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THIS MONTH'S PROGRAM

Dale Turner

That Obscure Object of Desire –The Search for *Phrynosoma ditmarsii*

7:15 PM; Wednesday, 19 September 2018

Tucson City Council Ward 3, 1510 East Grant Road, Tucson, AZ 85719

Dale Turner first connected with wildlife by playing with Texas horned lizards as a kid. He grew up to become a conservation activist and wildlife biologist, including 17 years (so far) with The Nature Conservancy. His work is focused on restoration projects in the Colorado River Delta in Mexico, and leading teams to plan conservation efforts across whole watersheds such as the binational San Pedro River. Dale completed an MS in Wildlife and Fisheries Science at University of Arizona, with a thesis on ecology of the Yuman Desert Fringe-toed Lizard, *Uma rufopunctata*, in Arizona's Mohawk Dunes. He has written a wide variety of scientific and popular articles, but is happiest when out chasing lizards in the desert. Dale is a past president of the Tucson Herpetological Society.

For more than a century, the Sonoran endemic Rock Horned Lizard, *Phrynosoma ditmarsii*, has been an enigma and a lure for herpetologists. It was named from specimens collected in 1897 with a locality described as "a short distance over the border of Arizona, in old Mexico, state of Sonora." The species was not found again until 1970, and was located after an intensive study of stomach contents from the holotype and paratype. That stirred new interest but only seven localities were known by 1984, scattered widely across the eastern half of Sonora. Another 18 years passed before the next observation.



Dale Turner in the field.

Thanks largely to a program of biological inventories now called the Madrean Discovery Expeditions, a dozen new localities in the past decade have brought better understanding of the species' true distribution, and hints of their ecology. Dale will share what we currently know about *P. ditmarsii*, along with photos and stories of the search in the beautiful mountains of Sonora.

FUTURE SPEAKERS

- 17 October 2018—Brandon La Forest: "Technology and Mexican Herpetology" and "A Tale of Three Vipers: Mexico's Horned Pitvipers of the Genus *Ophryacus*"
- 21 November 2018— Ross Maynard: Reserva Río Manduriacu: A Mine for Threatened Herpetofauna

RESEARCH ARTICLES

- 38 "Notes on Reproduction of Colorado River Toads, *Incilius alvarius* (Anura: Bufonidae), from Pima County, Arizona" by Stephen R. Goldberg
- 40 "Horned Lizards (*Phrynosoma*) of Sonora, Mexico: Distribution and Ecology" by Cecilia Aguilar-Morales and Thomas R. Van Devender
- 51 "Crypsis and Flight Initiation Distance in Horned Lizards" by William E. Cooper, Jr., and Wade C. Sherbrooke

NATURAL HISTORY

- 56 "Late Spring Mining of Minerals by Female Sonoran Desert Tortoises" by Brian K. and Elizabeth A. Sullivan
- 58 "Two species of foam nest forming *Rachophorus* frogs found in different twigs of a Guava Tree in Waynand, Kelara" by Suman Pratihar

Notes on Reproduction of Colorado River Toads, *Incilius alvarius* (Anura: Bufonidae), from Pima County, Arizona

Stephen R. Goldberg, Whittier College, Department of Biology, Whittier, CA; sgoldberg@whittier.edu

Incilius alvarius (Girard, 1859) (Fig. 1) occurs from central Arizona to extreme southwest New Mexico, extreme southeast California south to northwest Sinaloa, Mexico (Stebbins 2003). Breeding usually occurs in seasonal or permanent pools, cattle tanks and irrigation ditches (Green et al. 2013). Although they may still be abundant in Arizona, *I. alvarius* numbers appear to have declined in New Mexico and California (Green et al. 2013). The biology of *I. alvarius* (as *Bufo alvarius*) is summarized in Fouquette (1970). In the current paper I present data from a histological examination of *I. alvarius* gonadal material from Pima County, Arizona. Utilization of museum collections for obtaining reproductive data avoids removing additional animals from the wild.

A sample of 43 *I. alvarius* collected 1958 to 1999 from Pima County, Arizona (Appendix) consisting of 17 adult males (mean SVL = 122.9 mm \pm 8.9 SD, range = 108–143 mm), 25 adult females (mean SVL = 132.6 mm \pm 17.3 SD, range = 88–160 mm), one juvenile female (SVL = 74 mm) was examined from the herpetology collection of the Natural History Museum of Los Angeles County (LACM), Los Angeles, California, USA (Appendix). An unpaired *t*-test was used to test for differences between adult male and female SVLs (Instat, vers. 3.0b, Graphpad Software, San Diego, CA).

A small incision was made in the lower part of the abdomen and the left testis was removed from males and a piece of the left ovary from females. Gonads were embedded in paraffin, sections were cut at 5 μ m and stained with Harris hematoxylin followed by eosin counterstain (Presnell and Schreiber 1997). Histology slides were deposited in LACM.

The testicular histology of *I. alvarius* is similar to that of other anurans as described in Ogielska and Bartmanska (2009a). Within the seminiferous tubules, spermatogenesis occurs in vesicles called cysts which remain closed until the late spermatid stage is reached; cysts then open and differentiating sperm reach the lumina of the seminiferous tubules (Ogielska and Bartmanska 2009a). All males examined from the following months were undergoing spermiogenesis: June (*n* = 1), July (*n* = 11), August (*n* = 3), September (*n* = 2). In spermiogenesis, the lumen of each seminiferous tubule contained sperm and/or open sperm cysts with sperm



Figure 1. Juvenile *Incilius alvarius*, Rancho El Aribabi, Sonora. Photo by Jim Rorabaugh.

tails projecting into the lumina. Wright and Wright (1949) reported males of *I. alvarius* are mature at 80 mm SVL. My smallest mature male *I. alvarius* (*sensu* Wright and Wright 1949) measured 108 mm SVL (LACM 115165) was from late in the reproductive season (September) and contained mainly spermatogonia. It presumably produced sperm earlier in the year.

The mean SVL of *I. alvarius* females was significantly larger than that of males ($t = 2.1$, $df = 40$, $P = 0.041$). The ovaries of *I. alvarius* are typical of other anurans in being paired organs lying on the ventral sides of the kidneys which in adults are filled with diplotene oocytes in various stages of development (Ogielska and Bartmanska 2009b). Mature oocytes are filled with yolk droplets; the layer of surrounding follicular cells is thinly stretched. Two stages were present in the spawning cycle (Table 1): (1) “Ready to Spawn” condition in which mature oocytes predominated; (2) “Not in Spawning Condition” in which early diplotene oocytes predominated. However, an exception is the one July female (LACM 181334) in the “Not in Spawning Condition” category (Table 1) which contained yolk-filled oocytes that were smaller than those in “Ready to Spawn” females. These were similar to Secondary Growth Stage 5 “progressive accumulation of yolk platelets” (Uribe 2011). It is not known when these smaller yolk-filled oocytes would have spawned. In one non-breeding August female (LACM 87031, SVL = 137 mm) mature oocytes were deteriorating (atresia) (Table 1). The other four non-breeding females in Table 1 (two from August, two from September) con-

Incilius alvarius (Girard, 1859) (Fig. 1) occurs from central Arizona to extreme southwest New Mexico, extreme southeast California south to northwest Sinaloa, Mexico (Stebbins 2003). Breeding usually occurs in seasonal or permanent pools, cattle tanks and irrigation ditches (Green et al. 2013).

tained immature diplotene oocytes, but no mature oocytes. These findings (Table 1) likely indicate the reproductive period of *I. alvarius* is coming to a close. Wright and Wright (1949) reported *I. alvarius* females of 87 mm SVL were mature. The smallest mature female in my sample (*sensu* Wright and Wright 1949) measured 88 mm SVL (LACM 145654) was from September and contained only early diplotene oocytes. It presumably completed spawning earlier in the year. One smaller female (LACM 87033, SVL = 74 mm) contained early diplotene oocytes in its ovary and was considered to be a juvenile.

Varying amounts of atresia were noted in 12/19 (63%) of spawning *I. alvarius*. Atresia is a widespread process occurring in the ovaries of all vertebrates (Uribe 2009). It is common in the amphibian ovary (Saidapur 1978) and is the spontaneous digestion of a diplotene oocyte by its own hypertrophied and phagocytic granulosa cells which invade the follicle, and eventually degenerate after accumulating dark pigment (Ogielska and Bartmanska 2009b). In early atresia, the granulosa cells enlarge and project into the follicle lumen. In late atresia mature follicles are replaced by brown staining amorphous masses. Incidences of follicular atresia increase late in the reproductive cycle (Goldberg 1973). Saved energy will presumably be utilized in a subsequent reproduction.

Incilius alvarius move overland to breeding sites with the start of the summer monsoon (Fouquette et al. 2005). Sullivan and Malmos (1994) reported *I. alvarius* breeding occurred in one night following a rainfall > 25 mm, although breeding might be delayed until the second or third night after extensive flooding. While it is evident (Table 1) that the reproductive cycle of *I. alvarius* is timed to coincide with the summer monsoon season in Arizona, Stebbins (2003) reported *I. alvarius* was not dependent on rainfall for breeding. Consequently there are reports of breeding before the onset of summer rainfall in June in New Mexico and tadpoles in October, indicating a prolonged breeding season may, in some cases, occur (Degenhardt et al. 1996).

