainfall patterns in which rainfall is concentrated during the winter in the Mojave Desert but divided between winter and summer in the Sonoran Desert, greatly influences timing of activity in both species (Averill-Murray et al. 2002; Sullivan et al. 2016) and might have significant consequences for activity of very young SDTs throughout the year. Although winter activity has been recently documented in SDTs, including juveniles (Sullivan et al. 2014), little is known about the significance of this activity other than the benefits of exploiting favorable conditions for drinking water, an ecological necessity for tortoises occupying arid environments (Peterson 1996; Loehr

et al. 2009). Basking in the Speckled Cape Tortoise (*Homopus signatus*) allows them to opportunistically forage following winter rainfall events (Loehr et al. 2012), and Angulate Tortoises (*Chersina angulata*) will become surface active if water is available during typically arid summer months (Ramsay et al. 2002). Nonetheless, activity during winter may entail higher mortality risks from rapidly declining temperatures (Kuzmin 2002) or inability to escape predators (Riedle et al. 2010).

We initiated a radio-tracking study of SDTs in the Cave Buttes area of the Union Hills near Phoenix, in central Arizona, USA, in 2011. This afforded the opportunity to observe females during the egg-laying season (June), and target searches for emerging hatchlings and very young juvenile tortoises from those areas. In this study, we report on the space use and behavior of 13 very young SDTs that were free ranging. We followed tortoises for an average of 9 mo each, and we document variation in behavior and home range size.

MATERIALS AND METHODS

Study site.—Cave Buttes (CB) is a Maricopa County Flood Control District parcel of undeveloped land reserved for flood control purposes that has served as a long-term study site for amphibians and reptiles since 1980, and SDTs since 2011 (Sullivan et al. 2014, 2016). The site occupies the eastern margin of the Union Hills and the adjacent Cave Creek floodplain to the east on the northern edge of the Phoenix metropolitan area, Arizona, USA. Cave Buttes comprises a relatively low-elevation series of hills in a region of transition from Creosote (*Larrea tridentata*)-Bursage (*Ambrosia deltoidea*) flats to Saguaro (*Carnegiea gigantea*)-Palo Verde (*Parkinsonia microphylla*) dominated uplands. The hills rise to approximately 650 m elevation in the west from a surrounding area of flats of about 350 m in elevation to the east associated with the Cave Creek floodplain. Geologically, the hills comprise metavolcanic rocks with basaltic protoliths and various granitic rocks in lesser quantity. Within the site, tortoises are rarely encountered away from the slopes and the incised arroyos draining those hills, which are dominated by plants associated with the Arizona Upland Subdivision of the Sonoran Desert (Turner and Brown 1982). The arroyos have numerous exposed caliche formations into which tortoises and other organisms (e.g., White-throated Wood Rats, *Neotoma albigula*) had established burrows or nests. These burrows and nests were used by tortoises for refuges during both winter and summer. Unsurprisingly, given the limited availability of large rock outcrops, large juvenile (> 100 mm SLCL) and adult tortoises at CB do not typically take refuge under rock overhangs, as is commonly observed in other

SDT populations (Barrett 1990; Averill-Murray et al. 2002). Rather, SDTs at CB make use of caliche tunnels and occasionally, White-throated Wood Rat nests, and only rarely make use of relatively small rock overhangs (Sullivan et al. 2016, 2021).

Field methods.—We began radio-tracking adult SDTs at CB in the fall of 2011 (Sullivan et al. 2016). In 2012 we observed occasional hatchling or slightly larger juveniles (< 60 mm SLCL) in the central wash of our SDT study plot. This portion of the wash contained a deep caliche refuge typically used by five adult females in the late spring and early summer during our study, the period when nesting typically occurs (Averill-Murray 2002). In 2013 we began systematically searching this area, a roughly 25-m stretch of the 2–3 m wide wash and associated caliche banks draining the hills from west to east toward Cave Creek immediately southwest of the Cave Creek Dam. On each visit we moved through this area, we termed the nursery, scanning abandoned rodent burrows and scrutinizing small shrubs with shade producing canopies during 20–30 min Visual Encounter Surveys conducted by two individuals.

