

Temporal and Spatial Resource Partitioning in a Chihuahuan Desert Lizard Community

by

F. Michael Creusere and Walter G. Whitford

Department of Biology
New Mexico State University
Las Cruces, New Mexico 88003

Abstract

Activity patterns of the lizards in a Chihuahuan Desert creosotebush (*Larrea tridentata*) community were studied by walking fixed transects on a marked grid and recording activity of individual lizards. We found considerable spatial overlap in *Cnemidophorus tigris* and *Holbrookia texana*; however, individuals that overlapped spatially were active at different times. We distinguished five distinct activity patterns in *C. tigris* and *H. texana*, whereas *Uta stansburiana*, *Sceloporus magister*, *Phrynosoma modestum*, *P. cornutum*, and *Crotaphytus wislizenii* were bimodal. Individual activity patterns varied: some were active only in the morning, only in midday, only in the afternoon, morning and afternoon, or all day. Most lizards were active less than 25% of the days of observations. Exceptions were a few large male *H. texana* that were active between 40% and 70% of the days. We suggest that temporal separation of activity reduces intraspecific competition and increases carrying capacity in species for which food is probably not a limiting resource.

Recently there has been considerable interest in resource partitioning in lizard communities (Pianka 1973; Huey and Pianka 1977). Species typically divide resources along three dimensions: food type, habitat, and time (Pianka 1969); most studies have focused on habitat segregation, food size and body size, and daily and seasonal activity patterns (Schoener 1974). These studies, of necessity, have largely ignored differences in activity patterns among individuals in the populations of component species in order to focus on the overall patterns of resource partitioning. Several studies have shown that lizards in climatically varying habitats exhibit interspecific differences in activity periods (Inger 1959; Hillman 1969; Schoener 1970), but studies that have considered activity patterns of individuals have been limited to a single species (Irwin 1965; Simon and Middendorf 1976). Simon and Middendorf (1976) suggested that intraspecific partitioning may reduce competition, increase feeding efficiency, and increase carrying capacity. However, few studies have concentrated on temporal partitioning; Schoener (1974) indicated that temporal par-

tioning was much less important than food and habitat.

In studies of four sympatric species of Chihuahuan Desert ants, Whitford and Ettershank (1975) and Whitford (1978) showed that temporal partitioning was extremely important in species packing in Chihuahuan Desert ant communities; however, no attempt was made to follow the activity patterns of individual colonies.

Simon and Middendorf (1976) studied individual *Sceloporus jarrovi* and found that most adult activity was in the early morning and most juvenile activity occurred near noon. They also found that individual lizards were active an average of only 2.5 days per week.

In our studies of Chihuahuan Desert lizard communities (Whitford and Creusere 1977), we found seasonal differences in activity patterns of lizard species. We hypothesized that temporal partitioning might be as important in Chihuahuan Desert lizards as it seemed to be in the ants, and that there would be differences in activity patterns between juveniles and adults as suggested by Simon and Middendorf (1976). Therefore, we designed a study of the activity

patterns and microhabitat use of individual lizards of the eight species included in a Chihuahuan Desert lizard community. Here we report the results of that study.

Methods and Materials

The study area was on a watershed draining the southeast slopes of Mt. Summerford of the Doña Ana range on the New Mexico State University Ranch, 40 km NNE of Las Cruces, Doña Ana County, New Mexico. The watershed includes an alluvial fan (bajada) dissected by numerous ephemeral watercourses (arroyos) which drain into an ephemeral lake (playa). The soils on the bajada are shallow and sandy and the calcium carbonate deposition layer (caliche) occurs from a few centimeters to over a meter below the surface. The caliche layer is absent in arroyos that have complex soils varying from gravel to loam. The 50-year average precipitation for the area is 225 mm/year; peak rainfall occurs during July and August (Houghton 1972). Summer maximum air temperatures reach 40°C and freezing temperatures are recorded from October through mid-April (data from the Jornada Validation Site Weather Station).

The vegetation is typical of large areas in the northern Chihuahuan Desert. The well-drained areas on the bajada have an essentially monotypic cover of creosotebush, *Larrea tridentata* (23% cover), and all other species contribute about 1% cover. The arroyos are lined with a number of plant species including mesquite, *Prosopis glandulosa* (about 2% cover); tarbush, *Flourensia cernua* (1.5% cover); desert willow, *Chilopsis linearis* (< 1% cover); apache plume, *Fallugia paradoxa* (0.8% cover); and two yuccas, *Yucca elata* (0.2% cover) and *Y. baccata* (0.1% cover). The bajada slope varies from 5% to < 1%.

