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Diet Selection by a Lizard Ant-Specialist in an Urban System Bereft of Preferred Prey

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Abstract.—**Habitat loss, land-use transformation, climate change, and biological invasions all elevate the importance of plasticity in food selection for the continued persistence of dietary specialists. Horned lizards (*Phrynosoma* spp.) are myrmecophagic specialists and the abundance of ant prey make their populations vulnerable to habitat loss, as well as invasive ants and associated pest control programs. We studied ant use by *Phrynosoma cornutum* (Texas Horned Lizards) on an insular urban reserve in central Oklahoma that was bereft of harvester ants (*Pogonomyrmex* spp.), presumed to be their chief prey. The five most commonly available ant genera based on bait station captures were *Monomorium* (69%), *Forelius* (11%), *Pheidole* (10%), *Crematogaster* (7%), and *Tapinoma* (2%). Based on the examination of 124 scat samples from adult and juvenile *P. cornutum*, *Crematogaster* (81%), *Pheidole* (12%), *Formica* (6%), and *Monomorium* (1%) were used as prey. Consumption of prey in several ant genera by *P. cornutum* disproportionately to their availability was related to ant mass and presumed nutritional value. Among juveniles, gape size did not influence *Pheidole* use but may influence *Formica* use. We suggest that *P. cornutum* are adaptive ant specialists whose populations might be maintained in habitat fragments without harvester ants as long as abundant medium- and large-sized native ant communities are present. Therefore, urban reserves, when effectively managed for native fauna, can conserve declining native species by serving as habitat havens in an otherwise unsuitable landscape.**

Dietary specialization is presumed to increase foraging efficiency, resulting in high net nutritional gain (Beissinger, 1990) although such specialization is a biological trade-off. Morphological, physiological, and behavioral adaptations that are advantageous for hunting, capturing, handling, and assimilating specialized prey items (Lahti and Beck, 2008) may reduce hunting efficiency and extraction rates when specialists are forced to switch prey (Beissinger, 1990; Cooper and Secor, 2007). Rapid urbanization could be detrimental to the persistence of populations of native dietary specialists because their limited dietary plasticity may preclude the use of alternative prey.

In lizards, dietary specialization may change with life stage, fluctuations in prey abundance, or patchiness in prey distribution. Specialization may occur in localized populations (Fox and Morrow, 1981; Britt et al., 2006), or be a temporary phenomenon based on gape-size limitations of juveniles that enhance foraging efficiency through the selection of small, but numerous prey (Juanes and Conover, 1994; Lahti and Beck, 2008). Diets of juveniles may become less specialized as they grow and become less gape-limited (Drummond and Garcia, 1989); however, opportunistic specialization among dietary specialists that consume small insects, in response to seasonal and temporal changes in prey availability may occur (Roper, 1994; Elmhagen et al., 2000; Sales and Freire, 2015). When stressed, plasticity can lead to diet diversification in specialists (Beissinger, 1990) or diet contraction in generalists (Roper, 1994; Elmhagen et al., 2000).

Phrynosoma spp., or horned lizards, are typically cryptic, myrmecophage specialists that are distributed throughout the western United States and Canada through Mexico and Guatemala (Sherbrooke, 2003; Sherbrooke and Schwenk, 2008). Ant specialization has resulted in adaptations in skull morphology, tongue prehension, dentition, and pharyngeal processing (Pianka and Parker, 1975; Meyers et al., 2006; Vitt and Pianka, 2007; Sherbrooke and Schwenk, 2008). The relatively large size and expansive stomachs of *Phrynosoma* facilitate the consumption of large numbers of small, chitinous insects that are needed to fulfill energy requirements (Pianka and Parker, 1975).

Texas Horned Lizards (*Phrynosoma cornutum*) exist in relatively low-density populations in xeric habitats in western and central North America (Pianka and Parker, 1975). Harvester ants (*Pogonomyrmex* spp.) are the chief, even exclusive (Blackshear and Richerson, 1999; Eifler et al., 2012), prey of *P. cornutum*; and the presence of *P. cornutum* and harvester ants are strongly linked (Donaldson et al., 1994; Blackshear and Richerson, 1999; McIntyre, 2003). McIntyre (2003) suggested the use of the presence or absence of harvester ants for the determination of *P. cornutum* habitat suitability. Similarly, *P. solare* will persist in habitat patches across a range of sizes and disturbance levels, provided harvester ants are present (Sullivan et al., 2014).

Phrynosoma cornutum populations have experienced declines over much of their range because of habitat loss and destruction, as well as the aggressive use of pesticides to control ant populations (Donaldson et al., 1994). Furthermore, Sow et al. (2014) indicated that reptiles in arid environments may be especially vulnerable to climate change. Dietary specialization makes *P. cornutum* particularly sensitive to the removal of key prey species (Newbold and MacMahon, 2009), and the fate of *P. cornutum* populations is intimately linked to the prevalence and abundance of their food source (i.e., specific ant populations). In California, *Phrynosoma blainvillii* have steadily declined with the introduction and expansion of invasive Argentine ants (*Lenepithema humile*; Suarez et al., 2000). Another nonnative and non-prey ant species, red fire ants (*Solenopsis invicta*), have steadily expanded their range in the United States, sometimes out-competing native ant species on which *P. cornutum* forage (Blackshear and Richerson, 1999), and are known to depredate directly on reptiles (Reagan et al.,

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2000; Aresco, 2004). The red fire ant invasion has led to the widespread and indiscriminate use of pesticides to control all ant populations (Donaldson et al., 1994), which has resulted in the overall decline of ant prey abundance, having a deleterious effect on *P. cornutum* populations.

