The Southwestern Naturalist 57(1): 39–43 March 2012

HABITAT SELECTION BY FORAGING TEXAS HORNED LIZARDS, *PHRYNOSOMA CORNUTUM*

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Abstract—The Texas horned lizard, *Phrynosoma cornutum*, feeds primarily on harvester ants (*Pogonomyrmex*) across much of its range. We quantified behavior of *P. cornutum* foraging on *Pogonomyrmex* relative to habitat and time. For the duration of their morning activity, 14 lizards were observed; we determined their use of habitat and location of ants that were captured. Lizards spent most of their time under vegetation; the type of vegetation used varied throughout the morning. Most feeding took place in the open and involved ants dispersed away from colonies. When feeding under vegetation, most feeding took place under mesquites (*Prosopis*), and location of mesquites under which lizards fed was nonrandom with respect to distance from entrances to colonies of ants. Feeding at entrances to colonies was restricted to a shorter period of the morning than feeding on dispersed ants. Males and females differed in use of habitat and in foraging behavior, with males more likely to feed in the open and to feed at entrances of colonies than females.

Resumen—La lagartija cornuda texana, *Phrynosoma cornutum*, se alimenta principalmente de hormigas del género *Pogonomyrmex* a lo largo de mucho de su distribución. Cuantificamos la conducta de *P. cornutum* forrajeando para *Pogonomyrmex* en cuanto al hábitat y la hora del día. Observamos 14 individuos durante su actividad en las mañanas; determinamos su uso del hábitat y donde capturaron las hormigas. Las lagartijas pasaron la mayoría del tiempo bajo la vegetación; el tipo de vegetación utilizada varió durante la mañana. Forrajearon principalmente en espacios abiertos y comieron hormigas alejadas de sus colonias. Cuando forrajeaban bajo la vegetación, fue principalmente bajo mezquites (*Prosopis*), y la colocación de mezquites bajo los cuales comieron no fue al azar en cuanto a la distancia de entradas de colonias de hormigas. Forrajearon en las entradas de las colonias por un período más restringido que cuando comieron hormigas dispersas. Los machos y las hembras difirieron en su uso del hábitat y su conducta de forrajeo: los machos comieron más en el espacio abierto y en las entradas de colonias que las hembras.

Horned lizards (*Phrynosoma*) are diurnal insectivorous lizards from arid regions of North America. As a group, they are considered to be ant-specialists (Pianka and Parker, 1975) and to possess a suite of morphological, physiological, and behavioral adaptations for subsisting on a diet of ants (Pianka and Parker, 1975; Montanucci, 1989; Schmidt et al., 1989; Sherbrooke, 2003; Meyers et al., 2006). Living on ants can be a challenge; individual ants typically are low in nutritional value (Redford and Dorea, 1984), and ants individually or collectively may be capable of strong (potentially lethal) defensive behavior. Further, use of habitat by ants may impose risk to predators searching for active ants. Horned lizards foraging for ants must balance the need to harvest large numbers of prey with the associated risk of predation or prey-induced injury.

Given the abundance of prey, foraging at entrances to colonies may be the most efficient way to locate ants. However, foraging at entrances to colonies may be disadvantageous to horned lizards if risks of injury or predation are greater at entrances to colonies than locations where ants are more dispersed. Previous studies have examined how foraging by the Texas horned lizard, *Phrynosoma cornutum*, may be influenced by rates of harvest of ants (Munger, 1984). Other studies have indicated that choice of prey by *Phrynosoma* may be influenced by interspecific variation in aggressiveness by ants of the genus *Pogonomyrmex* (Rissing, 1981). No study has examined the extent to which efficiency of capturing prey and risk of injury may interact to influence foraging by *Phrynosoma*. To explore tradeoffs between these two factors, we undertook a study of foraging in the Texas horned lizard, which feeds largely on harvester ants (*Pogonomyrmex*) throughout much of its range (Whitford

and Bryant, 1979; Munger, 1984; Blackshear and Richerson, 1999). Previous research has confirmed low digestibility of *Pogonmyrmex* for *P. cornutum* (Whitford and Bryant, 1979). On our study area, the most common harvester ant was *Pogonomyrmex barbatus*, a species that readily attacks *P. cornutum* causing apparent distress and retreat.

Materials and Methods—We studied foraging by *P. cornutum* during 1–22 July 1999 in a desert scrubland ca. 5 km E Portal, Cochise County, Arizona (31°53.3′N, 109°3.8′W). Sampling of vegetation conducted during our study characterized the site as primarily open ground (66.9%), with interspersed shrubs, *Prosopis* (mesquite, 19.1%) and *Ephedra* (4.6%), or herbaceous plants, *Gutierrezia* (6.4%) and other species (2.9%).