Studies were conducted on a 160- × 60-m grid bisected by a large arroyo. Nearly all lizards in this area were captured by pitfall traps, noosing, or hand-capture. Each individual was toe-clipped, marked by a tricolored code with enamel paint on its dorsum, and released. Marking had no visible effect on activity patterns and permitted positive field identification of a lizard without subsequent handling. The paint remained intact from 4 to 8 weeks and lizards

were repainted when identification became difficult.

A buffer grid was established 60 m on all sides of the main grid. The buffer was used to obtain complete home ranges of animals captured on the primary grid. No pitfall traps were established in the buffer zone. All species except *Cnemidophorus tigris* were either noosed or hand-captured and color-coded. Data for species activity was obtained from the main grid, whereas patterns of activity of individuals included data from both.

A predetermined transect across both grids was walked each hour to record individual activity throughout the day. When a lizard was observed, its color code, location, and time of observation were recorded. Data reported here are based on 100 15-h days of observation from May through October 1975. Climatic data for the periods of observation were obtained from a standard weather station on the site.

When a lizard is "active" on the surface, it spends time searching or waiting for prey alternating with or combined with thermoregulatory behavior. Data obtained from transects provided information only on the type of activity the individual was engaged in at that time. Therefore, we could not divide activity into component behaviors as is possible if individual lizards are followed for extended periods of time. In this study we define "activity" as any behavior occurring on the surface.

We could not use the method of Tanner and Krogh (1974) to evaluate activity. Their method assumes equal probability of sighting for all species. The Jornada is more densely vegetated than the Nevada Test Site studied by Tanner and Krogh (1974), particularly in the arroyos where large perennials block vision. Lizards were often heard but could not be identified before disappearing into shrubs or a burrow.

Behavioral characteristics of species had an effect on the reliability of the data. For example, some sightings of *C. tigris* could not be included in the analysis because the individual could not be identified. *Cnemidophorus tigris* was extremely wary and ran into a burrow if approached too closely. We were unable to approach this species to noose it, and had to rely on can traps for capture and painting. Even with binoculars it was difficult to identify individuals when they were running. There was also a high probability of missing cryptic species such as

Crotaphytus wislizenii and *Phrynosoma modestum*. *Holbrookia texana* was much less wary than *C. tigris* and could often be approached to within 10 m.

To compare species occurring at different densities, we weighted activity by setting the largest sum of all observations for an hour equal to 1.00 and expressing the activity in all other hours as a percentage of that sum.

Spatial overlap was determined by plotting the sightings of individual lizards on maps of the study area. Boundary lines were drawn connecting the outermost sightings for each individual, thereby enclosing the "area of activity." Area overlap between individuals of the same or different species was then taken from these plots. If all sightings of a given lizard were completely within the boundaries of the area of activity of another lizard, the spatial overlap was set at 1.00. Spatial overlap less than 1.00 was set as the percentage of activity area common to both lizards.

Results

Species Activity Patterns

Five species (*Crotaphytus wislizenii*, *Phrynosoma cornutum*, *P. modestum*, *Sceloporus magister*, and *Uta stansburiana*) had bimodal activity patterns. *Cnemidophorus tessellatus* had unimodal activity (in the morning only); *C. tigris* and *Holbrookia texana* were active most of the day (Fig. 1). *Cnemidophorus tessellatus* and *C. tigris* exhibited maximum activity between 0800 and 0900 h. *Sceloporus magister* had its maximum activity at 0730 h and *P. modestum* was most active at 1730 h. *Crotaphytus wislizenii* and *H. texana* exhibited peak activity between 1000 and 1100 h, and *Phrynosoma cornutum* was most active between 0730 and 0930 h. The afternoon peak activity was usually considerably shorter than the morning peak for all species; however, *U. stansburiana* was most active shortly after sunrise (0630 h) and between 1800 and 1900 h on days when cloud cover reduced insolation. Cloud cover appeared to depress the activity of all species except *U. stansburiana*. Nearly all individuals of this species were active on cloudy afternoons but were rarely encountered on clear afternoons. The most frequently observed lizard species were *H. tex-*