Acknowledgments—I thank G.B. Pauly (LACM) for permission to examine *I. alvarius*.

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Table 1. Two monthly stages in the ovarian cycle of 25 adult female *Incilius alvarius* from Pima County, Arizona.

Month	<i>n</i>	(1) Ready to Spawn	(2) Not in Spawning Condition
July	16	15	1
Aug.	6	3	3
Sept.	3	1	2

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Incilius alvarius move overland to breeding sites with the start of the summer monsoon (Fouquette et al. 2005). Sullivan and Malmos (1994) reported *I. alvarius* breeding occurred in one night following a rainfall > 25 mm, although breeding might be delayed until the second or third night after extensive flooding.

Appendix: Forty-three *Incilius alvarius* from Pima County, Arizona examined from the herpetology collection of the Natural History Museum of Los Angeles County (LACM), Los Angeles, California, USA.

LACM: 926, 87018, 87020, 87029, 87031, 87033, 87034, 87036, 87042, 107297, 107298, 115165, 115166, 123204, 123205, 132621, 132622, 145654, 145655, 146797–146800, 146802–146806, 146808, 146809, 150918, 150919, 150922, 150923, 150928, 150930, 150932, 150935–152737, 152738, 181334, 181335.

Horned Lizards (*Phrynosoma*) of Sonora, Mexico: Distribution and Ecology

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Mexico is recognized globally as a mega-diversity country. The state of Sonora has very diverse fauna, flora, and vegetation. The diversity of horned lizards in the genus *Phrynosoma* (Phrynosomatidae) in the state of Sonora is a reflection of the landscape and biotic diversity. In this paper, we summarize the distribution and ecology of eight species of *Phrynosoma* in Sonora.

Methods

Study area

The great biodiversity of Sonora is the result of complex biogeography and ecology. The elevation in Sonora ranges from sea level at the Gulf of California to over 2600 m in the Sierras Los Ajos and Huachinera (Mario Cirett-G., pers. comm., 2017). The Sierra Madre Occidental (SMO) reaches its northern limits in eastern Sonora and western Chihuahua. North of the SMO, the Madrean Archipelago or Sky Islands Region extends to the Mogollon Rim in central Arizona. Sky Islands are isolated mountain ranges with crowns of oak woodland and/or pine-oak forest surrounded by lowland 'seas' of desertscrub, desert grassland, foothills thornscrub, or tropical deciduous forest (Van Devender et al. 2013). There are 55 Sky Islands and Sky Island complexes connected by oak woodland in the Madrean Archipelago, 32 of them in Sonora (Deyo et al. 2013).

Six biotic provinces with characteristic animals, plants, and vegetation converge in the Madrean Archipelago. The Rocky Mountains and Colorado Plateaus to the north have cold temperate climates. To the northeast, winter rainfall-dominated Mediterranean chaparral extends from California east to central Arizona. In the mid-continent, Great Plains grassland occurs from Canada south to the Mexican Plateau, and west to southern New Mexico, southeastern Arizona, and northeastern Sonora. The Chihuahuan biotic province reaches its southwestern limit in northeastern Sonora. In much of this area, Chihuahuan desertscrub occurs on rocky slopes adjacent to grassland in the adjacent valleys. The desert grassland of southeastern Arizona is replaced by foothills thornscrub about 100 kilometers south of the Arizona border as winter freezing temperatures decline. This ecotone is really the transition between the New World tropics and northern temperate biotas. Tropical deciduous forest is on the lower slopes

of the Sierra San Javier, the southernmost Sky Island (Van Devender et al. 2013). The Sierra Madre Occidental reaches its northern limit in eastern Sonora, with Madrean species present in the oak woodland and pine-oak forests in the higher elevations of the Sky Islands. West of the Madrean Archipelago, desertscrub vegetation is present in the Sonoran Desert lowlands of western and central Sonora.

Phrynosoma records

Eight species of *Phrynosoma* are reported from Sonora (Enderson et al. 2010; Rorabaugh and Lemos 2016). Distribution records from various sources and many photo vouchers are publicly available in the Madrean Discovery Expeditions (MDE) database (madreandiscovery.org)

Results

Phrynosoma cornutum, Texas Horned Lizard (Harlan, 1824)

In the United States, *Phrynosoma cornutum* ranges from Colorado and Kansas south to Texas and west to Arizona. Texas horned lizards may also be native to Louisiana and Arkansas. Introduced populations are found in the Carolinas, Georgia, northern Florida, and in the Honolulu area on Oahu Island in Hawaii (Hunsaker and Breese 1967). In Mexico, it is found throughout the Mexican Plateau as far south as Aguascalientes, San Luis Potosí, and Zacatecas (Arenas et al. 2014). In Sonora, *P. cornutum* is known in Chihuahuan desertscrub and desert grassland at 1136 to 1492 m elevation close to the Arizona border in the Agua Prieta-Naco area (Figs. 1 and 2). The southernmost record at Fronteras (49 km south of the border) was collected in June 1935 by Barry Campbell from the University of Michigan. He was in route to the Sierra El Tigre, where he made an important herpetological collection, including the first state records for Mexican Plateau Horned Lizard (*P. orbiculare*), Twin-spotted Rattlesnake (*Crotalus pricei*), and Ridge-nosed Rattlesnake (*C. willardi*). One animal was seen on Mesa las Víboras 30 km east of Agua Prieta. In this area, the vegetation is a unique dwarf (less than a meter tall) velvet mesquite (*Prosopis velutina*) scrub on reddish clay soils.

Mexico is recognized globally as a mega-diversity country. The state of Sonora has very diverse fauna, flora, and vegetation. The diversity of horned lizards in the genus *Phrynosoma* (Phrynosomatidae) in the state of Sonora is a reflection of the landscape and biotic diversity.



Figure 1. *Phrynosoma cornutum*. **A.** South of Ojinaga, Chihuahua, July 1972. Photo by Thomas R. Van Devender. **B.** Pat Hills, south of Willcox, Arizona, May 2015. Photo by Chris Roll. **C.** Mesa Las Víboras, east of Agua Prieta, Sonora, April 2008. Photo by Thomas R. Van Devender. **D.** Pat Hills, Arizona, May 2015. Photo by Chris Roll.

***Phrynosoma ditmarsii*, Rock Horned Lizard (Stejneger, 1906)**

Phrynosoma ditmarsii is endemic to the state of Sonora (Fig. 2). The species was first collected on the Carl S. Lumholtz expeditions to Mexico in 1890–91 from “Sonora.” Two additional specimens collected “a short distance over the border of Arizona, in old Mexico, state of Sonora” in 1897 were described as a new species by Stejneger (1906). The species was not found again for 73 years, when mining engineer Paul Geiger discovered it on Rancho El Alacrán in the Sierra Manzanal (now called the Sierra Alacrán) southeast of Cananea (Lowe et al. 1971). Today it is known from the Sierras Alacrán and Manzanal near Cananea south through the Sierras la Púrica, Nacozari (Burkhardt and Trageser 2015), la Madera, Babiácora, Lampazos, and Murrieta (Turner et al. 2017; Fig. 3). It is recorded from the western edge of the Sierra Madre Occidental near Nácori Chico and Ónavas (Perrill 1983), and was recently found in lowland areas at Bacerac, Colonia Aribabi, and Subitatchi. It typically lives in desert grassland-oak woodland transition, but has been found in oak woodland, desert grassland, foothills thornscrub, and tropical deciduous forest at 950 to 1679 m elevation. *P. ditmarsii* is only occasionally encountered in rocky habitats away from paved roads.

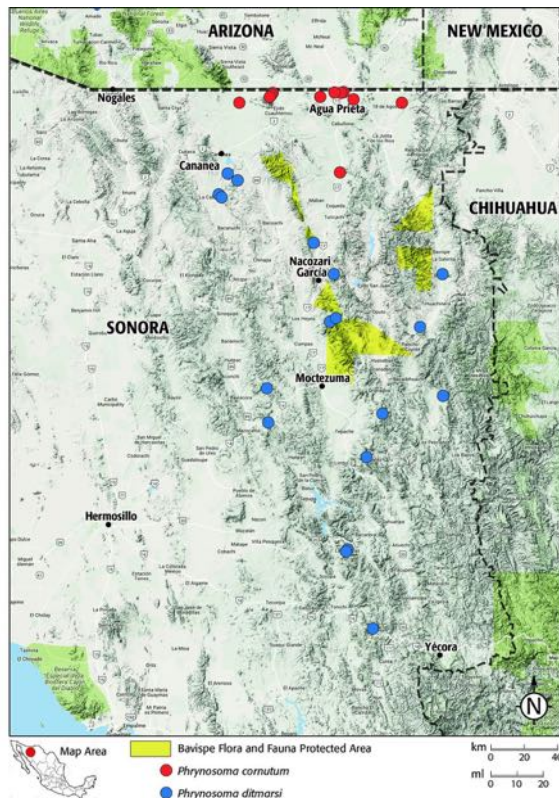


Figure 2. Known distribution of *Phrynosoma cornutum* and *P. ditmarsii* in Sonora, Mexico.