Each of 14 adults (six males, eight females) was equipped with a radiotransmitter (model BD2; Holohil Systems Ltd., Carp, Ontario, Canada) fastened to the lizard with a harness (Richmond, 1998). Radiotransmitters with their harness weighed an average 2.21 g (range 1.85–2.40 g), which averaged 4.3% of mass of lizards (range 2.5–6.6%).

Each morning, we located a predetermined subset of lizards and attempted to observe them throughout their morning activity period. Lizards were active ca. 0700–1130 h. Activity in afternoons was minimal for these animals; we conducted limited monitoring in afternoons, but feeding was so infrequent that we did not use these data in analyses. Once a lizard was located, observers proceeded to compile focal observations of its behavior. At 5-min intervals, habitat occupied by the focal lizard was characterized; for each feeding on a *Pogonomyrmex*, we recorded time, habitat, location, and capturing technique. For characterizations of habitat, we recorded whether the lizard was in the open or under one of four types of plants: *Prosopis*, *Ephedra*, *Gutierrezia*, or other plant. For the location of feeding events, we distinguished between *Pogonomyrmex* taken at an entrance to a colony, along a foraging trail, or while dispersed. Ants were captured by lizards using two techniques: either the lizard moved toward the prey to capture it (approach) or consumed an ant that came within one length of its body (snap). Observers were able to readily distinguish *Pogonomyrmex* (harvester ants) from other ants in the field.

We determined relative availability of harvester ants in different habitats using pitfall traps (9 cm diameter, 12 cm deep; $n = 89$ traps) that we installed level with the ground in all types of habitat. For types of habitat associated with plants, we placed traps completely under the randomly selected canopy. For mesquites, which exhibited a wide range in size, we recorded maximum length of canopy for each plant hosting a trap.

We determined whether colonies of harvester ants where lizards fed represented a distinguishable subset of colonies at the site. For colonies of harvester ants that were visited and a sample of 50 other colonies in the study area, we determined distance from entrances of colonies to the nearest vegetation and to the nearest mesquite. We also determined whether proximity to colonies characterized mesquites under which lizards were observed feeding by measuring distance to nearest entrance to a colony for those mesquites and for a random selection of mesquites from within the study area.

For statistical analyses of use of habitat and feeding habitat, we excluded the category of other plants because they were too few. For analysis of daily patterns of consumption of harvester ants, only dispersed ants and ants at colonies were compared; the number of harvester ants captured from foraging trails was too few for analyses. Observations of diet for the population were corroborated by collecting scats (fecal deposits) produced by animals during handling and observations and identifying their contents using a microscope.

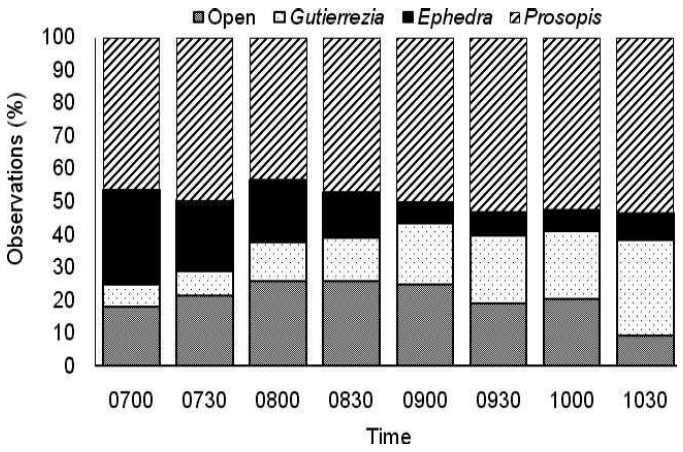

Fig. 1—Use of habitat during morning activity by the Texas horned lizard *Phrynosoma cornutum* near Portal, Cochise County, Arizona.

Results—During 48 observation periods, 14 Texas horned lizards were observed for a total of 139 h (total observation time per lizard, mean 9.9 h, range 3.6–15.8 h). Analyses of 25 scats produced 1,821 prey items; 99.95% were ants and 97.69% of prey was harvester ants. Only one prey item of the 1,821 was not an ant; it was a small Coleoptera (beetle).