We visited the nursery site for surveys at least twice and as many as five times per week, and we made every effort to visit after each rainfall event (> 2.5 mm). When we detected a juvenile tortoise, we attempted to increase the search effort over subsequent days to relocate the free-ranging subject, given that their small size precluded radio-tracking. When we first encountered a juvenile tortoise, we attempted to minimize disruption by avoiding all unnecessary handling, especially as we did not want to stimulate bladder voiding. We measured SLCL by placing a ruler above the subject when stationary and marking it uniquely on one scute of the carapace with a distinctive mark using a black permanent marker. Because we could not radio-track these small SDTs, our observations were based on our ability to detect individuals and biased by our efforts to search after rainfall events. Thus, if young SDTs varied in their propensity to remain near refuges, our ability to detect them was increased accordingly. Nonetheless, our data are a glimpse into space use and behavior of an otherwise little-known age-class of SDTs.

We recorded activity by noting the status (in a refuge or basking at a refuge, moving, feeding, or drinking water) of all individuals each time they were encountered. We defined basking at a refuge as a stationary position within the refuge opening, or immediately outside the opening with two or more limbs extended laterally, the plastron resting on the ground, and the head extended (eyes closed in many instances). Feeding was indicated by biting of plants; moving entailed direct observation of walking without feeding.

We calculated home ranges by plotting locations of each individual in ArcGIS 10.8.1 (Esri, Redlands, California, USA). We then generated Minimum Convex Polygons (MCP) using the Minimum Bounding Geometry Tool in ArcToolbox (Esri). To determine mean daily speed (MDS), we first ensured that locations were arranged chronologically, and then used the Points to Line Tool in ArcToolbox to generate a single line for each juvenile. We then used the Split Line by Vertices Tool in ArcToolbox and calculated the length of each line segment. We sorted movement measurements by the calendar month in which they occurred. We divided the total distance moved in a month by the number of days in that particular month. Because these methods incorporate straight-line distances, our MCP and movement values may be underestimates.

We obtained air temperatures (high/low °C) and daily rainfall from three weather stations at the northern, eastern, and southern boundaries of CB (Maricopa County Flood Control District) and for individual tortoises at basking sites using a Schulthesis Quick Recording thermometer (Weber & Miller; New York, New York, USA). Because of sample size limitations, and the absence of independence given the repeated sampling of the same individuals and wide variation in the number of repeated measurements among individuals, we used nonparametric statistical tests (Spearman's rho, Mann-Whitney U) for all comparisons ($\alpha = 0.05$).

RESULTS

Behavioral observations.—We encountered 28 juvenile SDTs (median SLCL: 50 mm; range, 44–62

mm) in the nursery (and one at a more distant wash to the north) from 2012–2021 (Table 1). Of these, we subsequently observed 13 on eight or more occasions, and we used these data to generate an estimate of home range size for each (see below). Overall, of 314 observations on these 13 juvenile SDTs, 75% (236) were in late winter and early spring (February, March, April). We recorded 88% of feeding observations in March and April alone. By far the most frequent activity noted during observation was basking or resting within a refuge (239), while moving (51) and feeding (24) were less commonly encountered.

As an example of consistent winter activity, one individual (Fig. 1) was initially seen on 2 January 2013, and last seen 31 March 2013, having remained in the same general area near three burrows 25 m apart. On some occasions, it was basking in the open, completely exposed, while on others it was next to some object, partially hidden, but in an apparent basking posture, with limbs extended at awkward angles and eyes closed as if sleeping (Fig. 1). It was basking consistently, morning after morning in sequence (e.g., 2–6 February), at much lower temperatures (minimum air temperature of 4° C) and on overcast mornings at earlier hours (0900 at 5° C) than adults. The beak was green whenever visible, indicative of recent feeding (Sullivan et al. 2014, 2016).