Phrynosoma ditmarsii is endemic to the state of Sonora (Fig. 2). The species was first collected on the Carl S. Lumholtz expeditions to Mexico in 1890–91 from “Sonora.” Two additional specimens collected “a short distance over the border of Arizona, in old Mexico, state of Sonora” in 1897 were described as a new species by Stejneger (1906).



Figure 3. *Phrynosoma ditmarsii*. **A.** Rancho la Palma, east-northeast of San José de Babiácora, Sonora, September 2004. Photo by Erik F. Enderson. **B.** Top of head. Rancho Subitatchi, Sonora, November 2016. Photo by Ana L. Reina-Guerrero. **C.** Rancho las Tierras de Jimenez, Sierra de Murrieta, Sonora, August 2014. Photo by Stephen L. Minter. **D.** Side view of head. Rancho Subitatchi, Sonora. Photo by Ana L. Reina-Guerrero. **E.** *Sceloporus*-like keeled scales on chest. Rancho Subitatchi, Sonora. Photo by Ana L. Reina-Guerrero. **F.** Front view of head. Rancho Subitatchi, Sonora. Photo by Ana L. Reina-Guerrero.

***Phrynosoma goodei*, Goode's Horned Lizard (Stejneger, 1893)**

Phrynosoma goodei occurs from Punta Sargento on the coast of the Gulf of California to the Colorado River in western Sonora and north to the Gila River and east to the Tucson area in Arizona. It is found in sandy and rocky habitats in Sonoran desertscrub (Figs. 4 and 5). Formerly, it was considered a subspecies of *P. platyrhinos*.

***Phrynosoma hernandesi*, Greater Short-Horned Lizard (Girard, 1858)**

Phrynosoma hernandesi ranges from Alberta and Saskatchewan in Canada to North Dakota and Montana

south to Utah, Nevada, Arizona, and New Mexico in United States, and Chihuahua, Durango, and Sonora in Mexico. The taxonomy of the *P. douglasii* species complex, including *P. hernandesi*, was reviewed by Montanucci (2015). In Sonora, it is known in the Municipalities of Agua Prieta, Cananea, Cumpas, Fronteras, Ímuris, Naco, Nacozari de García, and Nogales, where it lives at 1294 to 2470 m elevation in desert grassland, plains grassland oak woodland, and pine-oak forest (Fig. 6 and 7). *P. hernandesi* can tolerate cooler temperatures than most other Sonoran horned lizards.

***Phrynosoma mcallii*, Flat-tailed Horned Lizard (Hallowell, 1852)**

Phrynosoma mcallii species occurs in northwestern

Phrynosoma goodei occurs from Punta Sargento on the coast of the Gulf of California to the Colorado River in western Sonora and north to the Gila River and east to the Tucson area in Arizona. It is found in sandy and rocky habitats in Sonoran desertscrub (Figs. 4 and 5). Formerly, it was considered a subspecies of *P. platyrhinos*.



Figure 4. *Phrynosoma goodei*. All Pinacate Biosphere Reserve, Sonora. **A.** February 2008. Photo by James O. Rorabaugh. **B.** Top of head. March 2012. Photo by Thomas R. Van Devender. **C.** Photo by Thomas R. Van Devender. **D.** Side of head. March 2012. Photo by Thomas R. Van Devender. **E.** Front view of head. Photo by Thomas R. Van Devender. **F.** Detail of scales on back. March 2012. Photo by Thomas R. Van Devender.

Sonora, northeastern Baja California, southwestern Arizona, and southeastern California (Figs. 5 and 8). It lives in sandy Sonoran desertscrub at 0 to 300 m elevation (Rodríguez 2002). This species has an unusually flattened body, a long, broad, flat tail, dagger-like horns, no external openings, and color matches the soil very well.

***Phrynosoma modestum*, Round-tailed Horned Lizard (Girard, 1852)**

Phrynosoma modestum ranges from southeastern Colorado, western Texas, and southern New Mexico to southeastern Arizona in the United States. In Mexico, it occurs on the Mexican Plateau from Chihuahua and Coahuila south to Aguascalientes, San Luis Potosi, and Zacatecas. In Sonora, it has been found only near Agua Prieta at 1211 to 1326 m elevation in Chihuahuan

desertscrub and desert grassland (Figs. 9 and 10). Neonate *Phrynosoma* are more similar to each other than adults. *P. modestum* is a small, paedomorphic species, where the adults retain juvenile morphology in plain color patterns, simple dorsal scales, and modest horn development. Adults match the color of the soil very well, and simply hide among the stones in the open to avoid predators.

***Phrynosoma orbiculare*, Mexican Plateau Horned Lizard (Linnaeus, 1758)**

Phrynosoma orbiculare is a Mexican species that ranges from the Sierra Madres Occidental and Oriental and the Mexican Plateau south to Puebla and Veracruz, and to western Chihuahua and the Yécora area in easternmost Sonora (Enderson et al. 2014, Van Devender et al. 2017; Fig. 7). A disjunct population in the Sierra

Phrynosoma modestum ranges from southeastern Colorado, western Texas, and southern New Mexico to southeastern Arizona in the United States. In Mexico, it occurs on the Mexican Plateau from Chihuahua and Coahuila south to Aguascalientes, San Luis Potosi, and Zacatecas.

el Tigre, Municipality of Nacozari de García is 225 kilometers north of Yécora (Van Devender et al. 2015). It was recently found in between these two populations near Mesa Tres Ríos, Municipality of Nácori Chico in the northernmost Sierra Madre Occidental 149 km north-northeast of Yécora (Cabrera-H. et al., in press). In Sonora, this species lives in pine-oak forest at 1720 to 2412 m elevation (Fig. 11). It is common in the Sierra el Tigre, but less so in the Yécora area.

***Phrynosoma solare*, Regal Horned Lizard (Gray, 1845)**

Phrynosoma solare ranges from southwestern New Mexico and Arizona in the United States south through Sonora to northern Sinaloa in Mexico. In Sonora, it lives from near sea level to 1400 m elevation in Chihuahuan and Sonoran deserts scrub, desert grassland, coastal and foothills thornscrub, tropical deciduous forest, and open oak woodland (Figs. 10 and 12). It occurs on Tiburón Island in the Gulf of California. It is very widely distributed and the most common species in Sonora. The basic body coloration can be shades of gray, tan, brown, orange, or red, generally re-



Figure 5. Known distribution of *Phrynosoma goodei* and *P. mcallii* in Sonora, Mexico.

Phrynosoma solare ranges from southwestern New Mexico and Arizona in the United States south through Sonora to northern Sinaloa in Mexico. In Sonora, it lives from near sea level to 1400 m elevation in Chihuahuan and Sonoran deserts scrub, desert grassland, coastal and foothills thornscrub, tropical deciduous forest, and open oak woodland.



Figure 6. *Phrynosoma hernandesi*. **A.** Cañada el Pinalito, Sierra Elenita, Sonora, September 2015. Photo by Thomas R. Van Devender. **B.** Front view of head after squirting blood from eye. Sierra la Púrica, July 2013. Photo by Charles Hedgcock. **C.** Sierra la Púrica, July 2013. Photo by Charles Hedgcock. **D.** Side view of head. Sierra la Púrica, July 2013. Photo by Charles Hedgcock. **E.** Sierra la Púrica, July 2013. Photo by Charles Hedgcock. **F.** Juvenile color matching stones in bare area in desert grassland near Cananea, Sonora, September 2014. Photo by Thomas R. Van Devender.

flecting local substrates. The back can be patternless, or with various pattern elements, including an oval mid-dorsal light area, spots, three transverse bands, and a mid-dorsal stripe (Figs. 12A, C, E, and G.). The head can be the same color as the body, but the four largest horns are typically a contrasting reddish brown.

Discussion

Diversity and Habitat

The state of Sonora with eight species has the greatest diversity of *Phrynosoma* of any state in Mexico or the United States. The most commonly encountered species are *P. hernandesi* and *P. solare* in the east and *P. goodei* and *P. mcallii* in the west. *Phrynosoma goodei*, *P. mcallii*, and *P. solare* live in sparse desertscrub in the Lower Colorado River Valley subdivision of the Sonoran Desert from the Gulf of California in western Sonora inland to Arizona, California, and Baja California. *P. goodei* and *P. solare* are in the Central Gulf Coast subdivision of the Sonoran Desert along the coast of the Gulf of California. *P. solare* is the only horned lizard present in the Arizona Upland and Plains of Sonora subdivisions in northern and central Sonora, but also lives in desert grassland and tropical vegetation to the east. *P. cornutum* and *P. modestum* occur in Chihuahuan desertscrub and desert grassland near Agua Prieta and Naco.

There are three upland species of *Phrynosoma* in Sonora. *P. hernandesi* is common in desert grassland near Cananea, plains grassland east of Agua Prieta, and oak woodland and pine-oak forests in the Sky Islands (Sierras los Ajos, Avispas, Azul, Buenos Aires, Elenita, Madera [Oposura], Mariquita, Pan Duro, Púrica, and San Luis). *P. orbiculare* is a pine-oak forest species found in the Mexican Plateau and Sierra Madre Occidental reaching Sonora in the Yécora and Mesa Tres Río areas and in the Sierra el Tigre. Interestingly *P. hernandesi* has not been found in these areas.

