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SPATIAL DISTRIBUTION OF A POPULATION OF TEXAS HORNED LIZARDS (*PHRYNOSOMA CORNUTUM*: PHRYNOSOMATIDAE) RELATIVE TO HABITAT AND PREY

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ABSTRACT—The spatial distribution of a Texas horned lizard population was quantified with respect to habitat and prey. Horned lizard spatial distribution was clustered in three specific areas, whereas ant mounds belonging to their primary prey, *Pogonomyrmex barbatus*, were randomly distributed in the study area. An analysis of vegetation cover relative to horned lizard spatial distribution suggests that habitat, not prey, governed the spatial distribution of this population. In particular, horned lizards selected disturbed areas where ground cover was less dense. Horned lizards occurred at a density of one lizard/3,636 m^2 or nearly three lizards/ha. *Pogonomyrmex barbatus* mounds occurred at a density of 15.9 mounds/ha, equivalent to about 196,492 ants/ha. Relative to harvester ants, horned lizards occurred at a ratio of one lizard per six ant mounds or one lizard per 74,148 ants. Compared with a previous study in New Mexico, harvester ant density was considerably greater, however, horned lizard density was less. This may be related to prey availability; although ants are less abundant at the New Mexico site, more individuals may be available for consumption due to habitat differences.

Phrynosoma cornutum is a widespread and well-known component of the Texas herpetofauna, with certain conservation concerns (Price, 1990), yet little quantitative ecological information is available for Texas populations (but see Pianka and Parker, 1975). Consequently, an 87-day study, during May–August 1989, was conducted 9.3 km northeast of Millersview, Concho County, Texas (elev. 495 m), to investigate the distribution of this lizard in relation to habitat and to prey resources.

Texas horned lizards inhabit arid and semiarid areas, characterized by open country of scant vegetation. Habitats often consist of grasses interspersed with cacti, yucca, mesquite, and other assorted woody shrubs and small trees (Sherbrooke, 1981). The lizards have a dietary preference for ants, specifically harvester ants (*Pogonomyrmex* sp.) (Pianka and Parker, 1975; Whitford and Bryant, 1979; Sherbrooke, 1981; Munger, 1984*a*, 1984*b*, 1984*c*; Montanucci, 1989), although numerous other insects are included in their diet (Milne and Milne, 1950).

The nonrandom spatial distribution of horned lizards, often patchy, in relation to specific habitat variables and/or food sources, has been previously demonstrated (e.g., Munger, 1984*a*). Texas horned lizards have restricted home ranges, resulting in important ramifications for foraging strategies. In particular, individual *P. cornutum* would be expected to restrict themselves to discrete subpopulations of ant colonies (Munger, 1984*a*). This condition, coupled with exclusive use of a resource, are the two conditions necessary for the evolution of a "prudent" foraging strategy in horned lizards (Munger, 1984*a*, 1984*b*). Whitford and Bryant (1979) hypothesized a "prudent" foraging strategy for Texas horned lizards; such that *P. cornutum* limits its harvesting bouts at any one ant colony to maintain prey activity and availability for future harvesting. Munger (1984*b*) subsequently showed that *P. cornutum* forages in a manner that maximizes the short-term yield of ants. Because harvester ants are the principle food source of this lizard (op. cit.), we investigated the relationship between liz-