As an example of the use of multiple refuges consistently during the winter, a second individual was first observed foraging in the leaf litter of an Ironwood Tree (*Olynea tesota*) 5 October 2014, and then on and off throughout early June 2015. After observing this hatchling throughout October, despite considerable search effort, we were unable to detect this hatchling over the entire month of November, a warm but dry four-week period in

TABLE 1. Juvenile Sonoran Desert Tortoises (*Gopherus morafkai*) from Maricopa County, Arizona, USA, radio-tracked from 2013 – 2021, their straight-line carapace lengths (SLCL), the number of days between first and last fixes, number of fixes, and size of minimum convex polygon (MCP) home ranges.

Tortoise ID	SLCL (mm)	Date Detected	Date last seen	Days	Number of fixes	MCP (ha)
#5	48	2 January 2013	31 March 2013	88	13	0.002
#7	45	5 October 2014	8 June 2015	247	29	0.003
#11	50	21 May 2015	19 April 2017	700	18	0.012
#15	48	7 July 2016	22 February 2017	231	19	0.003
#16	62	3 August 2016	3 April 2017	244	29	0.014
#18	53	4 August 2016	5 April 2018	610	23	0.002
#19	48	7 September 2016	9 April 2017	215	17	0.055
#20	53	8 September 2016	9 April 2017	214	47	0.017
#24	55	14 December 2019	26 May 2020	165	38	0.017
#25	44	18 February 2020	2 May 2020	74	21	0.006
#26	51	5 March 2020	29 June 2020	116	30	0.007
#27	53	24 March 2020	14 February 2021	327	14	0.013
#29	48	6 April 2020	22 June 2020	77	8	0.002



FIGURE 1. Juvenile Sonoran Desert Tortoise (*Gopherus morafkai*) #5 from Maricopa County, Arizona, USA, basking at what we called a branch overhang refuge, 4 February 2013. Note the forelimb extended during basking. (Photographed by Brian Sullivan).



FIGURE 2. Juvenile Sonoran Desert Tortoise (*Gopherus morafkai*) #7 from Maricopa County, Arizona, USA, basking at burrow opening (burrow refuge) 9 December 2014. (Photographed by Brian Sullivan).

2014. Following 1.55 mm of rain 4 December 2014, we observed the tortoise on the first sunny day post rainfall, and each day thereafter for five consecutive days with morning (about 0900) air temperatures of 14° C to 24° C (Fig. 2). Unlike the individual described above, this second individual was always near (< 1 m) a burrow opening while basking. On some days, it would appear just inside the opening, appearing to bask in the sun with eyes closed (Fig. 2), without exiting the burrow. Despite frequent searches, we could not detect this individual again until 7 February 2015, when we found it just outside the same burrow, basking (air temperature = 18° C, ground = 23° C) on a sunny, dry day. Over the next four weeks, we observed this hatchling during each of our site visits. When it was not present at the burrow, it was at a second refuge, 4 m to the south, a small depression at the base of a Bursage, where it was difficult to detect unless viewed directly from above (Fig. 3). Thus, this individual was basking consistently, and even shifted between refuges at least once, probably repeatedly, from November through February.

It is also significant that we did not observe these two juvenile SDTs, as well as the other 11 individuals, taking refuge in the same larger caliche formations used by adults. Rather, they consistently made use of small, individual burrows as described above (Fig. 2). These juveniles also differed from adults in that when they detected our approach, they always moved quickly to the shade of a shrub or a burrow. The 13 SDTs we observed used 23 unique refuges: 74% were burrows, and the remainder were of rock and branch overhangs except for a single pallet (small scrape under a shrub). We never observed a juvenile in the process of excavating a burrow.