We studied an insular population of *P. cornutum* that exists in isolated patches of habitat within an urban environment (Wolf et al., 2013). Body size of prey and lizard are positively correlated in *Phrynosoma* spp. (Rissing, 1981; Suarez et al., 2000; Suarez and Case, 2002; Lahti and Beck, 2008), and *P. cornutum* may avoid small ants regardless of availability (Blackshear and Richerson, 1999). Therefore, because our study site lacked harvester ants, we predicted that the diet of *P. cornutum* would consist of a large proportion of relatively large-bodied, native ants. Furthermore, we predicted that the relatively large female lizards would consume larger proportions of large-bodied ants when compared to males, and we expected that juvenile lizards would consume a high proportion of smaller native ants attributable to gape-size limitations relative to adults.

Materials and Methods

Study Site.—Tinker Air Force Base (TAFB) is a largely urban base on the outskirts of Oklahoma City (35°24′58″N, 97°24′41″W; datum NAD83; Fig. 1). Approximately 500 ha of the 2,000-ha base are natural habitat that is dominated by mixed oak-hardwood forests and a mixture of native and nonnative grasslands. Core Reserve Area 3 (CRA3; known as Wildlife Reserve 3 in Endriss et al., 2007; Wolf et al., 2014) is a natural area (approximately 15 ha; Fig. 2) on the southwestern side of TAFB, dominated by grassland with patches of woody vegetation and gravel trails and includes residential housing and industrial facilities. Dominant vegetation on CRA3 include big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), plains bluestem (*Bothriochloa ischaemum*), indiangrass (*Sorghastrum nutans*), sideoats grama (*Bouteloua curtipendula*), Maximilian sunflower (*Helianthus maximiliani*), tall fescue (*Lolium pratense*), and eastern redcedar (*Juniperus virginiana*) (Endriss et al., 2007).

Field Methods.—We collected ants at 400 stations in 20-mL scintillation vials baited with millet and peanut butter in summers 2010 and 2011. We deployed vials at 200 bait stations (Bait Station Set 1) in May and July and at the other 200 bait stations (Bait Station Set 2) in June and August. We used the Hawth's Tools extension for ArcGIS 9.3 (ESRI, Redlands, CA) to randomly select locations throughout the study site for bait stations (Fig. 2). Vials were deployed between 0600 and 1200 h for 3–4 h on a single day per month on days with no precipitation. We preserved ants in 95% ethanol and later sorted and identified them to genus under a dissecting microscope. Ants were counted, cleaned, dried, and weighed using an Accu-124 analytical balance (Thermo-Fisher Scientific, Inc., Waltham, CA) accurate to 0.0001 mg. We estimated the mean mass of a single ant in each genus by regressing the mass of each sample on the number of ants in the sample, using the resulting regression line to extrapolate the mass of 100 ants, then dividing this number by 100.

We collected *P. cornutum* fecal samples ($N = 75$) opportunistically when found on the study site. Additionally, fecal samples ($N = 49$) were obtained from individuals held overnight for PIT tagging (12.5 mm tags; Biomark Inc., Boise, ID); these known scat samples were used as a reference in field collections. All samples ($N = 124$) were hydrated with 95% ethanol and contents examined for identification. Ant heads were counted and identified to genus. Other invertebrates found in bait stations and fecal samples were identified to order.

Phrynosoma cornutum hatchlings emerge during late summer and in the fall, develop into juveniles in their second year, and reach adulthood and sexual maturity in their third year (Montgomery and Mackessy, 2003). *Phrynosoma cornutum* at TAFB were categorized into age classes based on snout–vent length (SVL), with adult females measuring > 63 mm, and adult males > 49 mm (Endriss et al., 2007). Yet, because juveniles collected late in the year often were the same size as adults (and presumably had similar gapes and stomach capacity), we defined size classes as follows: large lizards with SVL > 50 mm ($N = 26$; adult males, adult females, and large juveniles); medium lizards with SVL between 30 and 50 mm ($N = 15$; juveniles); and small lizards with SVL < 30 mm ($N = 8$; hatchlings).

Statistical Analyses.—We tested for differences between use and availability of prey using log-likelihood ratio tests, also known as *G*-tests (Zar, 1999). We conducted an overall *G*-test with all scat samples pooled across lizard sizes and sexes to test for a population-wide difference between use and availability. Although bait stations were placed site-wide encompassing all of CRA3, we defined availability based only on bait stations within the area occupied by *P. cornutum* (Fig. 2). The lizard-occupied area was calculated with a 95% kernel density estimate (Kernohan et al., 2001) for all lizard locations, using the Home Range Tools Version 1.1 (Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, ON, Canada) extension for ArcGIS 9.3 with the reference smoothing parameter. We also used a *G*-test to test for differences in prey use between biologically relevant pairs of subgroups using *G*-tests of independence, such as differences between adult males and females, or between different size classes.