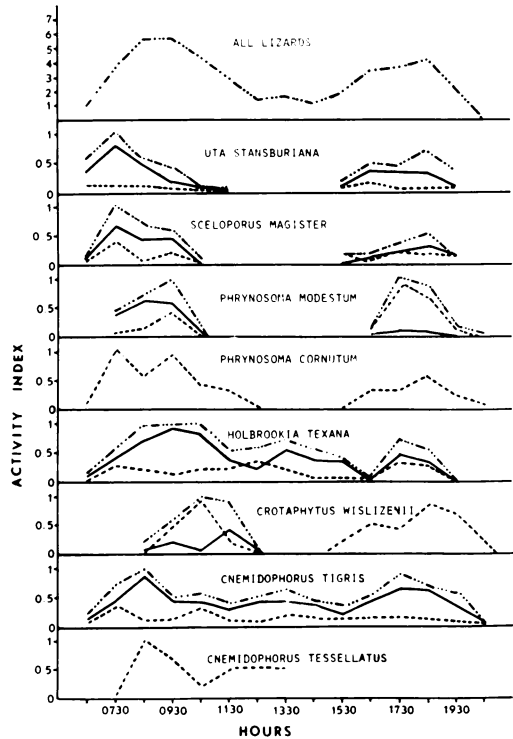


Fig. 1. Activity patterns of the lizards in a Chihuahuan Desert community. The activity index was derived by setting the largest number of observations equal to 1.00 and expressing the number of observations for all other hours as a fraction of 1.00. Dashed lines represent activity of females, solid lines the activity of males, and dot-dash lines the sum of the activity of all individuals seen, some of which were not sexed.

ana and *C. tigris*, which were also the most abundant (Whitford and Creusere 1977). We usually saw more males than females (Fig. 1).

Several hundred hours of observations yielded only 11 interspecific encounters. Seven of these resulted in both individuals fleeing a short distance, then immediately continuing their search for food. Three encounters between male *U. stansburiana* and *C. tigris* of both sexes resulted in the larger *C. tigris* ignoring the bobbing of the former and continuing its search for termites. The only successful interspecific defense of an area occurred when a female *P. cornutum* charged and pursued a large male *C. tigris* that had wandered into her territory while she was depositing eggs.

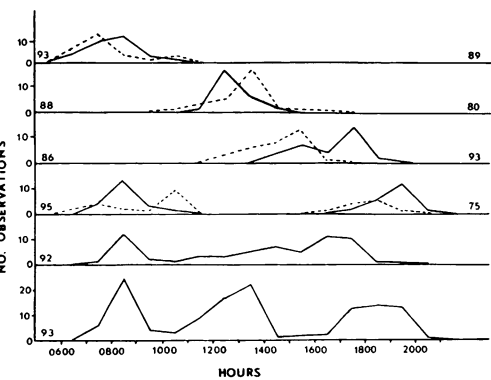


Fig. 2. Activity of the 10 most frequently encountered *Cnemidophorus tigris*. Dashed lines represent females, solid lines males. Snout-vent (S-V) lengths of males are on the left, S-V lengths of females on the right.

Individual Activity Patterns

Individuals in each species consistently maintained a preferred time of activity that made up only a portion of the total activity for the species. Within the populations of *C. tigris* and *H. texana*, we found five main patterns of daily activity: (1) early morning only, (2) midday only, (3) afternoon only, (4) both early morning and late afternoon, and (5) activity throughout most of the day (Figs. 2 and 3). The activity patterns of *U. stansburiana* are typical of species having a bimodal activity pattern. Individual lizards of bimodal species showed three patterns of activity: (1) morning only, (2) afternoons only, and (3) both morning and afternoon (Fig. 4). *Cnemidophorus tessellatus* was restricted to morning and midday activity on the study site but was observed to be active throughout the day in adjacent areas.