Home range.—Home ranges varied from 0.002 to 0.055 ha, with a median value of only 0.007 ha (Table

1). Home range size was not significantly correlated with the number of observations ($r_s = 0.42$, $P = 0.156$, $n = 13$), the length of the observation period ($r_s = 0.22$, $P = 0.465$, $n = 13$), or the size of the tortoise ($r_s = 0.45$, $P = 0.122$, $n = 13$). Movement data by month indicate that these small tortoises moved < 1 m per day (median = 0.30 m). These comparisons are limited by the small sample size but do indicate that none of these variables dramatically influenced the size of the home range of the tortoises we observed. The home ranges of 12 of the 13 juvenile SDTs are shown in Fig. 4 (the home range of subject #5 was outside of the area depicted in this image).

Mean daily speed (MDS) per month ranged from 0.03 m/day to 3.29 m/day across 31 monthly periods for the 13 subjects. Median daily speed in the late winter and early spring period of increased activity (February



FIGURE 3. Juvenile Sonoran Desert Tortoise (*Gopherus morafkai*) #7 from Maricopa County, Arizona, USA, basking in dappled light of Bursage (*Ambrosia deltoidea*) 26 February 2015. This represents a small rock overhang refuge. (Photographed by Brian Sullivan).

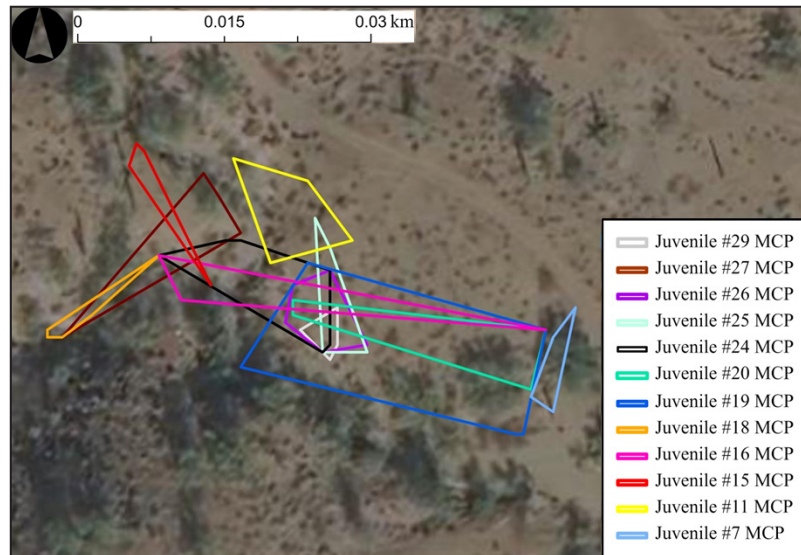


FIGURE 4. Home ranges (ha) of 12 of 13 juvenile Sonoran Desert Tortoise (*Gopherus morafkai*) at Cave Buttes, Arizona, USA, 2013–2021. Note the degree of overlap of home ranges; points of intersection at the edges of two or more polygons represent refuges used by more than one juvenile tortoise across sequential years.

through April) was 0.55 m/day ($n = 21$ monthly estimates for 11 individuals). This was significantly greater ($U = 27$, $Z = 3.27$, $P = 0.001$) than the median (0.08 m/day, $n = 10$ monthly estimates for seven individuals) during the remainder of the year (May–January).

DISCUSSION

The young SDTs we observed occupied very small home ranges, apparently near (within 30 m) nest sites used by their mothers. They were especially active in the late winter and early spring (about 75% of observations were February–April). Movement rates were highest in the late winter and early spring, but overall, these juveniles moved very little while under observation. Unlike adults that typically freeze when approached, juveniles we encountered in the open almost always moved quickly toward the shade of a shrub or to their burrow refuge, suggestive of a difference in anti-predatory behavior, perhaps because the juveniles are more brightly colored and thus less cryptic than adults. They spent considerable time basking and we observed them feeding in virtually every month of the year, although feeding observations were concentrated in the spring. Wilson et al. (1999) observed little feeding in very young MDTs during winter but most of the relatively few feeding events we witnessed were during late winter and early spring. Rain stimulated emergence regardless of temperature. During the hot summer months, we only detected very young SDTs following rain-fall events and at below average temperatures. The young SDTs we observed generally took refuge in burrows that we assume were co-opted

from rodents. Like adults (Sullivan et al. 2016; Sullivan 2021), juveniles made consistent use of the same refuge repeatedly spanning months and even years. Two made use of the same refuge occupied by a different juvenile in a prior year, and although we observed up to three individuals basking within 100 mm of one another, we never observed any in the same refuge simultaneously.