We described prey use with an electivity index (Lechowitz, 1982) that was defined as u_i / a_i, where u_i is the proportion of prey genus i used out of the total proportion of prey items in all scat samples, and a_i is the proportion of genus i available out of the total sample of available prey items. We calculated electivity indices for each prey genus using the availability sample based on the area occupied by *P. cornutum*. Although scaling each electivity index to the overall sample often is recommended (Lechowitz, 1982), the extreme skew in our availability and use data caused a few prey genera to dominate analyses. Hence, we used unscaled electivity indices for each genus. Therefore, our indices reflect whether a given prey genus was used or not used in relation to the availability of that genus but not in relation to other genera.

Results

Of the five most common ant genera found in lizard-occupied areas, four were found within the scats of lizards and with differing degrees of importance. We examined a total of 34,231 native ants (30–1,429 ants per sample) from 168 bait stations. In descending order of importance, the most common genera found included *Monomorium* (69%), *Forelius* (11%), *Pheidole* (10%), *Crematogaster* (7%), and *Tapinoma* (2%; Table 1), whereas harvester ants (*Pogonomyrmex* spp.) were infrequently sampled (0.0003%). During the same time frame, we collected 31,070 native ants from 124 *P. cornutum* scat samples. Again, in decreasing order of importance, the five most frequently

FIG. 1. Location of Tinker Air Force Base, Oklahoma. State boundaries are outlined in black. Inset: extent of location map in North America.

encountered genera were *Crematogaster* (81%), *Pheidole* (12%), *Formica* (6%), and *Monomorium* (1%; Table 1).

Lizards consumed prey species in different proportions than were available in their environments. Log-linear tests of independence of data ($G^2 = 60695.75$, $P < 0.0001$) indicated that *Crematogaster, Pheidole*, and *Formica* were consumed in greater proportions than their availability and that *Monomorium, Forelius*, and *Tapinoma* were used proportionately less than their availability (Table 1). Prey use by adult *P. cornutum* differed between the sexes ($G^2 = 295.58$, $P < 0.0001$). Females consumed *Pheidole* ants much more frequently than did males (Fig. 3) although there was high dietary overlap of *Formica* and *Crematogaster* in males and females (Fig. 3). The three size classes of lizards differed in their use of ant genera ($G^2 = 3.88$, $P < 0.0001$). Hatchlings used *Pheidole* to a greater extent than did medium and large lizards, and *Formica* was used more by large lizards when compared to lizards in the smaller size classes (Fig. 4).

Phrynosoma cornutum's disproportionate use of large native ants also was reflected in an electivity index. Values for Ivlev's electivity index ($E_i = [u_i - a_i] \: / \: [\, u_i + a_i]$) ranged from 1 (strong usage) to −1 (not used), whereas 0 indicated use in proportion to availability (Lechowitz, 1982). The most readily consumed ant prey represented the largest ant prey available at our study site, that is, *Formica* ($E_i = 1.00$), followed by *Crematogaster* ($E_i = 0.84$), and *Pheidole* ($E_i = 0.09$), whereas smaller ant species (e.g., *Forelius*, *Monomorium*, and *Tapinoma*) were not used (Fig. 5). Lizard size and ant mass were positively related, with a minimum ant threshold of 0.70 mg for consumption (Fig. 6).

DISCUSSION

Phrynosoma cornutum persisted on our urban study area (Wolf et al., 2014) without harvester ants, a primary and sometimes presumed exclusive prey species in other *P. cornutum* populations (Blackshear and Richerson, 1999; Eifler et al., 2012). Consistent with our predictions, *P. cornutum* disproportionately consumed large-bodied native ants. Prey consumption differed by sex and size class and was influenced by ant size, availability, and abundance.

Using biomass as a surrogate for nutritional value (Golley, 1961; Griffiths, 1975), *P. cornutum* focused their foraging activities on prey items that yielded the highest nutritional return, when balanced against foraging and digestive costs. Our results mirrored work on *P. platyrhinos* where ant consumption was regulated by encounter rate (i.e., prey abundance) and caloric intake (prey size [Newbold and McMahon, 2009]). In our