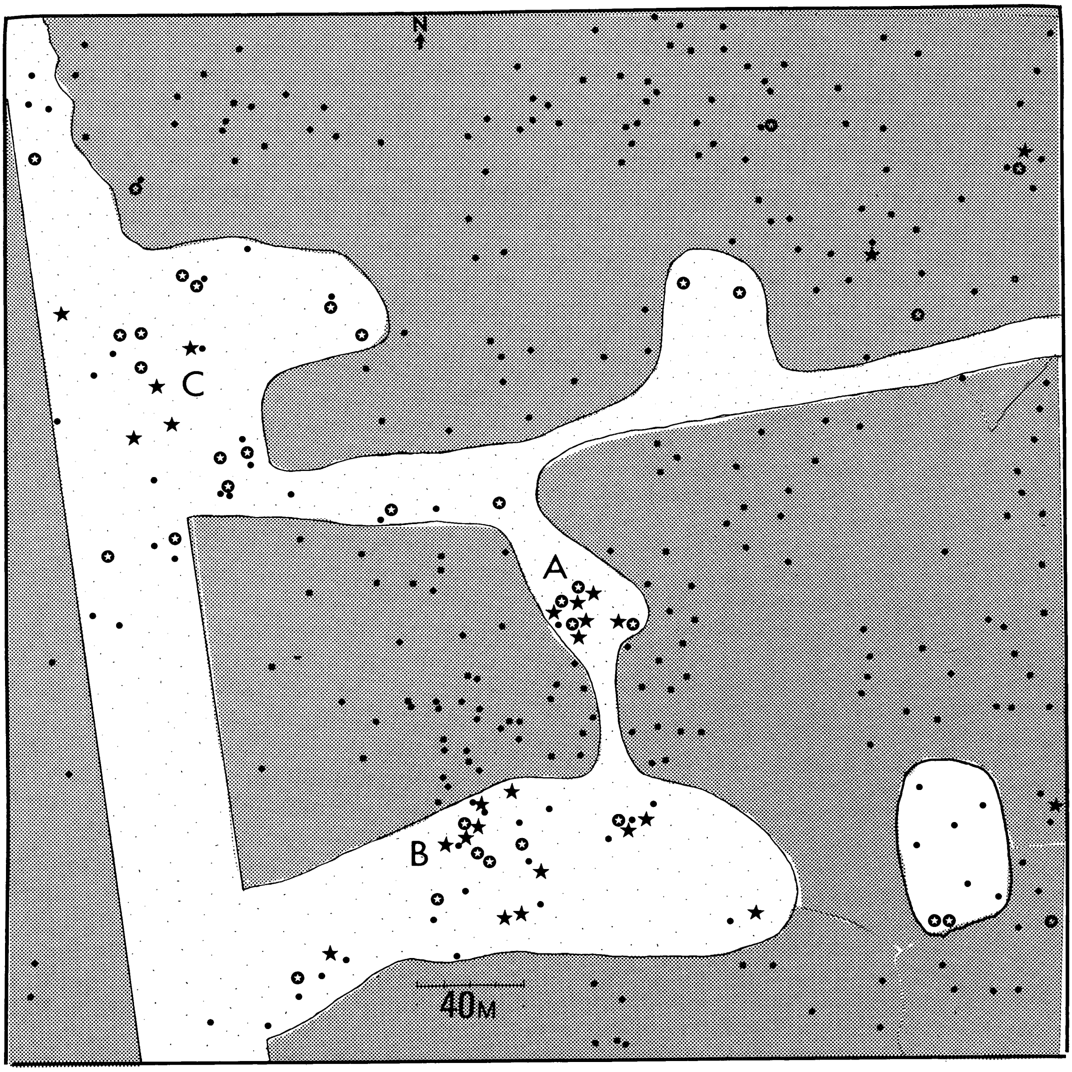

FIG. 1—Spatial distribution and relative abundance of horned lizards and harvester ants. The nonstippled areas are regions of disturbed habitat where vegetation is sparse. The westernmost area including C forms an airstrip. Dots indicate ant mounds, dots with stars first time lizard captures, and black stars show lizard recaptures. A, B, and C are areas of highest lizard abundance. Area A is caliche, area B clay; and area C is asphalt bordered by sandy soils.

ard density and prey density, and the spatial distribution of *P. cornutum* and its prey, *Pogonomyrmex barbatus*.