We made sufficient repeated observations on 30 of the 61 marked *C. tigris* to provide reliable estimates of individual activity patterns. Eight exhibited early morning activity, five were active only at midday, seven were active only in the afternoon, seven exhibited both morning and late afternoon activity, and three were active throughout most of the day. However, none of these individuals were seen on more than 25% of the days and most were seen only 10–15% of the days. The patterns of 10 of the most frequently encountered *C. tigris* are shown in Fig. 2. Of the 13 *H. texana*, 3 were active on-

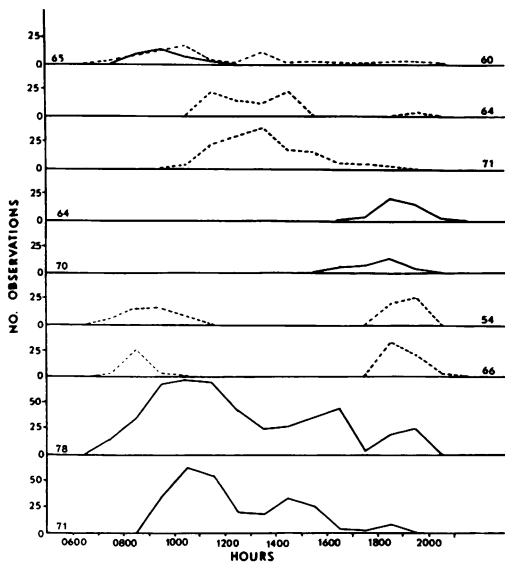


Fig. 3. Activity patterns of the 10 most frequently encountered *Holbrookia texana*. Dashed lines represent females, solid lines males. Snout-vent (S-V) lengths of males are on the left, S-V lengths of females on the right.

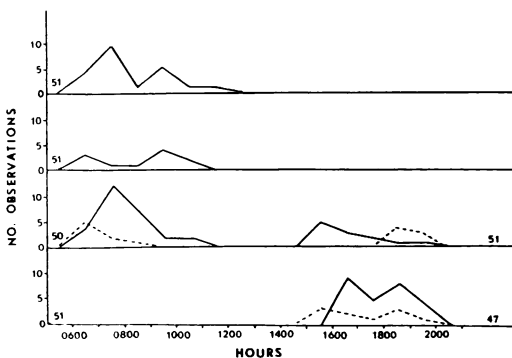


Fig. 4. Activity patterns of six *Uta stansburiana* selected to show the different activity patterns discussed in the text. Dashed lines represent females, solid lines males. Snout-vent (S-V) lengths of males are on the left, S-V lengths of females on the right.

ly in the mornings, 2 were active only in the afternoon, 3 were bimodal, and 5 were active throughout the day (Fig. 3). Three of the large male *H. texana* were seen on 60–70% of the days but the remainder were only seen on 15–40% of the days. Of the 13 *U. stansburiana*,

5 were active only in the morning, 4 were active only in the afternoon, and 4 were bimodal (Fig. 4). The three *P. modestum* and three *S. magister* were bimodal. Three *P. cornutum* were active only in the morning, one was active only in the afternoon, and one was bimodal. Two *C. tessellatus* were morning active only and one was active only at midday. Of the four *C. wislizenii*, two were bimodal, one was morning active, and one was afternoon active.

In previous studies (Whitford and Creusers 1977) we noted that the number of individuals observed hourly seldom exceeded 25% of the population based on mark-recapture estimates. When we increased the number of observers to six and walked a 60-m-wide transect across the site, we improved only slightly; 35% of the estimated population was observed. Previous pitfall trap data for 1970-74 indicated that many individuals were captured several times in one area followed by several weeks without recapture before being taken again in that area. We initially assumed that these lizards foraged in adjacent areas for a period of time before returning to the trapping grid. However, frequent sightings of individuals were followed by periods with no sightings on either the grid or buffer zone, which suggests these animals may have been aestivating. Some individuals of all species remained active throughout the summer.

The individuals that had short periods of activity were feeding during most of that period. Lizards with more extended activity periods fed in short spurts throughout the activity period, spending the remainder of the time at rest on the surface.

Spatial Patterns

To adequately interpret the temporal activity patterns of individual lizards, it is necessary to examine their spatial distribution. There was little spatial overlap in the species occurring at low densities, and here we present data only for *C. tigris* and *H. texana*.