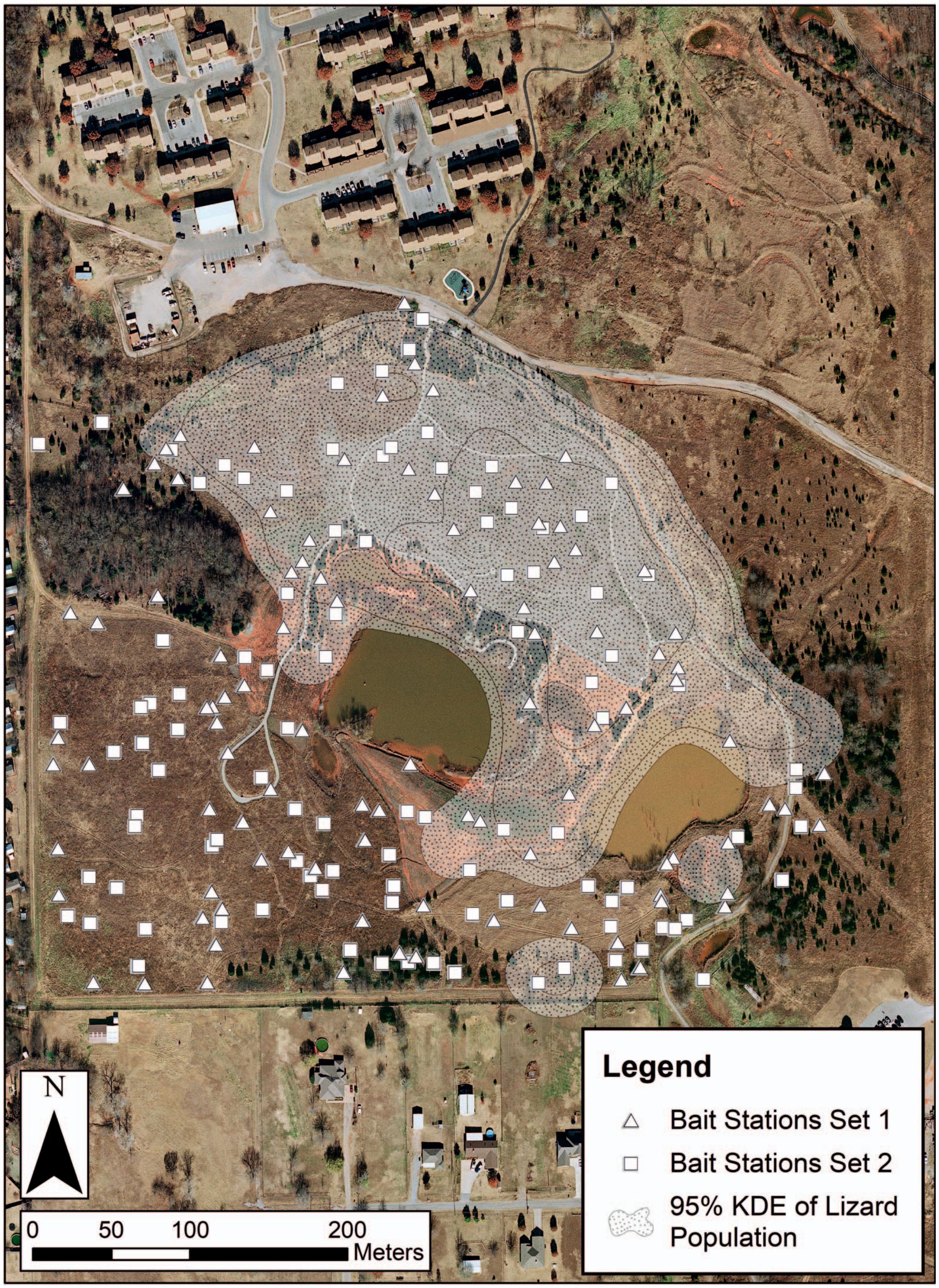

FIG. 2. Randomly placed ant bait stations at Core Reserve Area 3 at Tinker Air Force Base, Oklahoma. Availability was measured using bait-stations in lizard-occupied areas, as defined by a 95% kernel density estimate (KDE) of all lizard locations during 2010 and 2011. Bait stations ($N = 168$) occurred in lizard-occupied areas. Stippling indicates 95% KDE with 50% and 90% isopleths shown.

study, *Formica* was the largest native ant and was consumed when available, even though it was seldom encountered at our bait stations, possibly attributable to low colony sizes (Fisher and Cover, 2007), inappropriate sampling (Newbold and MacMahon, 2009), or solitary foraging strategy (Trager and Johnson, 1985; King and Trager, 2007; Trager et al., 2007). Solitary foraging ant species may be more vulnerable to *Phyrnosoma* predation, because they are less prone to mobbing behavior that could attract predators to the normally cryptic lizard (Rissing, 1981). Whitford and Bryant (1979), however, found that *P. cornutum* in southern New Mexico preyed on both solitary foragers (*Pogonomyrmex desertorum*) and column foragers such as *Pogonomyrmex rugosus*. Unlike *Formica*, *Crematogaster* form populous colonies and proved to be an abundant food resource among our study lizards (Fig. 5), similar to *Phrynosoma* populations in the Great Basin of the western United States (Newbold and McMahon, 2009).

Gape size may be an important factor in ant selection by *Phrynosoma*, affecting the consumption of *Formica*, which was used most frequently by large lizards and least by hatchlings.