Use of habitat by Texas horned lizards is nonrandom ($\chi^2 = 2{,}085.3$, $P < 0.001$, $df = 4$). Most notably, horned lizards were in the open less than expected and under mesquites more than expected. The most common location for a horned lizard was in association with a mesquite; indeed, lizards spent nearly one-half of their time near mesquites (46% of observations) despite mesquites occupying only 19% of available habitat. In addition, there was significant variation in use of habitat through the morning activity period ($\chi^2 = 143.8$, $P < 0.001$, $df = 21$; Fig. 1).

Colonies of harvester ants where lizards fed were neither closer to vegetative cover than other colonies in the area (one-tailed *t*-test: $t = 1.42$, $P = 0.082$, $df = 45$) nor were they any closer to mesquites (one-tailed *t*-test: $t = 0.38$, $P = 0.650$, $df = 30$). Mesquites under which lizards fed were not a random subset of available mesquites. They were significantly closer to colonies of ants than mesquites in general (4.8 versus 10.1 m, $t = 4.24$, $P < 0.001$, $df = 35$), but they were not the mesquites closest to colonies of harvester ants (average closest mesquite = 1.6 m; $t = 3.32$, $P = 0.005$, $df = 14$).

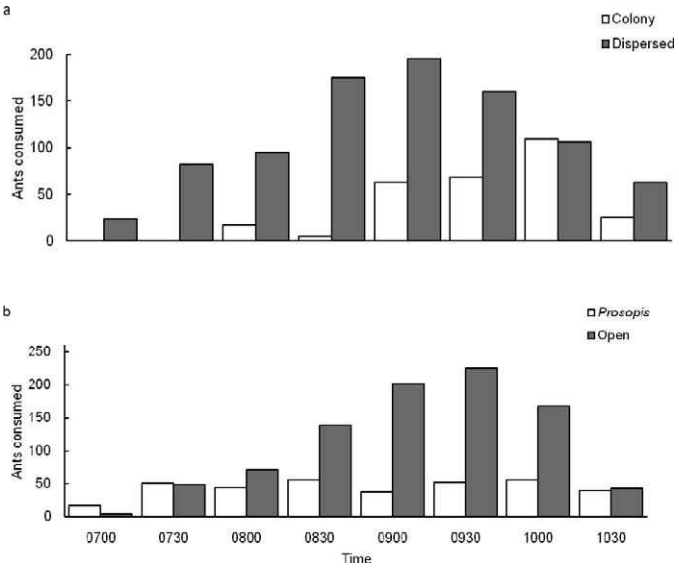

FIG. 2—a) Location of feeding sites of Texas horned lizards *Phrynosoma cornutum* and b) location (at colonies or dispersed from colonies) of harvester ants *Pogonomyrmex* that were consumed by these lizards near Portal, Cochise County, Arizona.

Most feeding occurred in the open (64.5%). When feeding under cover, most captures of harvester ants took place under *Prosopis* (67.6%; *Gutierrezia* 20.8%, *Ephedra* 6.5%, other 5.1%). Feeding that involved dispersed ants was more common than feeding at entrances to colonies or along foraging trails (dispersed, 67.5%; entrance to colonies, 27.2%; foraging trail, 5.3%). The daily pattern of consumption of harvester ants differed with location ($\chi^2 = 170.6$, $P < 0.001$, $df = 7$); feeding at entrances to colonies was restricted to a shorter period of the morning than feeding on dispersed ants (Fig. 2a). The daily pattern of consumption of harvester ants also differed with habitat (open versus mesquite, $\chi^2 = 124.384$, $P < 0.001$, $df = 7$; Fig. 2b).

The most common capturing tactic was to snap ants as they came within striking distance (66.0% snap versus 34% approach). There was a significant association between capturing technique and source of ants ($\chi^2 = 167.8$, $P < 0.001$, $df = 2$); almost all (92%) ants consumed at an entrance to a colony were snapped, while only 58% of dispersed ants and 34.8% of ants on trails were snapped. Capturing tactics were related to habitat ($\chi^2 = 12.4$, $P < 0.001$, $df = 1$), but this seems to be an outcome of feeding at colonies (all occurred in the open), which primarily were snaps. When evaluating captures at non-colonies, capturing tactics did not differ among habitats ($\chi^2 = 0.03$, $P = 0.864$, $df = 1$).

Pitfall traps in the open tended to catch more harvester ants than traps under cover (Mann-Whitney W = 804, $P = 0.049$, $n = 14$ in open and 75 under cover). There was no significant difference in abundance of harvester ants among the three types of vegetative cover ($F = 0.27$, $P = 0.761$, $df = 2, 72$). For mesquites, there was no indication that maximum width of canopy was related to abundance of harvester ants ($F = 0.09$, $P = 0.771$, $df = 1, 27$, $n = 39$).