The overlap of male and female *C. tigris* was almost complete (Fig. 5). Of the area occupied by males, 47% was used by only one male, 37% by two, 11% by three, and 5% by four. The average number of individuals using a given point within all the male activity areas was 1.7. Maximum overlap values for male *C. tigris* are

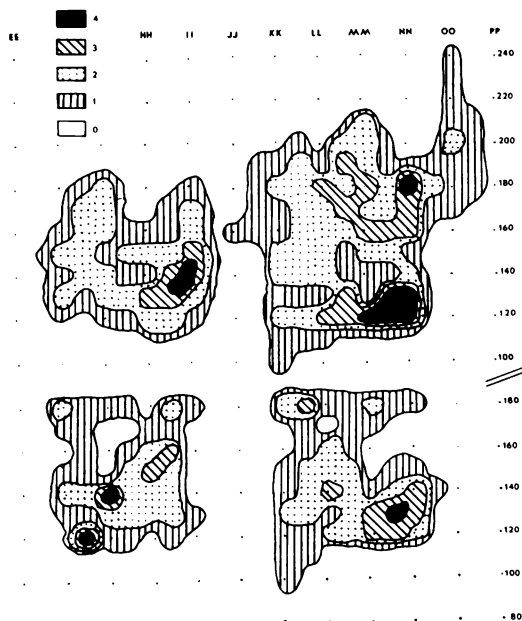


Fig. 5. Spatial overlap in *Cnemidophorus tigris*. The upper plots are for males and the lower plots for females. Different patterned areas indicate use by zero to four individuals of the same sex. Grid points are 20 m apart.

as follows: 1.00 overlap with at least one other male, 0.90 with at least two other males, and 0.50 with three or four other males (i.e., one male's activity area was completely contained in the areas of other males, 90% of one male's activity area fell into areas used by two or more other males, and 50% of one male's activity area was used by at least three other males).

Female use of space was similar: 51% of female activity areas was used by only one, 35% by two, 11% by three, and 4% by four. The average number of females using a given part of an activity area was 1.7—the same as for males. Maximum overlap for female activity areas was 0.81 with one or more other females, 0.45 with two or more others, and 0.45 with three or four others.

Among male *H. texana*, the maximum observed overlap was 0.62 with at least one other male, 0.50 with two or more others, and none overlapped with three others. There was virtually no overlap in *H. texana* females; the maximum overlap for any female activity area was 0.12 with one other.

In spite of overlaps, we almost never observed more than one individual of a species in proximity to another of the same species.

During the few weeks when both adults and juveniles were active, the adults tended to remain in the vicinity of denser vegetation and juveniles appeared to be relegated to more open vegetation. For example, adult *H. texana* were usually found in large arroyos having $>1\text{ m}^2$ of open stream bed, some rocks, and dense clumps of apache plume at the edge. Juvenile *H. texana* were found in the open upland areas of creosotebush until the adults ceased activity late in the season. The juveniles then migrated to the arroyos.

Discussion

The most intriguing result of these studies is that in the most numerous species individual lizards exhibited consistent but abbreviated patterns of activity. Many individuals in the population do not overlap temporally although these same individuals may overlap spatially. This temporal separation reduces intraspecific competition and increases carrying capacity probably by increasing feeding efficiency. This seems particularly likely in *C. tigris*, which occurs at densities of 30–40/ha (Whitford and Creusere 1977) and which have home ranges of about 0.57 ha (range 0.1–2.4 ha) in this study. *Onemidophorus tigris* feed primarily on termites (Pianka 1970) by rooting through accumulations of leaf litter. Although a morning feeder would disturb the termites and remove a small number, the subterranean galleries of the termites would be left undisturbed. If the litter is in a shaded, temperature-moderated area, the termites will reenter within a few hours (Johnson and Whitford 1975; W. G. Whitford, personal observation). Thus, individual lizards active at different times of the day could feed in the same location. Even at densities of 30–40/ha, *C. tigris* is not likely to deplete the termite population which we estimate conservatively to exceed $1,200/\text{m}^2$ (Johnson and Whitford 1975). With a food resource as large and temporally flexible as termites, *C. tigris* can exist at high densities avoiding intraspecific competition by utilizing the same space at different times of the day.