TABLE 1. Proportional abundance of ant genera at randomly placed bait stations ($N = 168$), proportions of ant genera ingested by *Phrynosoma cornutum* ($N = 124$ scat samples), average ant biomass per genera, and Ivlev's electivity index values for each ant genus (E_i) at Core Reserve 3 at Tinker Air Force Base in Oklahoma. Values for Ivlev's electivity index range from 1 (strong usage) to −1 (not used); 0 indicates usage in proportion to availability.

Ant genera	Proportion ants available	Proportion ants in diet	Ant biomass (mg)	E_i
Monomorium	0.69	0.01	0.29	−0.97
Forelius	0.11	0.00	0.46	−1.00
Pheidole	0.10	0.12	0.73	0.10
Crematogaster	0.07	0.81	0.73	0.84
Tapinoma	0.02	0.00	0.59	−1.00
Other	0.01	0.00	N/A	−1.00
Pogonomyrmex	0.00	0.00	4.01	−1.00
Formica	0.00	0.06	1.77	1.00

Size class of lizards is positively correlated with average prey size (Powell and Russell, 1984). Horned lizards seize prey with tongues and swallow ants whole (Sherbrooke and Schwenk, 2008), and gape-size limitations may prohibit *P. cornutum* hatchlings from consuming large *Formica* prey. A similar relationship between predator and prey size was observed in *P. douglasii* (Lahti and Beck, 2008), *P. douglasii brevirostre* (Powell and Russell, 1984), *P. platyrhinos* (Rissing, 1981), and *P. blainvillii* (Suarez et al., 2000; Suarez and Case, 2002). Furthermore, adult lizards may simply be superior competitors, dominating profitable static food sources (e.g., *Formica* ant mounds), while excluding smaller, inexperienced conspecifics. Although *Pheidole* have dimorphic castes (Wilson, 2003), all size classes of lizards exploited this food resource and gape size did not appear to be a limiting factor in *Pheidole* consumption.

Our results also suggested a minimum threshold in prey size for persistence of *Phrynosoma* populations. As a cryptic species, *Phrynosoma* may be more vulnerable to predation by selecting small ant species that would require a large foraging effort over extended periods (Suarez and Case, 2002). Despite their high relative abundance, *Monomorium* and *Forelius* were the smallest ants at our study site and were underused by *P. cornutum*. Suarez et al. (2000) found that *P. blainvillii* did not typically use small native ants (mean = 1.11 mm body length), and Whitford and Bryant (1979) found *P. cornutum* used only native ants measuring >5 mm in total length. *Monomorium minimum* (<2 mm) and *Forelius pruinosus* (~2 mm) are diminutive (Fisher and Cover, 2007), and members of both genera are known to swarm food resources and exclude competitors with chemical defenses (Adams and Traneillo, 1981; Scheffrahn et al., 1984); hence, their high numbers at our bait stations may be exaggerated. The small body size of *Monomorium* make it an unappealing choice for *P. cornutum*, whereas *Forelius* are thermophilic, foraging at peak environmental temperatures (Fisher and Cover, 2007) that coincides with inactivity of *P. cornutum*. Temporal partitioning may exclude *Forelius* as suitable prey, as Whitford and Bryant (1979) observed in *P. cornutum* and large nocturnal native ants.

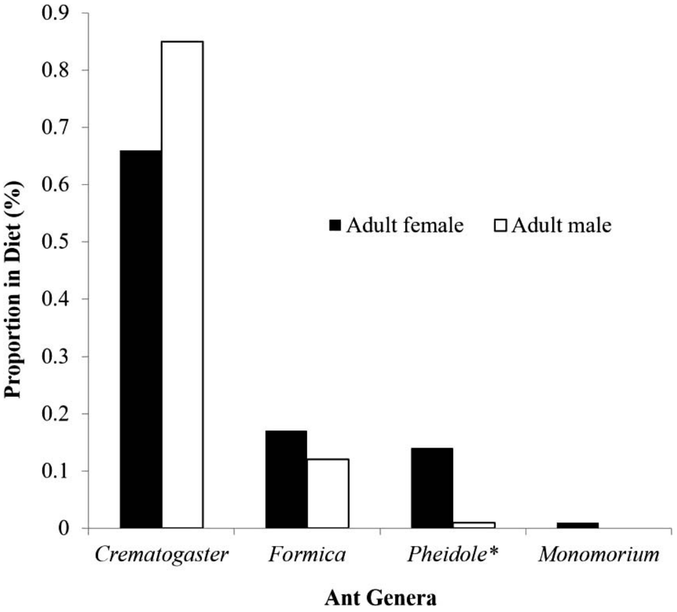

FIG. 3. Comparative diet use of four common ant genera by male and female *Phrynosoma cornutum* on Core Reserve Area 3 at Tinker Air Force Base, Oklahoma, in 2010 and 2011. * indicates significant difference in prey consumption among sexes based on a log-likelihood test.

Although common throughout the entire study area, *Tapinoma* spp. were rare at our bait stations. Fellers (1987) found *Tapinoma sessile* to be a consistently subordinate competitor at bait stations; thus, *Tapinoma* may be more abundant at our study site than we detected. Approximately 20% smaller than *Crematogaster*, *Tapinoma* may fall under a minimum ant biomass threshold below which foraging becomes unprofitable for *P. cornutum*.