Phrynosoma ditmarsii is endemic to Sonora (Turner et al. 2017). It is known from oak woodland and desert grassland from the Sierras Alacrán and Manzanal south of Cananea south through the Sierras la Púrica, Nacozari, la Madera, Babiácora, Lampazos, and Murrieta, and recently in desert grassland in the Río Bavispe Valley. Some of these localities are close to the western edge of the Sierra Madre Occidental, suggesting that it may eventually be found in Chihuahua.

Horned lizards are best known as desert-adapted lizards, and in Sonora five species occur in desertscrub in four subdivisions of the Sonoran Desert and the Chihuahuan Desert. But *Phrynosoma* also lives in desert grassland, coastal and foothills thornscrub, tropical deciduous forest, oak woodland, and pine-oak forest. Desert grassland with five species has the greatest diversity. *P. cornutum*, *P. modestum*, and *P. solare* are

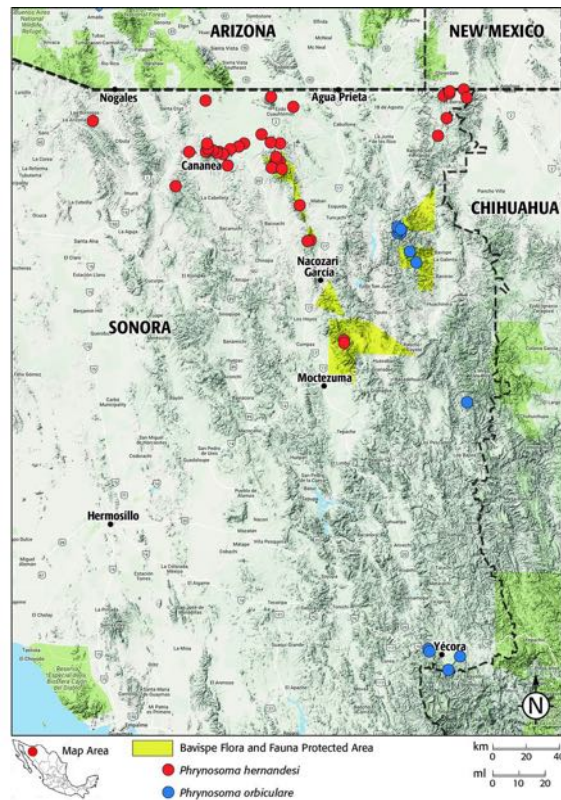


Figure 7. Known distribution of *Phrynosoma hernandesi* and *P. orbiculare* in Sonora, Mexico.

potentially sympatric near Agua Prieta in Chihuahuan desertscrub/desert grassland transition. *P. cornutum*, *P. ditmarsii*, and *P. hernandesi* are potentially sympatric in desert grassland in the Cananea area. *P. ditmarsii* and *P. solare* were found at the same locality in the Sierra Manzanal. *P. hernandesi* and *P. solare* both occur on Rancho el Aribabi in the Sierra Azul. In the Lower Colorado River Valley in northwestern Sonora and adjacent Arizona, *P. goodei*, *P. mcallii*, and *P. solare* potentially live in the same area. *Phrynosoma mcallii* prefers areas of fine-grained silica sand, while *P. goodei* specializes in granite-derived sands on desert bajadas (Rorabaugh pers. comm. 2018). They are sympatric in the sandy flats north of Puerto Peñasco. *Phrynosoma ditmarsii* and *P. hernandesi* both live in oak woodland and may co-occur in the Sierras Nacozari and la Púrica. *Phrynosoma hernandesi* and *P. orbiculare* both live in pine-oak forest, but not in the same areas.

Conservation Status

We think that most of these horned lizards are reasonably common and not seriously threatened by habitat destruction. Horned lizard populations are locally impacted by human activities including cattle grazing, buffelgrass planting, mining, and disturbance near rural towns. Human interest in horned lizards was reflected by sculptures and myths in various American indigenous groups (Sherbrooke 2003). Before rigorous protection laws, horned lizards were commonly sold as pets in the United States, even though they quick-

There are three upland species of *Phrynosoma* in Sonora. *P. hernandesi* is common in desert grassland near Cananea, plains grassland east of Agua Prieta, and oak woodland and pine-oak forests in the Sky Islands (Sierras los Ajos, Avispas, Azul, Buenos Aires, Elenita, Madera [Oposura], Mariquita, Pan Duro, Púrica, and San Luis).



Figure 8. *Phrynosoma mcallii*. **A.** Southeast of El Golfo de Santa Clara, April 2017. Photo by S. Campbell. **B.** Top view of head. Machorro Canyon, east-southeast of El Golfo de Santa Clara, March 2011. Photo by A. Ferrell. **C.** Near San Luis Río, 1980. Photo by R. Wayne Van Devender. **D.** Side view of head. Southeast of El Golfo de Santa Clara, April 2017. Photo by S. Campbell. **E.** Near San Luis Río, 1973. Photo by R. Wayne Van Devender. **F.** Top view of head. North-northwest of El Golfo de Santa Clara. Photo by E. Scott.

ly died. In Bacerac, Sonora on the Río Bavispe, people occasionally keep camaleones as pets. This is of special concern because a *P. ditmarsii* was recently found in this town.

In the 1970s, University of Arizona students Wayne Howard and Michael D. Robinson collected large series of *P. cornutum* and *P. modestum* near Agua Prieta and Naco. In recent decades of relatively intense biological inventories, only a few individuals have been seen in these areas. One *P. modestum* area is now part of urban Agua Prieta. These species may have declined in Sonora, but are widespread in Chihuahua, Coahuila, and Texas.

Protection Status

Only *Phrynosoma mcallii* and *P. orbiculare* are listed as Threatened (Amenazada) in the Mexican endan-

gered species law (NOM 059 SEMARNAT 2010). Curiously *P. ditmarsii* was also Threatened in earlier versions of the law, but delisted. The rest of the Sonoran species of horned lizards are not federally protected in Mexico or the United States. There has been an international effort to protect *P. mcallii* in the United States and Mexico. It is a high priority species in the Alto Golfo de California Biosphere Reserve in the Pinacate region of northwestern Sonora. It is illegal to collect *P. mcallii* in Arizona and California without a state scientific collection permit, and it has a Near Threatened status in the 2015 IUCN Red List. As a candidate for federal listing, it was extensively studied in Arizona and California, but not listed. Observations in the last eight years by vertebrate paleontologists prospecting for Pleistocene fossils in sedimentary badlands show that it is common near El Golfo de Santa Clara, Sonora (Fred Croxen, pers. comm. 2017).

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Figure 9. *Phrynosoma modestum*. **A.** Black Gap, Texas, June 1978. Photo by Thomas R. Van Devender. **B.** Side view of head. Black Gap, Texas, June 1978. Photo by Thomas R. Van Devender. **C.** Sierra Anibácachi, southwest of Agua Prieta, June 2007. Photo by R. Wayne Van Devender. **D.** Side view of head. Sierra Anibácachi, southwest of Agua Prieta, June 2007. Photo by R. Wayne Van Devender. **E.** Pat Hills, south of Willcox, Arizona, July 2010. Photo by Chris Roll. **F.** Top view of head. Pat Hills, south of Willcox, Arizona, July 2010. Photo by Chris Roll.

Protected Areas

Phrynosoma are present in protected areas in Sonora, although common or smaller species are not individually managed. There are six federal reserves managed by the Comisión Nacional de Áreas Naturales Protegidas (CONANP) in Sonora. *Phrynosoma hernandesi*, *P. ditmarsii* and *P. orbiculare* are in the Área de Protección de Flora y Fauna (APFF) Bavispe (formerly the Reserva Forestal Nacional y Refugio de Fauna Silvestre Ajos-Bavispe) in northeastern Sonora. *P. ditmarsii*, *P. cornutum*, *P. modestum*, and *P. solare* are known from nearby areas of conservation interest. *P. hernandesi* lives in the Área Natural Protegida Destinada Voluntariamente a la Conservación (ANPDVC) Sierra la Mariquita in northern Sonora. *P. hernandesi* and *P. solare* both occur on ANPDVC Rancho el Aribabi in northern Sonora. *P. solare* is in the proposed APFF Sierra Huérfana (= Sierra Mazatán) in central Sono-

ra, and the APFF Sierra de Álamos-Río Cuchujaqui in southern Sonora. *P. goodii*, *P. mcallii*, and *P. solare* are in the El Pinacate y Gran Desierto de Altar Biosphere Reserve (administered by CONANP) in western Sonora.

Phrynosoma are also present on private protected natural areas in Sonora. The Cuenca Los Ojos Foundation (cuencaalosojos.org/) owns six ranches in northeastern Sonora. *P. hernandesi* is common in plains grassland in the southern extension of the Animas Valley and in montane woodlands and forest in the nearby Sierra Pan Duro and San Luis. *P. solare* has been seen at Rancho Puerta Blanca. *P. cornutum* has not been reported from CLO but is likely to occur in Chihuahuan desertscrub on Rancho San Bernardino. *P. hernandesi* is on the Reserva los Fresnos owned by The Nature Conservancy near the Arizona border in northern Sonora, and *P. solare* is common in foothills thornscrub on the Northern Jaguar Reserve (www.northernjaguarpro-

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ject.org/northern-jaguar-reserve/) in east-central Sonora (Rorabaugh et al. 2011).