Simon and Middendorf (1976) presented the

only recorded example of spatial and temporal overlap in a single species of lizard and stated that little overlap has been described in any taxon. Here we document temporal and spatial overlap in *C. tigris* and *H. texana*. We suggest that such overlap may be the rule rather than the exception, particularly in species that achieve high densities. There are many species of organisms that use extremely abundant food resources and that occur at densities that should result in considerable intraspecific competition because of spatial overlap. Intraspecific interactions are energy expensive and, if agonistic, can be damaging. There appears to be remarkable lack of intraspecific agonistic behavior in harvester ants (Whitford 1976), and in *C. tigris* and *H. texana* as documented in this study. It seems likely that temporal separation could be behaviorally established early in a season and maintained throughout the season.

Spatial overlap of a male and female in sexually reproducing species is expected, but spatial overlap of several males is not. The relation between lizard body size and extent of activity suggests the behavioral establishment of a temporal hierarchy. In *H. texana*, the largest lizards exhibited the all-day pattern of activity. The smaller lizards had the more temporally restricted activity pattern. This could be interpreted as dominant-subordinate interaction; the subordinate is relegated to less favorable foraging times. The peak activity of ground and litter arthropods is in the early morning and evening when temperatures near the ground are more favorable for their activity (W. G. Whitford, unpublished data). Larger lizards may have to spend more time active on the surface to maintain body temperatures at preferred levels for digestion and other physiological processes, and they may require a longer time to fill their stomachs. This need for an extended feeding-digestion period seems to be a reasonable explanation for the body size–activity pattern in *H. texana*.

It is apparent from this study that individual lizards are not surface active every day; the data suggest that most are active about 2 days per week or less. Simon and Middendorf (1976) found that *Sceloporus jarrovi* were active on the average only 2.5 days per week. Even allowing for large errors in our data due to the limitations of the walking transect technique, we can state with confidence that individual lizards were ac-

tive less than 50% of the time with the few exceptions noted in *H. texana*. Considering a pattern of surface activity that is less frequent than daily and the reduced diel activity patterns of individual lizards, it is apparent that temporal partitioning is much more important than previously thought (e.g., Schoener 1974) and deserves further investigation to see if this results in a partitioning of food resources.

References

- Hillman, P. E. 1969. Habitat specificity in three sympatric species of *Ameiva* (Reptilia: Teiidae). *Ecology* 50:476-481.
- Houghton, F. E. 1972. Climatic guide, New Mexico State University, Las Cruces, New Mexico, 1851-1971. New Mexico State Univ. Agric. Exp. Stn. Res. Rep. 230:1-20.
- Huey, R. B., and E. R. Pianka. 1977. Patterns of niche overlap among broadly sympatric versus narrowly sympatric Kalahari lizards (Scincidae: *Mabuya*). *Ecology* 58:119-128.
- Inger, R. F. 1959. Temperature responses and ecological relations of two Bornean lizards. *Ecology* 40:127-136.
- Irwin, N. I. 1965. Diel activity and social interaction of the lizard *Uta stansburiana* Stejnegeri. *Copeia* 1965:99-101.
- Johnson, K. A., and W. G. Whitford. 1975. Foraging ecology and relative importance of subterranean termites in Chihuahuan Desert ecosystems. *Environ. Entomol.* 4:66-70.
- Pianka, E. R. 1969. Sympatry of desert lizards (*Ctenotus*) in western Australia. *Ecology* 50:1012-1030.
- Pianka, E. R. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology* 51:703-720.
- Pianka, E. R. 1973. The structure of lizard communities. *Annu. Rev. Ecol. Syst.* 4:53-74.
- Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408-418.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27-39.
- Simon, C. A., and G. A. Middendorf. 1976. Resource partitioning by an iguanid lizard: temporal and microhabitat aspects. *Ecology* 57:1317-1320.
- Tanner, W. W., and J. E. Krogh. 1974. Variations in activity as seen in four sympatric lizard species of southern Nevada. *Herpetologica* 30:303-308.
- Whitford, W. G. 1976. Foraging behavior of Chihuahuan Desert harvester ants. *Am. Midl. Nat.* 95:455-458.
- Whitford, W. G. 1978. Structure and seasonal activity of Chihuahuan Desert ant communities. *Insectes Soc.* 25:79-88.
- Whitford, W. G., and F. M. Creusere. 1977. Seasonal and yearly fluctuations in Chihuahuan Desert lizard communities. *Herpetologica* 33:54-65.
- Whitford, W. G., and G. Ettershank. 1975. Factors affecting foraging activity in Chihuahuan Desert harvester ants. *Environ. Entomol.* 4:689-696.