Phrynosoma cornutum was presumed to be a harvester ant specialist (Munger, 1984; Blackshear and Richerson, 1999; Eifler et al., 2012); however, our data suggested plasticity in foraging behavior when harvester ants are not available. Management

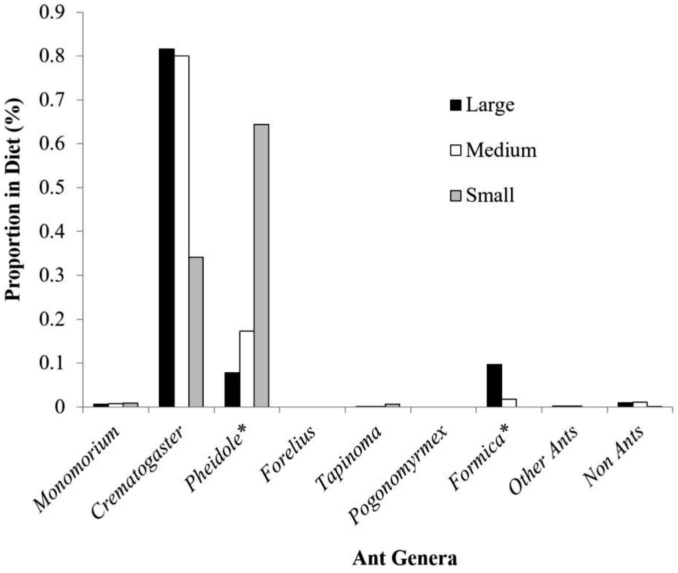

FIG. 4. Comparative diet use of ant genera by size classes of *Phrynosoma cornutum* on Core Reserve Area 3 at Tinker Air Force Base, Oklahoma, in 2010 and 2011. Size classes of lizards were defined as follows: large = adult and late juvenile lizards with SVL > 50 mm ($N = 26$); medium = juveniles with SVL between 30 and 50 mm ($N = 15$); and small = hatchlings with SVL < 30 mm ($N = 8$). Two medium-sized lizards in 2010 transitioned into large lizards in 2011, and were included independently as medium and large lizards. * indicates significant differences in prey consumption based on log-likelihood tests comparing lizard size classes.