Acknowledgments—We learned so much from horned lizard gurus Wade Sherbrooke and Richard Montanucci. We thank *GreaterGood.org* for supporting Madrean Discovery Expeditions biodiversity inventories and conservation in Sonora. We thank Ana Lilia Reina-Guerrero, James C. Rorabaugh, Fred Croxen, Dale S. Turner, Hugo Silva-Kurumiya, Frank W. Reichenbacher, R. Wayne Van Devender, Norberto León del Castillo, Charles Hedgcock, Chris Roll, Victor Hugo Cabrera-Hernández, Guillermo Molina-Padilla, Joseph Scheer, and Michael F. Wilson for sharing their observations and images of *Phrynosoma* in Sonora. Rorabaugh's careful editing improved the manuscript. We thank Mario Cirett-Galán, Francisco Isaias Ochoa-Gutiérrez, and APFF Bavispe guarda bosques for participating in MDE Expeditions. Financial support to Aguilar-Morales was from the Horned Lizard Conservation Society and the MDE Student Scholarship program. Ed Gilbert created the MDE database. Dennis Caldwell drafted the maps.

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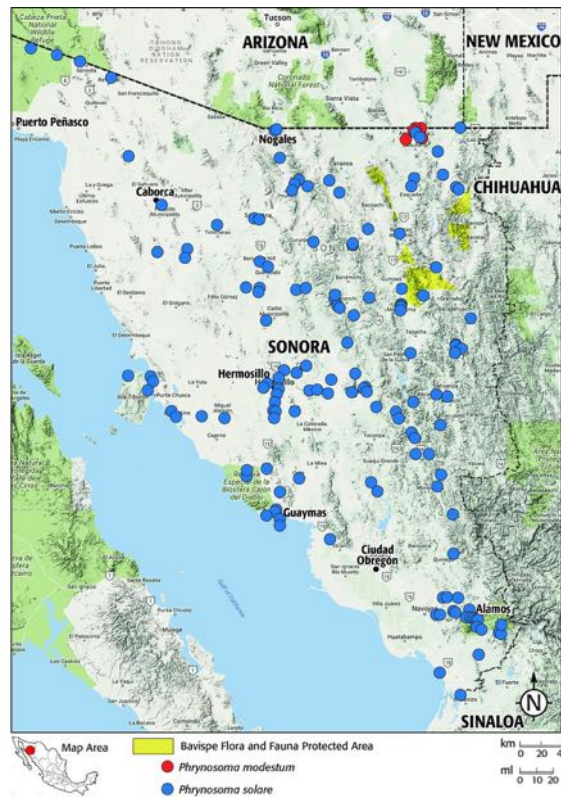


Figure 10. Known distribution of *Phrynosoma modestum* and *P. solare* in Sonora, Mexico.

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Figure 11. *Phrynosoma orbiculare*. **A.** Mesa del Campanero, west of Yécora, August 2010. Photo by Joseph Scheer. **B.** Side view of head of juvenile. Rancho el Tigre, Sierra el Tigre, August 2015. Photo by R. Wayne Van Devender. **C.** Rancho el Tigre, Sierra el Tigre, August 2015. Photo by R. Wayne Van Devender. **D.** Side view of head. Rancho el Tigre, Sierra el Tigre, August 2015. Photo by R. Wayne Van Devender. **E.** Pair found mating. Rancho el Tigre, Sierra el Tigre, August 2015. Photo by Guillermo Molina-Padilla. **F.** Rancho el Tigre, Sierra el Tigre, August 2015. Photo by R. Wayne Van Devender.

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Figure 12. *Phrynosoma solare*. **A.** La Mesa de San Patricio, south of Moctezuma, May 2012. Photo by Hugo Silva-Kurumiya. **B.** Top of head. West of Estancia, September 2012. Photo by Thomas R. Van Devender. **C.** North-northeast of Nácori Grande, July 2012. Photo by Thomas R. Van Devender. **D.** Side of head. West of Estancia, September 2012. Photo by Thomas R. Van Devender. **E.** East of Benjamín Hill, May 2009. Photo by Thomas R. Van Devender. **F.** Side of head. West of Estancia, September 2012. Photo by Thomas R. Van Devender. **G.** Hermosillo, July 2000. Photo by Thomas R. Van Devender. **H.** Dorsal pattern. West of Estancia, September 2012. Photo by Thomas R. Van Devender.

Crypsis and Flight Initiation Distance in Horned Lizards

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Abstract

Horned lizards of the genus *Phrynosoma* are unique within Phrynosomatidae in having broad, flat bodies, slow running speed and highly developed crypsis. Escape theory predicts that cryptic prey should allow predators to approach more closely than less cryptic prey before starting to flee, i.e., should have shorter flight initiation distance (FID). We measured flight initiation distance in three species of horned lizards found in the Sonoran and Chihuahuan Deserts and associated mountains, *Phrynosoma cornutum*, *P. hernandesii*, and *P. modestum*. Each of the three species had shorter FID than any of 66 other lizard species for which FID was comparably measured. A single origin of shortened FID in the common ancestor can account for available data. Chameleons appear to have similarities associated with altered body form, slow (often arboreal) running/escape speed and reduced FID, as may *Moloch horridus* and possibly other species discussed.

Introduction

Horned lizards (*Phrynosoma*) are exceptional among lizards in many ways, including their broad body form, slow running speed, and crypsis (Sherbrooke 2003). Their specialized ant diet is believed to have led to evolution of their specialized morphology, and their consequent slow running speed has favored natural selection enhancing crypsis (Pianka and Parker 1975). Escape behavior by lizards is influenced strongly by crypsis and habitat factors that make lizards difficult to detect. Cryptic lizards have short flight initiation distance (FID = distance between a prey and an approaching predator when the prey begins to flee; Stankowich and Blumstein 2005, Cooper 2015a, Samia et al. 2015). Because horned lizards are exceptionally cryptic, it may be predicted that they have shorter FID than typical lizards. Laboratory studies showed that round-tailed horned lizards (*Phrynosoma modestum*) are both highly cryptic and have very short FID, especially against a background that renders them inconspicuous (Cooper and Sherbrooke 2010a, 2012). Similarly a short FID has been reported for *Phrynosoma cornutum* (Cooper and Sherbrooke 2010b). However, because FID of horned lizards in the field has not been reported, it has not been possible to compare their FID to that of lizards having typical body form, running speed and conspicuousness.

In a recent comparative study of escape behavior by lizards (Cooper et al. 2014), phylogeny had no de-

tectable influence on flight initiation distance (FID). Although the study included more than 60 species and representatives of diverse lizard taxa, all species were typical lizards that rely on rapid running to escape, that lack morphological adaptations restricting running ability greatly, and that lack extreme crypsis. However, it is precisely in atypical groups of species relying more on crypsis than speed to avoid predation that shorter FIDs are likely to occur.

Obvious candidate lizards that might reveal reduced escape responses in association with specialized morphology, reduced running speed and heightened crypsis are the phrynosomatid horned lizards of the genus *Phrynosoma*, the agamid thorny devil (*Moloch horridus*), and members of Chamaeleonidae, with the possible exception of species such as the Namaqua chameleon (*Chamaeleo namaquensis*), which has greater running ability on the ground than other true chameleons, yet is not fast and stops to defend itself when overtaken (personal observations, WEC). Horned lizards and the thorny devil share a suite of traits including broad body shape, short legs, protection by spines and/or horns and slow escape running speed (Pianka and Pianka 1970, Pianka and Parker 1975, Sherbrooke 1981, 1999, 2003). They are also cryptic when not moving (Pianka and Pianka 1970, Cooper and Sherbrooke 2010a, 2012) and are often easy to catch by hand (WCS and WEC, personal observations).

Optimal escape theory (Cooper and Frederick 2007, 2010, Cooper 2015a) and another cost-benefit model (Ydenberg and Dill 1986) predict that FID increases as predation risk increases and decreases as the cost of fleeing increases. The major cost of fleeing is opportunity cost, i.e., the fitness lost by giving up opportunities to forage, engage in social behavior, or conduct other beneficial activities. Opportunity costs will not be discussed further. Predictions about the effects of various factors affecting both cost of fleeing and predation risk (= cost of not fleeing) have been verified in many studies (reviewed for lizards by Samia et al. 2015, and for all prey by Stankowich and Blumstein 2005, and Cooper and Blumstein 2015). Previous studies have shown that FID decreases when circumstances such as plant cover, shadows, and similarity of lizards to their backgrounds reduce the probability of being detected by a predator (reviewed by Samia et al. 2015, and Cooper 2015b).

Therefore, we predicted that FID in horned lizards would be shorter than that of other lizards because horned lizards are very cryptic. We conducted a field study of FID in three highly cryptic species of *Phryno-*

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soma. Here, we present the first field data on horned lizard FID and discuss the role of crypsis in escape behavior of these phrynosomatid lizards and in chameleons and discuss its possible importance in other lizard taxa.