MATERIALS AND METHODS—Horned lizards were surveyed within a study site 160,000 m² in total area which contained numerous patches of disturbed habitat in early stages of succession (Fig. 1). It included part of an asphalt airstrip, several dirt roads, grazed pastures, a section of mowed grass, and a house. Substrates consisted of asphalt, sandy soils, clay, and caliche. Vegetation within the study site consisted primarily of *Acacia greggii, Opuntia engelmannii, Prosopis glandulosa, Mimosa biuncifera, Nolina texana, Ephedra antisyphilitica, Hilaria* sp. (the dominant grass type), *Aristida* sp., *Bouteloua* sp., *Eriochloa* sp., *Panicum* sp., *Andropogon* sp., *Castela texana, Berberis trifoliolata,* and *Xanthocephalum dracunculoides.* The position of each ant mound, topographical features, and the locality of each lizard was mapped using a compass and measuring tape (Fig. 1). During each survey the entire study area was covered by foot, and lizards were sampled by hand. Sampling took place either in the morning or evening, coinciding with the activity time of *P. cornutum* (Creusere and Whitford, 1982). Several lizards were encountered randomly and are included in this analysis. Lizards were uniquely toe-clipped for future recognition (Ferner, 1979).

Quantitative data on basal (ground) cover was collected to test the prediction that horned lizards prefer sparsely vegetated, disturbed areas. Two general areas were sampled: (1) areas inhabited by lizards (nonstippled region of Fig. 1) and (2) areas in which lizards were thought to be absent (stippled region of Fig. 1). Basal cover was sampled randomly in each of these areas using a 0.25-m^2 plot frame, modified from Daubenmire (1959). A total of 30 samples was taken in each area, where a sample consisted of measuring (1) grass cover, (2) miscellaneous herbaceous vegetation cover, and (3) debris cover (e.g., leaf litter). The data were then analyzed using the chi-square test (PROC FREQ procedure; SAS Institute, 1985). Differences were considered significant at $P < 0.05$. Herbaceous vegetation and debris contributed very little to ground cover in both areas, additionally, debris such as leaf litter would not obstruct a lizard in most instances. Consequently, only differences in grass cover between the two areas are presented. Areas inhabited by horned lizards had significantly less vegetation in terms of ground cover than areas uninhabited by horned lizards ($\chi^2_3 = 16.63$, $P = 0.001$).

A distance method known as T-square sampling (Ludwig and Reynolds, 1988) was used to measure spatial patterning for both horned lizards and harvester ants. The BASIC program TSQUARE.BAS was used to compute C, the T-square index of spatial patterning, and I, the distance index of dispersion. A random pattern is obtained when I has an approximate expected value of 2, a uniform pattern for less than 2, and a clumped pattern for greater than 2. An approximate value of 0.5 for C indicates a random pattern, significantly less than 0.5 a uniform pattern, and significantly greater than 0.5 a clumped pattern.

RESULTS AND DISCUSSION—Ant mound distribution was random ($I = 1.87$, $Z = -0.43$; $C = 0.52$, $Z = 0.53$). Mounds were visible on sandy, stony, and asphalt substrates, suggesting that *P. barbatus* does not discriminate between substrate type. Seeds are the ants' principle food source (Rissing, 1981), and mounds were more dense in seed-producing areas. Horned lizards were sometimes found adjacent to these grassy areas in less dense vegetation, where they could potentially feed on foraging workers (Fig. 1).

Lizard distribution was clustered in three specific areas, A, B, and C of Fig. 1 ($I = 12.24$, $Z = 32.93$; $C = 0.82$, $Z = 6.58$). These disturbed areas contained invading forbs and grasses, and were connected by corridors. Disturbed areas contained less ground cover, allowing horned lizards a greater degree of movement. Area A consisted of caliche, area B, clay (fine consistency); and C was part of an asphalt airstrip bordered by sandy soil. Horned lizards were observed burying themselves in sandy and clay soils in these areas. Areas A and B were adjacent to relatively high concentrations of ant mounds, while area C was not. Area C was graded, compacted, mowed, and maintained as an airstrip (Fig. 1). It retained heat for longer than the surrounding soils. *Phrynosoma cornutum* was found there in the early morning and late evening, apparently using area C for thermoregulation. Of the 35 individual horned lizards captured, 30 were located in disturbed habitat (Fig. 1). Habitat selection was significantly greater for the disturbed areas ($\chi^2_1 = 49.64$, $P < 0.001$), where lizards could potentially move with less obstruction.