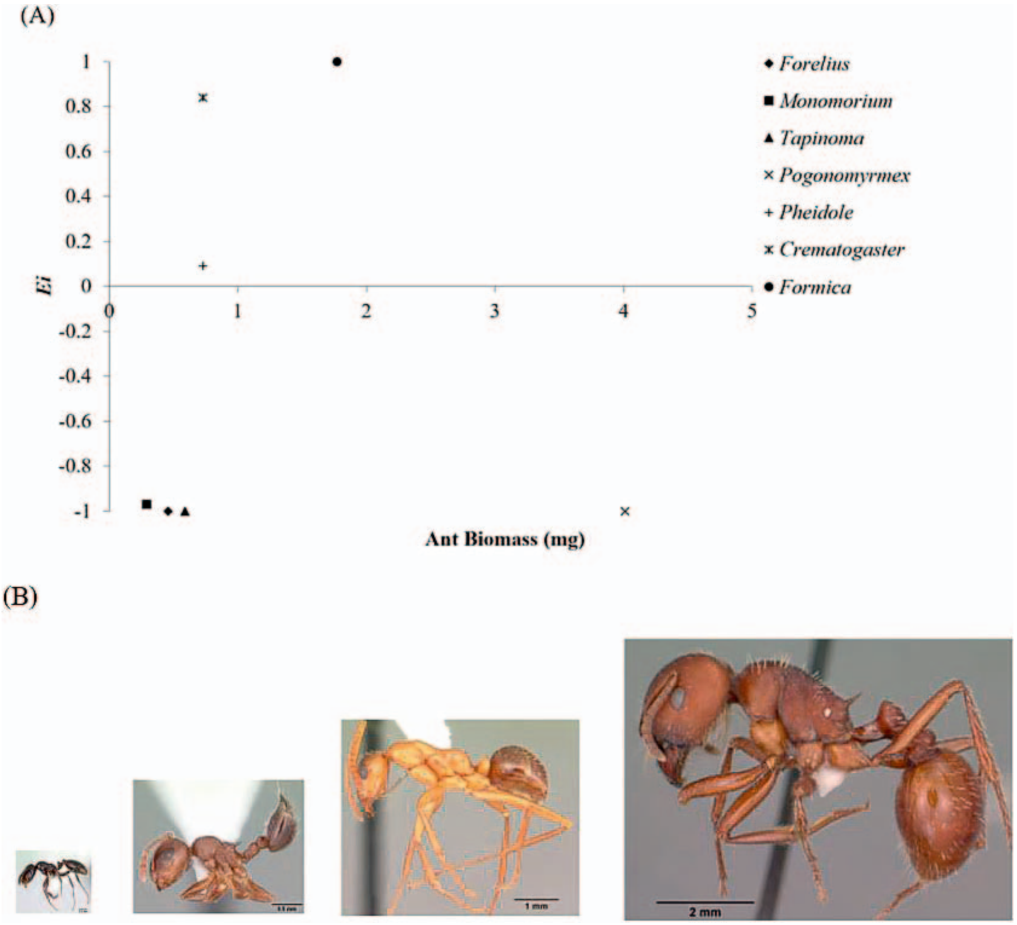

FIG. 5. (A) Ivlev's electivity index (E_i) of *Phrynosoma cornutum* for ant genera in relation to average mass of individual ants on Core Reserve Area 3 at Tinker Air Force Base, Oklahoma, in 2010 and 2011. Values for Ivlev's electivity index range from 1 (strong usage) to -1 (not used), whereas 0 indicates usage in proportion to availability. (B) (left to right) *Monomorium minimum*, *Crematogaster lineolata*, *Formica pallidefulva*, (photos from April Nobile), *Pogonomyrmex barbatus* (photo by Jen Fogarty) / from www.antweb.org. Accessed 1 May 2016. Photos are sized to show to relative size differences between species.

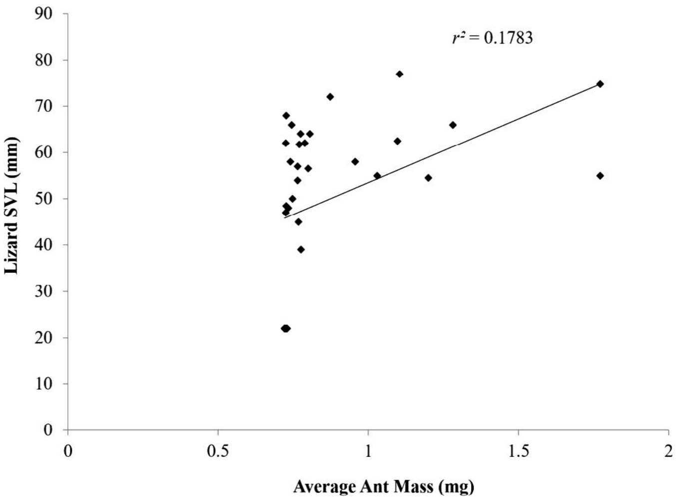

FIG. 6. Average mass of individual ants consumed by *Phrynosoma cornutum* ($N = 34$) across lizard size classes on Core Reserve Area 3 at Tinker Air Force Base, Oklahoma, in 2010 and 2011. Size classes were based on snout–vent lengths (SVL) and defined as follows: large = SVL > 50 mm; medium = SVL 30–50 mm; small = SVL < 30 mm. Two medium-sized individuals in 2010 transitioned into large lizards in 2011 and were plotted independently as medium and large lizards.

efforts to conserve or re-establish *P. cornutum* populations should expand their habitat suitability assessments beyond simply the presence/absence of harvester ants and, instead, consider habitat fragments with abundant medium- and large-sized native ant communities.

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Literature Cited

Adams, E. S., and J. F. A. Traneillo. 1981. Chemical interference competition by *Monomorium minimum* (Hymenoptera: *Formicidae*). Oecologia 51:265–270.

Aresco, M. J. 2004. Reproductive ecology of *Pseudemys floridana* and *Trachemys scripta* (Testudines: *Emydidae*) in northern Florida. Journal of Herpetology 38:249–256.

Beissinger, S. R. 1990. Alternative foods of a diet specialist, the snail kite. Auk 107:327–333.

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

Britt, E. J., J. W. Hicks, and A. F. Bennett. 2006. The energetic consequences of dietary specialization in populations of the garter snake, *Thamnophis elegans*. Journal of Experimental Biology 209:3164–3169.

Cooper, W. E, and S. Secor. 2007. Strong response to anuran chemical cues by an extreme dietary specialist, the eastern hog-nosed snake (*Heterodon platirhinos*). Canadian Journal of Zoology 85:619–625.

Donaldson, W., A. H. Price, and J. Morse. 1994. The current status and future prospects of the Texas horned lizard (*Phrynosoma cornutum*) in Texas. Texas Journal Science 46:97–113.

Drummond, H., and C. M. Garcia. 1989. Limitations of a generalist: a field comparison of foraging snakes. Behaviour 108:23–43.

Eifler, D. A., M. A. Eifler, and T. K. Brown. 2012. Habitat selection by foraging Texas horned lizards, *Phrynosoma cornutum*. Southwest Naturalist 57:39–43.

Elmhagen, B., M. Tannerfeldt, P. Verucci, and A. Angerbjörn. 2000. The arctic fox (*Alopex lagopus*): an opportunistic specialist. Journal of Zoology 251:139–149.

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

Fellers, J. H. 1987. Interference and exploitation in a guild of woodland ants. Ecology 68:1466–1478.

Fisher, B. L., and S. P. Cover. 2007. Ants of North America. University of California Press, USA.

Fox, L. R., and P. A. Morrow. 1981. Species property or local phenomenon? Science 211:887–893.

Griffiths, D. 1975. Prey availability and the food of predators. Ecology 56:1209–1214.

