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Behavioral Responses of a Predator, the Round-tailed Horned Lizard, Phrynosoma modestum and Its Prey, Honey Pot Ants, Myrmecocystus spp.

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ABSTRACT: The round-tailed horned lizard *Phrynosoma modestum* was active and feeding throughout the day from 2 hr after sunrise until sunset. *Phrynosoma modestum* remained in the shade of large mesquite during midday where they preyed on honey pot ants *(Myrmecocystus depilis/mimicus)* which were foraging in the canopy and moving across the shaded substrate. *Phrynosoma modestum* fed at an average of 3.9 ± 2.2 ants • bout^{-1} and an average of 7.0 ± 1.7 bouts • hr^{-1}. The species diversity of the diet of *P. modestum* doubled ($H' = 0.78$ to $H' = 1.41$) following rainfall when many species of small ants extended their activity to overlap with the activity of *P. modestum*. Honey pot ants *Myrmecocystus mimicus/depilis* were, however, the only dependable prey. Simulated predation of 20 ants • day^{-1} and 40 ants • day^{-1} affected activity of *M. mimicus/depilis,* while simulated predation of 10 ants • day^{-1} had no effect. We estimate that *P. modestum* removes approximately one-half of the early summer standing crop of *M. mimicus/depilis* during the summer.

INTRODUCTION

Lizards of the genus *Phyrnosoma* are known to be primarily myrmecophagous (Pianka and Parker, 1975), but few studies have examined any of the relationships between species of lizards and species of ants (Roth, 1971; Whitford and Bryant, 1979). Roth (1971) identified the prey species in stomachs of preserved *P. ditmarsi* and, using the distribution of the ants as a clue, was able to aid in the rediscovery of that species (Lowe *et al.,* 1971). Whitford and Bryant (1979) studied the behaviors of the horned lizard *Phrynosoma cornutum* and the responses to simulated predation of its prey, harvester ants of the genus *Pogonomyrmex*. They found that feeding behavior of the lizards was related to the behaviors of the ants. They also suggested that predation by *P. cornutum* accounted for annual turnover of the forager populations of three *Pogonomyrmex* species.

A cogener of *Phrynosoma cornutum, P. modestum,* which is approximately one-half the size of *P. cornutum,* is sympatric with the larger species over much of southern New Mexico, southwestern Texas and N-central Mexico. For these lizards to coexist we hypothesized that they would differ in foraging behavior or prey species or both. Here we report studies designed to test this hypothesis and to examine the responses to simulated predation on the major prey species of *P. modestum.*

SITE DESCRIPTION

Studies were conducted on the Jornada Validation Site 40 km NNE of Las Cruces, Dona Ana Co., New Mexico. A 4-ha site was selected for study on the NW corner of the fringe of a playa lake described by Schumacher and Whitford (1976). On this site, the dominant plants are mesquite (*Prosopis glandulosa*) and soaptree yucca (*Yucca elata*). Subdominant shrub species include longleaf mormon tea (*Ephreda trifurca*) and snake weed (*Gutierrezia sarothrae* and *G. microcephala*).

Soils on the site are sandy with a caliche (calcium carbonate) layer of about 100 cm below the surface. Average annual rainfall is 215 mm • $year^{-1}$, most occurring in July-September as intense thunderstorms.

METHODS

Phrynosoma modestum occur at densities of only 2 • ha^{-1} (Whitford and Creusere, 1977) and their cryptic coloration makes them difficult to find. For this reason we were able to obtain only 13 animals from the local area for this study. Between May and September 1978 and between April and July 1979 we observed a total of 13 *P. modestum* for 1 or more days each. After capture, lizards were returned to the laboratory for collection of fecal pellets. After the animals were postabsorptive (approximately 1 week after capture) they were marked with yellow paint on the head and back and released in the field. Most observations on the horned lizards were limited to between 0800 and 1700 hrs because in this area *P. modestum* feeds mostly in the morning and early afternoon. Lizards were observed with binoculars from a distance of 6 to 8 m and types and duration of behaviors recorded. Additional fecal pellets were collected in the field as lizards defecated. Diet composition was determined by examination of fecal pellets with a Nikon dissecting microscope. Diet diversity (Shannon-Weaver, H′) was calculated on the composition of the fecal pellets collected in 1979.