Our data on space use by very young SDTs are similar to those obtained for free-ranging Gopher Tortoises (Pike 2006) and Texas Tortoises (Hellgren et al. 2000), as well as Spur-thighed Tortoises, which have very small home ranges for up to eight months following hatching. Pike (2006) documented that Gopher Tortoises move little in their first fall and increase movements the following spring. Together, these studies suggest that hatchling tortoises may remain relatively inactive after they hatch and emerge from the nest in the summer or early fall and become more active the following spring. Our results comport with these findings.

Bjurlin and Bissonette (2004) found that hatchling MDTs moved little and suffered little mortality for the first few months after hatching. They argued this was attributable to reduced movement and use of yolk reserves for energy needs rather than foraging. We observed that like adult SDTs (Sullivan et al. 2014), very young SDTs emerge to bask and drink on winter days at temperatures as low as 4° C although ground temperatures reached as high as 30° C on these days. Previous researchers have generally assumed that MDTs remain inactive inside their burrows through the winter months (Nagy and Medica 1986; Rautenstrauch et al. 1998; Duda et al. 1999); however, populations now recognized as SDTs experience much different

climatic conditions than MDTs, leading to differences in activity and behavior (Van Devender 2002). From a conservation standpoint, it is important to recognize that SDTs can be active in the winter more often than previously recognized. It is also critical to note that winter activity in very young MDTs, especially after rains, may be more common than has been assumed. Detailed observations during rainfall events will be required to evaluate this hypothesis.

Advancements in very-high frequency (VHF) radio transmitters, including considerable reductions in size and weight, now permit fine-scale detail of movement data and habitat selection by hatchling and juvenile desert tortoises. In their examination of habitat needs and selection by neonate and juvenile MDTs, Todd et al. (2016) radio-tracked very young tortoises for 2 y and found individuals to select for, among other things, areas of greater canopy cover (especially from Creosote), greater coverage of perennial plants, and areas with a greater number of small-mammal burrows. Given significant geological, topographical, and vegetative differences between the Mojave and Sonoran deserts, future studies on very young SDTs could help to fill similar knowledge gaps. Fine-scale research on SDT habitat use can increase our understanding of microhabitats and potentially reduce anthropogenic impacts to high-quality juvenile tortoise habitat as well as enhance habitat restoration efforts for SDTs.

Acknowledgments.—We thank Keith and Elizabeth Sullivan for assistance in the field. Audrey Owens and David Germano shared their knowledge of tortoises. Observations were conducted under authority of permits (#SP 639140 to BKS) provided by the Arizona Game and Fish Department (AGFD). Collecting methods were approved as part of an Institutional Animal Care and Use Committee protocol (#20-1738R to BKS) of Arizona State University (BKS) for surveying reptiles. Maricopa County Flood Control personnel, especially Dennis Duffy, Dianna Cunningham, and Diana Stuart, provided considerable assistance at CB, as did Rob Patterson of the Phoenix Parks Department, and Roger Moncayo provided assistance with site protection. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the Arizona Game and Fish Department.