Males and females differed in several aspects of their foraging strategy. Both males and females captured harvester ants from habitats in proportions that differed from availability of habitat (males, $\chi^2 = 26.7$, $P < 0.001$, $df = 1$; females, $\chi^2 = 12.5$, $P < 0.001$, $df = 1$), but they also differed from each other ($\chi^2 = 19.7$, $P < 0.001$, $df = 2$). Males were more likely to feed in the open than females ($\chi^2 = 4.8$, $P = 0.029$, $df = 1$). In addition, sexes differed in location where they took harvester ants ($\chi^2 = 28.05$, $P < 0.001$, $df = 2$). Males fed more at entrances to colonies than expected, while females relied more on dispersed ants than expected.

DISCUSSION—In the population we studied, foraging *P. cornutum* must deal with the threat of prey-induced injury and predation. Feeding on harvester ants, particularly near entrances to colonies, can lead to ants climbing onto and stinging Texas horned lizards, which elicits frantic behavior as lizards hop about in apparent discomfort, or in an attempt to dislodge ants. Aside from physical injury, responses to attacks by ants potentially increase the risk of being detected by predators. Potential predators such as the greater roadrunner (*Geococcyx californianus*), loggerhead shrike (*Lanius ludovicianus*), and raptors often were encountered in the study area and rely on vision for detecting prey. Thus, while entrances to colonies of harvester ants were all in the open and pitfall trapping suggests that dispersed harvester ants are also more abundant in open areas, there are disadvantages associated with foraging in the open or near entrances to colonies. Many aspects of foraging by Texas horned lizards seem to reduce risks associated with feeding on harvester ants.

Choice of habitat by *P. cornutum* involves a preferential use of cover. Use of cover reduces risk of detection by predators. Mesquites are the largest plants in the area with the most effective canopy for obscuring activity from visual searches by predators. Choosing mesquites close to colonies of ants, but not as close as possible, may reduce risk of both prey-induced injury and predation, while increasing proximity to reasonable densities of ants. While we did not quantify this behavior, it was common for Texas horned lizards under mesquites to temporarily leave cover to capture an ant that was in the open. Lizards foraging in the open that approach prey for capture put themselves at greater risk of detection. Most captures of harvester ants involved snaps, which typically require little more movement than a twist of the head or tilt of the body and extension of the tongue.

Most feeding occurs in the open but near entrances to colonies. Relying on snaps and sallying from mesquites to capture prey may reduce exposure to predators. Timing

of visits to colonies may mitigate risk of attack by ants. While colonies of harvester ants may be active all morning, intensity of activity near the entrance to the colony may vary by time of day or from day to day and be related to factors such as weather (Gordon, 1983, 1991). Daily activity of harvester ants initially is focused near entrances to colonies and initial parts of trails (Gordon, 1983, 1991). Texas horned lizards tend to feed at colonies later in the morning, perhaps avoiding times of peak activity of ants near entrances to colonies.

Differences between sexes in use of habitat or foraging are common in lizards (Eifler and Eifler, 1999; Eifler et al., 2007). Females in our study were larger than males. They may need different amounts of food or have different thermal requirements. Further, most or all females were gravid during part of our study. Behavioral shifts in horned lizards may occur as a result of reproductive status (Cooper et al., 1990; Downes and Bauwens, 2002), with gravid females becoming more cautious. Males in our study tended to feed in more exposed areas (i.e., in the open and near entrances to colonies); whether differences in foraging behavior between sexes exist outside of the reproductive period is unknown. Not every aspect of foraging by Texas horned lizards is necessarily a response to risk of physical harm. Munger (1984) observed that Texas horned lizards feeding on *Pogonomyrmex desertorum* tended to feed at or near to entrances of colonies, with the tendency stronger for females. Interspecific variation in behavior and size of colonies may make some species of *Pogonomyrmex* a greater threat than others (Rissing, 1981). For example, *P. desertorum* has much smaller colonies than *P. barbatus* and foraging near entrances of their colonies may be less risky. In another study area, where *P. desertorum* and *P. rugosus* were heavily relied upon as food, most feeding occurred away from colonies (Whitford and Bryant, 1979).