Methods

To study flight initiation distance in the vast majority of species for which observations of actual predator-prey encounters are rare, a human researcher approaches a prey, simulating approach by a potential predator. This procedure not only has the advantage of making it possible to collect data in a feasible time frame, but also is useful because human beings can approach over rough terrain containing obstacles that would block terrestrial approach by mechanical simulated predators. A large literature on flight initiation distance is based on human simulation of predators (Cooper and Blumstein 2015, Blumstein et al. 2015). Although antipredatory responses of some lizards may differ among predator types (Stuart-Fox et al. 2008, including *Phrynosoma*: Sherbrooke 2008, 2013, Sherbrooke and May 2008), such effects have not been detected with respect to FID (Cooper 2008).

In most circumstances walking through a habitat is an extremely inefficient way to detect horned lizards that have not previously received radio-telemetry transmitters. Nevertheless, the data for *P. hernandesi* were collected while walking through its natural habitat in the Chiricahua Mountains of southeastern Arizona in the Coronado National Forest near the Middle Fork of Cave Creek, 1,620 m. Data were collected whenever the opportunity arose during several field seasons in the mid- to late 2000s devoted primarily to field studies of more abundant sympatric lizards. Additional data were collected during the summer of 2016 in the Santa Catalina Mountains, 2,390 m, of the Coronado National Forest north of Tucson, Arizona.

When a *P. hernandesi* was sighted, WEC approached it directly at a practiced speed of ca. 0.7 m/s until it fled, then measured FID to the nearest 2.5 cm. Starting distance, the distance between predator and prey when approach begins was ca. 6 – 10 m. In many species FID increases as starting distance increases. However, starting distance does not affect FID at all or has only a minimal effect on FID at such a slow approach speed in other phrynosomatid species (Cooper 2005, Cooper et al. 2014). Flight initiation distance was recorded to the nearest 2.5 cm for all species. To ensure that lizards of all three species were aware of the investigator's presence and approach, the investigator always began the approach from a direction affording the lizard a clear view of him and ascertained that the lizard's visible eye was open.

To collect data for the other species, we located lizards by driving slowly (maximum speed ca. 56 km/hr)

along roads with little traffic in Hidalgo County, New Mexico on warm mornings in May and June of 2015–2018. At this time of year males move extensively, resulting in highly male-skewed sex ratios (Sherbrooke 2002a) and facilitating data collection by encounters on roads. When a lizard was sighted, the driver stopped the vehicle. When both of us were in the vehicle, we both got out and ascertained that the lizard had not fled from the car. We did not attempt to measure FID of lizards that had fled. One of us then stood still while well separated from the other at least 5 m from the lizard, usually at a considerably longer distance (5 – 10 m). Then one of us approached the lizard directly at ca. 0.7 m/s. Starting distance, the distance between predator and prey when approach begins, was ca. 6 – 12 m. In other cases, only WCS was present.

Summary statistics and statistical analyses were computed using Statistica. Data are presented as means \pm 1.0 SE. We tested for possible interspecific differences using analysis of variance for independent groups. We avoided pseudoreplication for *P. cornutum* and *P. modestum* by collecting all specimens following measurement of FID for use in other projects. Because *P. hernandesi* in the Chiricahuas were encountered sporadically and were not marked, it is possible that some individuals might have been measured more than once. The *P. hernandesi* data from near Tucson were independent data points collected in less than one hour on the same day in a single field where it was clear each FID was associated with a different individual.

To examine species differences in the proportions of lizards that did not flee (i.e., had FID = 0) we conducted Fisher exact probability tests for each of the three species pairs. We report the raw probability values, but the pattern of significance is the same as when the p values are adjusted for the number of tests conducted (Wright 1992).

We examined the data for conformity with the assumptions of homogeneity of variance using Levene's test and of normality using *d*. The estimate of effect size was η^2 . The ANOVA test was conducted two-tailed with $\alpha = 0.05$.

To make a preliminary assessment of the probability that horned lizards have shorter FID than other lizards in the comparative aspect of our study, as in the study of island tameness (Cooper et al. 2014), we conducted binomial tests in which the probability of FID being greater in horned lizards than in each of the other 66 species provide independent data points, which is false, but the result is informative regarding the extreme shortness of FID in horned lizards. In a second such test, we compared the FID of horned lizards to the mean FID for each of the 11 families represented in the island tameness study (Phrynosomatidae, Agamidae, Gekkonidae, Cordylidae, Scincidae, Teiidae, Lacertidae, Tropiduridae, Crotaphytidae, Iguanidae, and Polychrotidae.

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Results

The lizards typically gave no intension movements indicating readiness to flee, but at least one cocked its head toward an approaching researcher. The FID was very short in all three species (Fig. 1). Some individuals did not flee at all, allowing the researcher's foot to pass over their bodies (FID = 0). All 5 *P. modestum* (1.00), 5 of 36 (0.14) of *P. cornutum*, and 1 of 13 (0.08) *P. hernandesii* had FID = 0. The proportion that fled was significantly lower in *P. modestum* than in either of the other two species (Fisher exact $P = 0.019$ each. The proportion that fled did not differ significantly between *P. cornutum* and *P. hernandesii* (Fisher $P > 0.10$).

In an independent groups ANOVA, *P. modestum* was excluded due to zero variance and small sample size. For the two species having adequate sample sizes for adults, variances of FID were homogeneous (Levene's $F_{1,47} = 0.08$, $P = 0.78$) and the distribution did not deviate significantly from normality (Kolmogorov-Smirnov $d = 0.13$, $P > 0.05$). Flight initiation distance did not differ significantly between *P. cornutum* and *P. hernandesii* ($F_{1,47} = 1.05$, $P = 0.31$). The effect size was very small ($\eta^2 = 0.022$).

Mean FID of each of the horned lizard species was shorter than that of any of the 66 species included in the comparative lizard study, shorter even than the FIDs of lizard species inhabiting islands distant from the mainland. If FID data for all of the horned lizard species are pooled, their FID is the shortest of 67 entries. Assuming that FID is equally likely to be greater in horned lizards and each of the other species, the binomial probability that horned lizards have the shortest FID is < 0.0001 . This is clearly indicating that within Phrynosomatidae, the horned lizard FID is significantly shorter than that of the other lizards. This is a crude test because it does not take into account phylogenetic relationships among the other species. Nevertheless, the difference is robust because the other species in the sample include a broad diversity of lizards. In a binomial test of the mean FID for the three horned lizard species against the family means, including that of Phrynosomatidae, the binomial probability that the FID of horned lizards is the shortest among the families is $P = 0.001$.

Using FID = 0 for *Chamaeleo chamaeleo*, the probabilities are the same as for the two binomial test for horned lizards.

Discussion

Flight initiation distance by horned lizards when approached by a human simulated predator is shorter than that of all other lizards for which FID has been measured as describe in Cooper et al. (2014). In studies of typical lizards all individuals flee, but some individuals of the three species of *Phrynosoma* that we studied did not flee at all or did not flee until the pred-

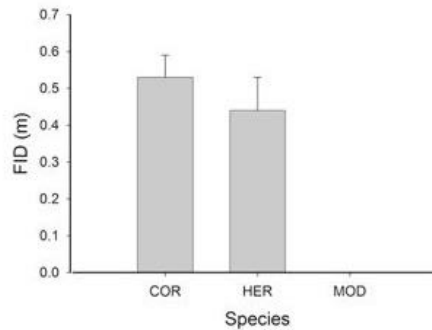


Figure 1. Mean flight initiation distance (FID) of three species of horned lizards: *Phrynosoma cornutum* – COR, *P. hernandesii* – HER, *P. modestum* – MOD. Error bars represent 1.0 SE.

ator had reached them, i.e., FID = 0. Such behavior strongly suggests that the escape responses of the three horned lizard species differ from those of other lizards, indicating that they rely more heavily than other lizards on crypsis to avoid being detected rather than on escape by fleeing. Flight initiation distance did not differ between *P. cornutum* and *P. hernandesii*, and the FID of *P. modestum* was significantly shorter than for the other two species.

The shorter FID of *P. modestum* might be a consequence of small sample size not adequately reflecting the behavior of *P. modestum*. This is credible because many individuals of *P. modestum* flee when approached in large enclosures (Cooper and Sherbrooke 2010a, 2012). However, the difference may be for two other reasons. *Phrynosoma modestum* is considered to be a stone mimic that relies heavily on this resemblance to avoid detection (Sherbrooke and Montanucci 1988, Sherbrooke 2003, Cooper and Sherbrooke 2010a, 2012). Also, FID increases as body length increase in lizards (Cooper et al. 2014) and *P. modestum* is the smallest of the three species.

Can very short FID be accounted for by something other than crypsis? Extreme habituation may lead to similar behavior in lizards exposed to extremely frequent human traffic. For example, FID of *Cordylus niger* at the Cape of Good Hope National Park in South Africa is exceptionally long for individuals located at least 200 m from the main trail to the southern overlook, but very short along the trail from the main tourist parking lot to the overlook; some individuals there could be touched if approached very slowly (Cooper and Whiting 2007). The *P. cornutum* and *P. modestum* in the present study were all from sparsely populated rural areas where contact with human beings was extremely infrequent or nonexistent. The *P. hernandesii* were found on or near trails in the Chiricahua Mountains where some human hikers and campers pass and in a field in the Catalina Mountains where people occasionally deposit debris. At neither site was exposure to human beings nearly as frequent as that at sites where pronounced habituation occurs that is associated with shortened FID. Furthermore, stripe plateau lizards (*Sceloporus virgatus*) from the same sites retain

The lizards typically gave no intension movements indicating readiness to flee, but at least one cocked its head toward an approaching researcher. The FID was very short in all three species (Fig. 1). Some individuals did not flee at all, allowing the researcher's foot to pass over their bodies (FID = 0). All 5 *P. modestum* (1.00), 5 of 36 (0.14) of *P. cornutum*, and 1 of 13 (0.08) *P. hernandesii* had FID = 0.

longer FID than in areas having greater human presence (Cooper 2009).