LITERATURE CITED

- Averill-Murray, R.C. 2002. Reproduction of *Gopherus agassizii* in the Sonoran Desert, Arizona. *Chelonian Conservation and Biology* 4:295–301.
- Averill-Murray, R.C., B.E. Martin, S.J. Bailey, and E.B. Wirt. 2002. Activity and behavior of the Sonoran Desert Tortoise in Arizona. Pp.135–158 *In* The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. Van Devender, T.R. (Ed.). University of Arizona Press and Arizona Sonora Desert Museum, Tucson, Arizona, USA.
- Barrett, S.L. 1990. Home range and habitat of the Desert Tortoise (*Xerobates agassizi*) in the Picacho Mountains of Arizona. *Herpetologica* 46:202–206.
- Bridges, A., H.L. Bateman, A.K. Owens, C.A. Jones, and W. Miller. 2016. Microhabitat selection of juvenile Sonoran Desert Tortoises (*Gopherus morafkai*) in central Arizona. *Chelonian Conservation and Biology* 15:219–230.
- Bjurlin, C.D., and J.A. Bissonette. 2004. Survival during early life stages of the Desert Tortoise (*Gopherus agassizii*) in the south-central Mojave Desert. *Journal of Herpetology* 38:527–535.
- Campbell, S.P., R.J. Steidl, and E.R. Zylstra. 2015. Recruitment of desert tortoises (*Gopherus agassizii* and *G. morafkai*): a synthesis of reproduction and first-year survival. *Herpetological Conservation and Biology* 10:583–591.
- Duda, J.T., A.T. Krzysik, and J.E. Freilich. 1999. Effects of drought on Desert Tortoise movement and activity. *Journal of Wildlife Management* 63:1181–1192.
- Hellgren, E.C., R.T. Kazmater, D.C. Ruthven, III, and D.R. Synatzske. 2000. Variation in tortoise life history: demography of *Gopherus berlandieri*. *Ecology* 81:1297–1310.
- Keller, C., C. Diaz-Paniagua, and A.C. Andreu. 1997. Post-emergent field activity and growth rates of hatchling Spur-thighed Tortoises, *Testudo graeca*. *Canadian Journal of Zoology* 75:1089–1098.
- Kuzmin, S.L. 2002. *The Turtles of Russia and Other ex-Soviet Republics*. Edition Chimaira, Frankfurt, Germany.
- Loehr, V.J.T. 2012. High body temperatures in an arid, winter-rainfall environment: thermal biology of the smallest tortoise. *Journal of Arid Environments* 82:123–129.
- Loehr, V.J.T., M.D. Hofmeyr, and B.T. Henen. 2009. Small and sensitive to drought: consequences of aridification to the conservation of *Homopus signatus signatus*. *African Journal of Herpetology* 58:116–125.
- Lovich, J.E., R.C. Averill-Murray, M. Agha, J.R. Ennen, and M. Austin. 2017. Variation in annual clutch phenology of Sonoran Desert Tortoises (*Gopherus morafkai*) in central Arizona. *Herpetologica*, 73:313–322.
- Murphy, R.W., K.H. Berry, T. Edwards, A.E. Leviton, A. Lathrop and J.D. Riedle. 2011. The dazed and confused identity of Agassiz's land tortoise, *Gopherus agassizii* (Testudines, Testudinidae) with the description of a new species, and its consequences for conservation. *Zookeys* 113:39–71.