Several previous studies have investigated use of habitat by *P. cornutum* and detected preferences that may be unrelated to foraging and risk of predation. Whiting et al. (1993) suggested that for a population of *P. cornutum* in Texas, habitat influenced distribution; areas of dense grass, which could impair locomotion, usually were avoided. Burrow et al. (2001) observed *P. cornutum* using bare ground and vegetation during morning activity in proportion to availability but noted changes in use of habitat in the afternoon that they attributed to temperature. Most vegetation in our study area would not impede locomotion by *P. cornutum* but could represent different thermal regimes as the morning progresses. The changes in use of habitat that we observed through the morning may reflect changes in temperature. Our sampling of harvester ants was not designed to detect temporal patterns in availability of ants among habitats, but such temporal patterns may exist.

We thank K. Bott, G. Close, S. Hernandez, N. Jordi, V. Morris, and A. Pilyavskaya for assistance with fieldwork. We thank R. Green for allowing this study to be conducted on his land. Support was provided by EarthWatch, the Durfee Foundation, and the Southwestern Research Station of the American Museum of Natural History.

Literature Cited

Blackshear, S. D., and J. V. Richerson. 1999. Ant diet of the Texas horned lizard (*Phrynosoma cornutum*) from the Chihuahuan Desert. Texas Journal of Science 51:147–152.

Burrow, A. L., R. T. Kazmaier, and E. C. Hellgren. 2001. Microhabitat selection by Texas horned lizards in southern Texas. Journal of Wildlife Management 65:645–652.

Cooper, W. E., Jr., L. J. Vitt, R. Hedges, and R. B. Huey. 1990. Locomotor impairment and defense in gravid lizards (*Eumeces laticeps*): behavioral shift in activity may offset costs of reproduction in an active forager. Behavioral Ecology and Sociobiology 27:153–157.

Downes, S. J., and D. Bauwens. 2002. Does reproductive state affect a lizard's behavior toward predator chemical cues? Behavioral Ecology and Sociobiology 52:444–450.

Eifler, D. A., and M. A. Eifler. 1999. The influence of prey distribution on the foraging strategy of the lizard *Oligosoma grande* (Reptilia: Scincidae). Behavioral Ecology and Sociobiology 45:397–402.

Eifler, D. A., M. A. Eifler, and E. N. Eifler. 2007. Habitat use and movement patterns in the graceful crag lizard, *Pseudocordylus capensis*. African Zoology 42:152–157.

Gordon, D. M. 1983. The relation of recruitment rate to activity rhythms in the harvester ant, *Pogonomyrmex barbatus* (F. Smith) (Hymenoptera: Formicidae). Journal of the Kansas Entomological Society 56:277–285.

Gordon, D. M. 1991. Behavioral flexibility and the foraging ecology of seed-eating ants. American Naturalist 138:379–411.

Meyers, J. J., A. Herrel, and K. C. Nishikawa. 2006. Morphological correlates of ant eating in horned lizards (*Phrynosoma*). Biological Journal of the Linnaean Society 89:13–24.

Montanucci, R. R. 1989. The relationship of morphology to diet in the horned lizard genus *Phrynosoma*. Herpetologica 45:208–216.

Munger, J. C. 1984. Optimal foraging? Patch use by horned lizards (Iguanidae: *Phrynosoma*). American Naturalist 123:654–680.

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

Redford, K. H., and J. G. Dorea. 1984. The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. Journal of Zoology (London) 203:385–395.

Richmond, J. Q. 1998. Backpacks for lizards: a method for attaching radio transmitters. Herpetological Review 29:220–221.

Rissing, S. W. 1981. Prey preferences in the desert horned lizard: influence of prey foraging method and aggressive behavior. Ecology 62:1031–1040.

Schmidt, P. J., W. C. Sherbrooke, and J. O. Schmidt. 1989. The detoxification of ant (*Pogonomyrmex*) venom by a blood factor in horned lizards (*Phrynosoma*). Copeia 1989:603–607.

Sherbrooke, W. C. 2003. Introduction to horned lizards of North America. University of California Press, Berkeley.

Whitford, W. G., and M. Bryant. 1979. Behavior of a predator and its prey: the horned lizard (*Phrynosoma cornutum*) and harvester ants (*Pogonomyrmex* spp.). Ecology 60:686–694.

Whiting, M. J., J. R. Dixon, and R. C. Murray. 1993. Spatial distribution of a population of Texas horned lizards (*Phrynosoma cornutum*: Phrynosomatidae) relative to habitat and prey. Southwestern Naturalist 38:150–154.

Submitted 8 June 2009. Accepted 12 June 2011.
Associate Editor was Geoffrey C. Carpenter.