Golley, F. B. 1961. Energy values of ecological materials. Ecology 42:581–584.

Juanes, F., and D. O. Conover. 1994. Piscivory and prey size selection in young-of-year bluefish: predator preference or size-dependent capture success? Marine Ecology Progress Series 114:59–69.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pp. 125–166 in J. J. Millspaugh and J. M. Marzluff (eds.), Radio Tracking and Animal Populations. Academic Press, USA.

King, J. R., and J. C. Trager. 2007. Natural history of the slave-making ant, *Polyergus lucidus*, sensu lato in northern Florida with its three *Formica pallidefulva* group hosts. Journal of Insect Science 7:1–14.

Lahti, M. E., and D. D. Beck. 2008. Ecology and ontogenic variation of diet in the pigmy short-horned lizard (*Phrynosoma douglasii*). American Midland Naturalist 159:327–339.

Lechowitz, M. J. 1982. The sampling characteristics of electivity indices. Oecologia 52:22–30.

McIntyre, N. E. 2003. Effects of conservation reserve program seeding regime on harvester ants (*Pogonomyrmex*), with implications for the threatened Texas horned lizard (*Phrynosoma cornutum*). Southwest Naturalist 48:274–277.

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

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

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

Newbold, T. A., and J. A. MacMahon. 2009. Spatial and seasonal dietary patterns of the desert horned lizard (*Phrynosoma platyrhinos*): harvester ant specialist or generalist ant feeder? Canadian Journal of Zoology 87:112–123.

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

Powell, G. L., and A. P. Russell. 1984. The diet of the eastern short-horned lizard (*Phrynosoma douglassi brevirostre*) in Alberta and its relationship to sexual size dimorphism. Canadian Journal of Zoology 62:428–440.

Reagan, S. R., J. M. Ertel, and V. L. Wright. 2000. David and Goliath retold: fire ants and alligators. Journal of Herpetology 34:475–478.

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

Roper, T. J. 1994. The European badger *Meles meles*: food specialist or generalist? Journal of Zoology 234:437–452.

Sales, R. F. D., and E. M. X. Freire. 2015. Diet and foraging behavior of *Ameivula ocellifera* (Squamata: *Teiidae*) in the Brazilian semiarid Caatinga. Journal of Herpetology 49:579–585.

Scheffrahn, R. H., L.A. Gaston, J. J. Sims, and M. K. Rust. 1984. Defensive ecology of *Forelius foetidus* and its chemosystematic relations to *F. pruinosus* (Hymenoptera: Formicidae: Dolichoderinae). Environmental Entomology 13:1502–1506.

Sherbrooke, W. C. 2003. Introduction to Horned Lizards of North America. University of California Press, USA.

Sherbrooke, W. C., and K. Schwenk. 2008. Horned lizards (*Phrynosoma*) incapacitate dangerous prey with mucus. Journal of Experimental Zoology 309:447–459.

Sow, A. S., F. Martiinez-Freiria, H. Dieng, S. Fahd, and J. C. Brito. 2014. Biogeographical analysis of the Atlantic Sahara reptiles: environmental correlates of species distribution and vulnerability to climate change. Journal of Arid Environments 109:65–73.

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

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

Sullivan, B. K., K. O. Sullivan, D. Vardukyan, and T. Suminki. 2014. Persistence of horned lizards (*Phrynosoma spp.*) in urban preserves of Central Arizona. Urban Ecosystems 17:707–717.

Trager, J. C., and C. Johnson. 1985. A slave-making ant in Florida: *Polyergus lucidus* with observations on the natural history of its host *Formica archboldi* (Hymenoptera: *Formicidae*). Florida Entomologist 68:261–266.

Trager, J. C., J. A. MacGown, and M. D. Trager. 2007. Revision of the Nearctic endemic *Formica pallidefulva* group. Pp. 610–636 in R. R. Snelling, B. L. Fisher, and P. S. Ward (eds.), Advances in Ant Systematics (Hymenoptera: *Formicidae*): Homage to E. O. Wilson—50 years of Contributions. American Entomological Institute, USA.

Vitt, L. J., and E. R. Pianka. 2007. Feeding ecology in the natural world. Pp. 141–172 in S. M. Reilly, L. D. McBrayer, and D. B. Miles (eds.), Lizard Ecology: The Evolutionary Consequences of Foraging Mode. Cambridge University Press, USA.

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.

Wilson, E. O. 2003. Pheidole in the New World: A Dominant, Hyperdiverse Ant Genus. Harvard University Press, USA.

Wolf, A. J., E. C. Hellgren, V. Bogosian III, and R. W. Moody. 2013. Effects of habitat disturbance on Texas horned lizards: an urban case study. Herpetologica 69:265–281.

Wolf, A. J., E. C. Hellgren, E. M. Schauber, V. Bogosian III, R. T. Kazmaier, D. C. Ruthven III, and R. W. Moody. 2014. Variation in vital-rate sensitivity between populations of Texas horned lizards. Population Ecology 56:619–631.

Zar, J. H. 1999. Biostatistical Analysis. 4th ed. Prentice Hall Publishers, USA.

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