Habituation cannot be the reason that the horned lizards exhibited such short FID. We can think of no credible explanations for the extremely short FIDs unrelated to crypsis. Horned lizards are not aposematically colored. Their defenses include horns, spines and squirting of noxious blood from orbital sinuses at some mammalian predators. Nevertheless, these defenses do not prevent predation by a variety of reptilian, avian and mammalian predators (Sherbrooke 2003, 2013). Flight initiation distance increases as snout-vent length increases across lizard species, but the FIDs of the horned lizards are shorter than those of other lizards having comparable body length (Cooper et al. 2014, Samia et al. 2015; this paper).

The unusual adaptive suite of horned lizard characteristics that includes crypsis presumably led to the evolution of short FIDs in *Phrynosoma*. Because all species of *Phrynosoma* have wide and flattened bodies and are slow runners, crypsis should be favored by natural selection over fleeing to avoid predation. Horned lizards appear to flee only when the probability that they have been detected is very high. Once they flee, they are much easier to capture by pursuit than typical lizards. The balance between reliance on immobility, cryptic body form and coloration (Sherbrooke and Montanucci 1988, Sherbrooke and Frost 1989, Sherbrooke 1997, Sherbrooke 2002b) on the one hand and on fleeing on the other hand has shifted markedly toward crypsis in these lizards. Because the three species that we studied are widely distributed within the phylogeny of *Phrynosoma* (Leaché and McGuire 2006) and share the body form, slow running speed and cryptic coloration with the remaining species, we expect that future studies will demonstrate that FIDs are atypically short throughout the genus.

Short flight initiation distance appears to be associated with the combination of crypsis and slow running speed. The most extreme form of this trait combination occurs in the horned lizards, *Moloch* and *Chamaeleo*. Another lizard in which it might occur is *Cordylus cataphractus*, which has a broad body, is a slow runner, and is known for defending itself by biting its spiny tail, increasing its diameter to avoid being swallowed (Branch 1998). Among cordylid lizards, species having heavier armor are slower runners and run shorter distances when fleeing (Losos et al. 2002). We may expect that FID is shorter in slower, more heavily armored species such as *C. cataphractus*.

Chameleons are another very promising group for testing the relationship of the suite of horizontally or vertically compressed body form, reduced running speed and crypsis to FID. In contrast to horned lizards and thorny devils, chameleons have deep, narrow bodies and feet adapted for gripping branches rather than running rapidly (Pianka and Vitt 2003). Typical chameleons are extremely cryptic and rely on crypsis rather

er than fleeing to avoid predation. *Chamaeleo chamaeleo* is so cryptic that it is very difficult to detect and has therefore been collected for study at night when it is more visible under illumination by flashlight (Cuadrado et al. 2001, J. Martín, personal communication). In a study of escape behavior by *Chamaeleo chamaeleo*, flight initiation distance could not be used to measure escape response because the lizards did not flee when initially approached (Cuadrado et al. 2001). Consequently, the investigators used an alternative procedure of approaching and standing close to a chameleon, which sometimes induced the lizard to drop from the bush, usually with substantial latency. If the lizard did not drop or retreat, the investigator pointed at it for a time. If it still did not move, the investigator moved closer and repeated the process. The FID in this species is essentially zero.

We did not conduct a formal comparative analysis due to the small sample size of slow, cryptic taxa having short, measured FID, but it seems highly likely that crypsis and short FID are evolutionarily correlated. It seems clear that single evolutionary transitions to the suite of slow running, altered body form, crypsis and short flight initiation distance has occurred once in the common ancestor of *Phrynosoma*. The same may be true of *Moloch* and the Chamaeleonidae, but there are no data to establish this for chameleons. We encourage collection of FID data for *Moloch* and diverse chameleons, as well as for *Cordylus cataphractus*, twig anoles, and other highly cryptic species to facilitate a broad comparative study.

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Late Spring Mining of Minerals by Female Sonoran Desert Tortoises

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In 2011 we initiated a long-term radio-tracking study of Sonoran Desert Tortoises (= SDTs; *Gopherus morafkai*) on the eastern slopes of the southern Union Hills, on the northern edge of the Phoenix Metropolitan region (-33.73° N, 112.06° W). While recording feeding behavior over the past eight years, we have observed consumption of small bits of caliche and other mineral deposits by adult female SDTs (straight-line carapace length > 225 mm). Consumption of calcium rich items, including bone, rocks and soil layers, has been well documented in desert tortoises of the southwest (see review in Walde et al. 2007). Our observations suggest that at least for the Union Hills population of SDTs, females consume caliche and mineral deposits during the late spring and very early summer, consistent with the notion that developing eggs drive this behavior even though it occurs at a time when conditions are especially harsh with respect to water balance. Watching female SDTs consume hard, dry bits of caliche when they have had no access to free-standing water for months provides convincing evidence that the need for minerals is extreme.

Since 2011 we have radio tracked 15-25 adult SDTs each year, attempting to gather detailed observations on annual variation in space use and activity. Beginning in 2014, we opportunistically used video recording to document feeding behavior, and collected dozens of feeding episode videos over the past five years. We observed feeding during every month of the year; we obtained video recordings of feeding sequences for subsequent analysis during nine months of the year (February through October). Over eight years of observations, we occasionally observed consumption of small bits of caliche, or what we termed “caliche frag-

ments” encountered apparently at random along the wash bed and adjacent slopes. Examining these videos of feeding behavior, we determined that consumption of caliche fragments occurred on eight days from 26 May to 27 June in five years (2014-2018), by four different females. If one assumes that these caliche consuming events should have been randomly distributed across the nine months of our feeding observations on an annual basis, the clustering during this four-week period in late spring and early summer is highly significant ($P < 0.005$, Fisher’s Exact test).

The general behavior of SDTs during these caliche consuming events was similar in that females appeared to exhibit typical foraging behavior, walking slowly forward, touching their snout to the ground regularly. Immediately prior to consuming caliche fragments, after touching their snouts to the ground, females repeatedly pressed their snout against a particular caliche fragment (or whitish pea-sized stone), as if ascertaining the suitability of the fragment for consumption (Fig. 1). Often, a fragment was passed over after a few apparent (closed mouth) sampling efforts, but others were grasped and bitten, with audible scraping and crunching sounds produced (Fig. 1). On multiple occasions pea-sized bits were consumed after 5-10 seconds of mastication. On a few occasions, females consumed bits of dry grass and other vegetation over a 5-10 minute period of filming, with repeated consumption of caliche fragments interspersed among those events. On one occasion, a female sampled dry, white powder lining the surface of a small (1 meter diameter) former pool where a wash opened up and water regularly evaporated from a small catchment, leaving behind the salt residue. While pressing her snout against the substrate she repeatedly grasped and bit small rocks coated

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Figure 1. Female with snout pressed against caliche fragment immediately prior to mouthing (12 June 2018), left panel. Female crushing and biting caliche fragment (13 June 2016), right panel.

with white mineral deposits (Fig. 2).

Some have observed that Mohave Desert Tortoises (*Gopherus agassizii*) will move significant distances to mine minerals (Marlowe and Tollestrup 1982), and that they will consume bones of various vertebrates (Walde et al. 2007). Our observations reveal that at least within a caliche rich wash system, SDTs may not need to move far to sample calcium (and phosphorus) sources, and that these consumption events are clustered close to the reproductive period in which egg laying follows. Lovich et al. (2017) documented that for SDTs, the average date of first appearance of eggs within reproductive tracts is 6 June, and the average date of last appearance is 26 June, which accords well with our dates of caliche consumption of 26 May to 26 June. Our observations are limited by the relatively small sample size of observations ($n = 8$), and even lower number of individual females ($n = 4$), but are suggestive of a relationship between egg-laying and mining of minerals, at least for a population of SDTs in a caliche lined wash. It is of interest to note that juvenile SDTs have been observed mining during the monsoon (July-August; A. Owens, pers. comm.); of two juveniles

(SLCL < 180 mm) in our study population, the female was observed scrapping minerals with its forelimbs while inside a large caliche refuge (cave), briefly, during July, but we were unable to confirm consumption. Additional study will be necessary to more fully evaluate our hypothesis of a temporal link between mining and egg production in SDTs.

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Figure 2. Female biting a mineral encrusted rock in an area of regular water evaporation (26 May 2015). Note the white powder coating the substrate and small rocks.