- Nagy, K.A., and P.A. Medica. 1986. Physiological ecology of Desert Tortoises in southern Nevada. *Herpetologica* 42:73–92.
- Peterson, C.C. 1996. Ecological energetics of the Desert Tortoise (*Gopherus agassizii*): effects of rainfall and drought. *Ecology* 77:1831–1844.
- Pike, D.A. 2006. Movement patterns, habitat use, and growth of hatchling tortoises, *Gopherus polyphemus*. *Copeia* 2006:68–76.
- Ramsay, S.L., M.D. Hofmeyr, and Q.I. Joshua. 2002. Activity patterns of the Angulate Tortoise (*Chersina angulata*) on Dassen Island, South Africa. *Journal of Herpetology* 36:161–169.
- Rautenstrauch, K.R., A.L.H. Rager, and D.L. Rakestraw. 1998. Winter behavior of Desert Tortoises in southcentral Nevada. *Journal of Wildlife Management* 62:98–104.
- Riedle, J.D., R.C. Averill-Murray, and D.D. Grandmaison. 2010. Seasonal variation in survivorship and mortality of Desert Tortoises in the Sonoran Desert, Arizona. *Journal of Herpetology* 44:164–167.
- Sullivan, B.K. 2021. Long-term trends in overwintering behavior of resident and translocated Sonoran Desert Tortoises, *Gopherus morafkai*. *Sonoran Herpetologist* 34:14–16.
- Sullivan, B.K., R.C. Averill-Murray, K.O. Sullivan, J.R. Sullivan, E.A. Sullivan, and J.D. Riedle. 2014. Winter activity of Sonoran Desert Tortoise (*Gopherus morafkai*) in central Arizona. *Chelonian Conservation and Biology* 13:114–119.
- Sullivan, B. K., A.K. Owens, K.O. Sullivan, and E.A. Sullivan. 2016. Spatial ecology of Sonoran Desert Tortoises (*Gopherus morafkai*): I. Fidelity in home range, refuge use, and foraging behavior. *Journal of Herpetology* 50:509–519.
- Todd, B.D., B.J. Halstead, L.P. Chiquoine, J.M. Peaden, K.A. Buhlmann, T.D. Tuberville, and M.G. Nafus. 2016. Habitat selection by juvenile Mojave Desert Tortoises. *Journal of Wildlife Management* 80:720–728.
- Tuberville, T.D., K.A. Buhlmann, R. Sollmann, M.G. Nafus, J.M. Peaden, J.A. Daly, and B.D. Todd. 2019. Effects of short-term, outdoor head-starting on growth and survival in the Mojave Desert Tortoise (*Gopherus agassizii*). *Herpetological Conservation and Biology* 14:171–184.
- Turner, R.M., and D.E. Brown. 1982. Sonoran desertscrub. Special Issue, *Desert Plants* 4:181–221.
- Van Devender, T. 2002. Natural history of the Sonoran tortoise in Arizona: life in a rock pile. Pp. 3–28 *In* The Sonoran Desert Tortoise: Natural History, Biology, and Conservation. Van Devender, T.R. (Ed.). University of Arizona Press and Arizona Sonora Desert Museum, Tucson, Arizona, USA.
- Wilson, D.S., D.J. Morafka, C.R. Tracy, and K.A. Nagy. 1999. Winter activity of juvenile Desert Tortoises (*Gopherus agassizii*) in the Mojave Desert. *Journal of Herpetology* 33:496–501.



BRIAN K. SULLIVAN received his B.A. in Zoology from the University of California, Berkeley, USA, in 1979, and his Ph.D. in Zoology from Arizona State University (ASU), USA, in 1983. Subsequently, he was a Lecturer at the University of Texas, Austin, USA, prior to his appointment as an Assistant Professor at the University of Maine, Orono, USA. Brian returned to ASU as an Assistant Professor in 1989. He served as the Editor of the *Journal of Herpetology* from 2000 through 2005. He has spent over 50 y investigating the behavior, conservation, ecology, and evolution of amphibians and reptiles of the Sonoran Desert. Brian has authored over 175 articles, book reviews, technical reports, and book chapters, including many coauthored with students and colleagues in the American Southwest. He retired in 2023, freeing up time for research, and is now an Emeritus Professor at ASU. (Photographed by Elizabeth Sullivan).



CHAD A. RUBKE is the Turtles Project Coordinator for the Arizona Game and Fish Department, Phoenix, USA. In this position, he works independently and with partner agencies to implement projects, conduct research, and better understand the conservation needs of turtle and tortoise species of Arizona. An Arizona native, Chad has spent the last 12 y conducting work on much of the flora and fauna of Arizona but has focused primarily on reptiles and amphibians. He holds a Bachelor's degree in Biology with a certificate in Wildlife Ecology and Management from Northern Arizona University, Flagstaff, USA. Chad is currently pursuing his Master's degree in Fish, Wildlife, and Conservation Biology from Colorado State University, Ft. Collins, USA. His interests include reading, hiking, camping, and exploring the backcountry of Arizona. (Photographed by Janet Johnson).