A total of 35 juvenile and adult lizards was caught, including three hatchlings. Hatchlings are excluded from analysis because of their high mortality (Ballinger, 1974), but are included in Fig. 1 to show spatial distribution within the study area. Population size was estimated to be 44 using the Schumaker-Eschmeyer (1943) method ($SE = 5.5$, 95% confidence interval = 33–55). Recapture success was 86% (30 out of 35 lizards were recaptured). Four lizards were each recaptured twice, two were recaptured three times, and one was recaptured five times. The sex ratio was male biased (1.5:1), but not significantly different from 1:1 ($\chi^2_1 = 1.29$, $P > 0.9$). Forty-four lizards in the 160,000-m^2 area equates to one lizard per 3,636 m^2 or nearly three lizards per hectare. Whitford and Creusere (1977) estimated 10 *P. cornutum*/ha at their site (Jornada) in the Chihuahan desert in New Mexico.

Two-hundred fifty-five *P. barbatus* mounds were mapped at a density of 15.9 mounds per hectare, providing a ratio of one lizard per six ant mounds. Whitford and Bryant (1979) reported that three species of *Pogonomyrmex* occurred at a density of 145 colonies/ha (one lizard per 14.5 colonies). Using Whitford and Bryant's (1979) data, we extrapolated ant density to be 117,040 ants/ha (1 lizard per 11,704 ants). Based on an estimate of colony size for *P. barbatus* (12,358 ants; Wildemuth and Davis, 1931), standing crop was calculated at 196,492 ants/ha (1 lizard per

74,148 ants). Ant density would therefore be greater for the Texas population, suggesting that factors other than prey density are limiting the population. Although ant density is less at the Jornada site, more ants may be available for consumption due to the nature of the habitat. The Jornada Plains are grassland, the cover is sparse, and past overgrazing has produced a desert-like environment (annual precipitation is less than 15 cm/year). In habitats where resources are more or less dispersed (Jornada Plains), trunk trails created by *Pogonomyrmex* are conspicuously absent, and ants diverge from the nest immediately (Hölldobler and Lumsden, 1980; Hölldobler and Wilson, 1990). The dispersal of ants in the absence of trunk trails would preclude lizards from foraging at these trails, but not from the region of the nest. If ants at the Texas site are foraging in dense grass (many of the mounds are in fact located in dense grass or weeds), they are less vulnerable to predation by a horned lizard compared to the Jornada Plain. Also, *P. barbatus* is a group forager (Davidson, 1977*a*). exploiting patchy resources and concentrating its foraging effort in a restricted area surrounding the nest (Davidson, 1977*b*; Hölldobler and Wilson, 1990). This type of foraging may inhibit predation of ants by horned lizards in the more vegetated areas of our site, where dense vegetation and a dorsally compressed body are probably not compatible.

The nonrandom spatial distribution of this lizard population, and the random distribution of ant mounds, would suggest that horned lizard spatial patterns are in response to factors other than prey. Our map data (Fig. 1) provides supporting evidence that vegetation density accounts for horned lizard spatial distribution. We considered that horned lizards would be harder to find in dense vegetation, but extensive searching in and around the study area yielded a low number of horned lizards. Finally, our data suggest that the spatial distribution of Texas horned lizards was dependent upon the presence of foraging harvesting ants, their principle food source, and open, partially vegetated habitat that facilitates locomotion, foraging, and thermoregulation.

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