Two Species of Foam Nest Forming *Rachophorus* Frogs Found in Different Twigs of a Guava Tree in Waynand, Kelara

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The Western Ghats is accepted worldwide as a region of significant importance for the conservation of biological diversity. A string of mountains running parallel to India's western coast, approximately 30-50 km inland, the Ghats traverse the States of Kerala, Tamil Nadu, Karnataka, Goa, Maharashtra, and Gujarat. These mountains cover an area of around 140,000 km² in a 1,600 km stretch that is interrupted only by the 30 km Palghat Gap at around 11°N. The Western Ghats is composed of extraordinary levels of plant and animal diversity and endemism. In particular, the level of endemism for some of the 4-5,000 plant species recorded in the Ghats is very high: of the nearly 650 tree species found in the Western Ghats, 352 (54%) are endemic. Animal diversity is also exceptional, with amphibians (up to 179 species, 65% endemic), reptiles (157 species, 62% endemic), and fishes (219 species, 53% endemic)

From 18 to 20 May 2018, during a search for amphibians on a rainy night within an abandoned mixed orchard, predominantly coffee plantations (11.8014° N, 76.0044° E, 2468 ft), Waynand district of Kerala, I observed two *Rachophorus* species in different twigs of a Guava Tree (*Psidium guajava*). The frogs were identified as *Rachophorus malabaricus* and *Rachophorus lateralis*.

The Old World tree frog family Rhacophoridae is one of the most diverse anuran families in the world (Frost 2013, Amphibia Web 2018). The Rhacophoridae (Asian Tree Frog) family has some 350 species in 16 genera of which 14 species are found in India. The Western Ghats mountain range is considered a distinct biogeographic unit (Biju and Bossuyt 2003, Bossuyt et al. 2004, 2006, Roelants et al. 2004, Bocxlaer et al. 2009), and contains four species of *Rachophorus* viz., *Rachophorus calcadensis* Ahl, *R. lateralis* Boulenger, *R. malabaricus* Jerdon, and *R. pseudomalabaricus* Vasudevan and Dutta, that are endemic to this chain of mountains.

Rachophorus malabaricus is a common species of frog from the Rhacophoridae family. It is a bright green frog with its back skin lightly granulated. Immature frogs have markings on their body, whereas adult frogs have no markings. The belly is more roughly granulated and it is mainly pale yellow. There are skin fringes between and along the long limbs. The webbing between fingers and toes is large and bright orange-reddish. The disks of fingers and toes are large. Snout is rounded and nostrils are located nearer to the end of the snout rather than near the eyes. It can glide short distances from branch to branch by stretching the webbing between its toes while jumping down from the top branches.

Rachophorus lateralis is restricted to two small areas of the southern Western Ghats of India in Kerala (Waynand) and Karnataka (Coorg). The frog was described by George Albert Boulenger in 1883 based on a single specimen from Kerala. For color-changing behavior, one immediately thinks of a chameleon, or an octopus, or even fall foliage (Grosjean et al. 2008). But nature has more than one 'trick' up her sleeve. *Rachophorus lateralis* has a spectacular behavior of color change. The background color of *R. lateralis* is green or reddish purple. Ventrally, the species is white or pinkish white. The head and back have dark dots, and colored parts of the limbs have dark cross lines. There is a white streak on each side from the nostril along the outer edge of the upper eyelid to the groin (Grosjean et al. 2008). Reproductive behavior is also quite unique. Nest construction in anurans with aquatic larvae has been interpreted as a method to protect early developmental stages against a high diversity of aquatic predators (Sayyed 2013). For this species, oviposition and fertilization occurs on a single leaf, after which the male leaves the female alone to roll the leaf containing foam and eggs into a purse-like nest. The



Fertilization in *Rachophorus* (photo by author, Western Ghats).



Rachophorus lateralis (photos by author, Western Ghats).

leaf folding pattern of behavior of *R. lateralis* may have evolved as an adaptive benefit since its loose foam needs the best security possible. This may be compared with the foam nest of other predominantly arboreal breeders among Indian Rhacophorid members (Sayyed 2013).

Adult *Rhacophorus malabaricus* are bright green colored. The species inhabits evergreen and semi-evergreen forests and builds arboreal foam nests. During spawning, the female extends its hind limbs and reverses them on to the back of the male. This brings the vent of the male closer to the female. After the completion of fertilization process the female holds the leaf containing the foam nest with its fore limbs and starts collecting leaves one after another from the surrounding area by stretching its hind limbs to cover the foam from all the sides. The foam itself acts as an adhesive for binding the leaves. The free end of the leaf holding the foam nest is folded by the frog to seal it from the lower end (Sayyed 2013).

In another case, spawning occurs on land. After the foam is formed, the male moves away from the site leaving the female and the foam. Immediately the female starts collecting the dead leaves from the surrounding area to cover the foam by stretching her limbs. Soon the foam nest is completely covered with litter (Sayyed 2013).

Rhacophorus pseudomalabaricus breeds on overhanging vegetation above the temporary water body, and tadpoles develop in these water bodies (Sayyed 2013).

Another frog species, *Rhacophorus nigropalmatus*, is a Moss Frog found in the Malay Peninsula, popularly known as Wallace's Flying Frog because Alfred R. Wallace collected the first specimen to be formally identified (Van Dijk et al. 2004). They also formed bubble nest on over-hanging twigs above water bodies. Females lay her eggs into the foam nest and at that time the male fertilizes these eggs (Van Dijk et al. 2004).

The production of foam nests has been reported in the genera *Polypedates*, *Rhacophorus*, *Chiromantis*, and *Chirixalus*. Animals form foams for many reasons, the most accepted being related to reproduction or protection of juveniles (Sayyed 2013). The largest such construction produced by land animals are the nests of species of frogs that form foam enclosures for their eggs and refuges for their hatched larvae. These nests are amazing for their constancy under harsh environmental conditions, and the diversity of sites in which they are produced, such as on the surface of water, in burrows, or suspended in vegetation. Foams require mechanical processing for the incorporation of air bubbles, and the processes and materials required may differ between types of foam (Sayyed 2013). Those produced by frogs that build nests floating on, and with, water face particular biophysical challenges; the foams must contain surfactant(s) to reduce the surface tension of water, and anti-microbial factors, all of which must be compatible with naked eggs and sperm. Foam nests are sometime directly deposited on the surface of pool or flowing water but often are found adjacent to water body (Sayyed 2013). Daily temperature deviation within foam nests resulted from the interaction of several factors: duration of direct solar radiation received by a nest, time of day, cloud cover, and extent of shading provided by surrounding vegetation. Terrestrial foam nests of anurans function to slow down desiccation of



Rhacophorus malabaricus (photos by author, Western Ghats).

eggs and larvae while apparently providing a thermally advantageous environment for rapid larval development (Sayyed 2013).

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MEETING MINUTES

BOD minutes can be found here:

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MEMBERSHIP

Membership Information

Individual	\$20	Sustaining	\$30
Family	\$25	Contributing	\$50
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The Tucson Herpetological Society would like to thank existing members and new members for renewing their membership. We appreciate your support and are always looking for members to actively participate in THS activities and volunteer opportunities. It is a great way to be involved with the conservation of amphibians and reptiles in the Sonoran Desert.

Including the THS in your will is an excellent way to support the value of this organization and the conservation of the herpetofauna of the Sonoran Desert. We would like to recognize and thank anyone who has included the THS in their will. Please contact us so we can express our appreciation. For information about designating the THS in your will, please contact Maggie Fusari, Treasurer, Tucson Herpetological Society, at maggiefusari@gmail.com.

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Thank you for your membership in the Tucson Herpetological Society. Renewal reminders for upcoming membership expiration will be emailed at the beginning of the month that your membership expires. If you have any questions about your membership or would like to be in touch with a THS member you do not know how to reach, please contact our Membership Coordinator, Robert Villa, by email: cascabel1985@gmail.com.

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Sonoran Herpetologist Natural History Observations

The Tucson Herpetological Society invites your contributions to our Natural History Notes section. We are particularly interested in photographs and descriptions of amphibians and reptiles involved in noteworthy or unusual behaviors in the field. Notes can feature information such as diet, predation, community structure, interspecific behavior, or unusual locations or habitat use. Please submit your observations to Howard Clark, editor.sonoran.herp@gmail.com. Submissions should be brief and in electronic form.

Local Research News

The *Sonoran Herpetologist* welcomes short reports for our Local Research News, a regular feature in our journal. We are interested in articles that can update our readers on research about amphibians and reptiles in the Sonoran Desert region. These articles need be only a few paragraphs long and do not need to include data, specific localities, or other details. The emphasis should be on how science is being applied to herpetological questions. Please submit your materials to Howard Clark, editor.sonoran.herp@gmail.com. Submissions should be brief and in electronic form.



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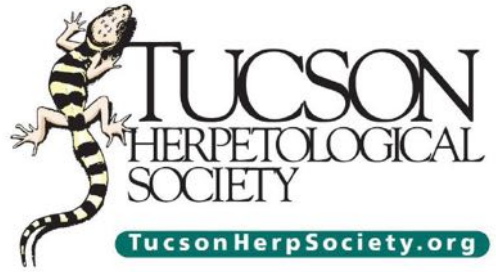
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Society Activities

Monthly Members Meeting

Jim Rorabaugh, Program Chair

jrorabaugh@hotmail.com

3rd Wednesday, 7:15 PM

Board of Directors Meeting

Last Wednesday of each month (except December), 7:00 PM

Speakers Bureau (scheduled presentations)

Robert Villa

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Sonoran Herpetologist, *Backyard Ponds* brochure,

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For more information about the THS and the reptiles and amphibians of the Tucson area visit
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