Preliminary examination of fecal pellets showed that honey pot ants (genus *Myrmecocystus* spp.) were the main prey of *Phrynosoma modestum* on the study site. Therefore, we studied activity patterns and responses of *Myrmecocystus* spp. to simulated predation. Forager population estimates were obtained by the Lincoln Index. Foragers were aspirated into a container, then cooled with ice. The terminal segment of one antenna was removed and the ants released (Whitford and Bryant, 1979). This marking procedure did not affect the ants in any way which might alter the population estimate. Simulated predation on 25 *Myrmecocystus* nests was conducted in July of 1978. Each day, for a 10-day period, a predetermined number of foragers was removed from each nest. Five colonies were assigned at random to each of the five predation-level groups; removal of 0, 5, 10, 20 or 40 ants • $nest^{-1}$ • day^{-1}. Number of ants active before simulated predation and the number of ants actually taken were recorded for each nest. Honey pot ant activity was monitored from April through June 1979. For this study, 21 colonies which had not been included in the predation studies of the preceding summer were examined. The activity of each nest was recorded hourly from 0700 to 1900 hr approximately biweekly.

RESULTS

Phrynosoma modestum exhibited most of the behaviors reported for *P. cornutum* by Whitford and Bryant (1979) (Fig. 1). In thermoregulatory sitting, *P. modestum* assumed one of two positions, "up" or "down." In the up position the lizard had its limbs extended with its body held up off the soil surface. In the down position all of the lizard's body, except for the head, was in contact with the soil surface. The up position was used most often to bask in full sun in the mornings, thus presumably avoiding excessive heat loss due to conduction to the cooler soil surface. The up position was also used both in the sun and in the shade throughout the rest of the day. The down position was used on several occasions to gain heat from a warmer substrate both in the sun and shade throughout the day. In random walking/running, *P. modestum* used a crawling gait typical of horned lizards, in which all four limbs are slightly bent, supporting the body ca. 1 cm above the soil surface. In elevated sitting, the lizard fully extended its front limbs with its tail and hind limbs in contact with soil surface. Like *P. cornutum*, *P. modestum* often placed its front feet on a tuft of grass or some other object when sitting, allowing the lizard to attain a height not otherwise possible. Unlike *P. cornutum*, *P. modestum* fed most often from a variety of positions (both "up" and "down" thermoregulatory positions as well as the elevated position) while under the shade of vegetation. As in *P. cornutum*, head tilting preceded ingestion of the prey when feeding occurred from a stationary position.

Encounters between two or more *Phrynosoma modestum* were not observed. *Phrynosoma modestum* moved between areas of shade and sun throughout the day (Fig. 1) to obtain both a suitable thermal microenvironment and ants. The horned lizards were not active before 0830 hr, approximately 2 hr after sunrise (Fig. 1). Feeding and other activities were greatest in the morning hours. A typical sequence of foraging behaviors was as follows: sitting/basking for a few seconds to several minutes, random walking with intermittent elevated sitting lasting for a few seconds to several minutes. Depending on the temperature of the soil surface, the lizard would then either repeat the sequence or seek shade. In the shade, the lizard would assume one of the thermoregulatory positions lasting from a few seconds to several minutes. Prey (ants) were most often encountered while in the shade, although any prey encountered while in the open were also readily taken. When the midday soil temperature exceeded 40 C, the lizards restricted their activity to the shaded areas under small shrubs and mesquite where the soil surface temperature was 35-40 C. However, because the active honey pot ants were restricted to the same areas, the lizards could continue to feed into the early afternoon hours (Fig. 1).

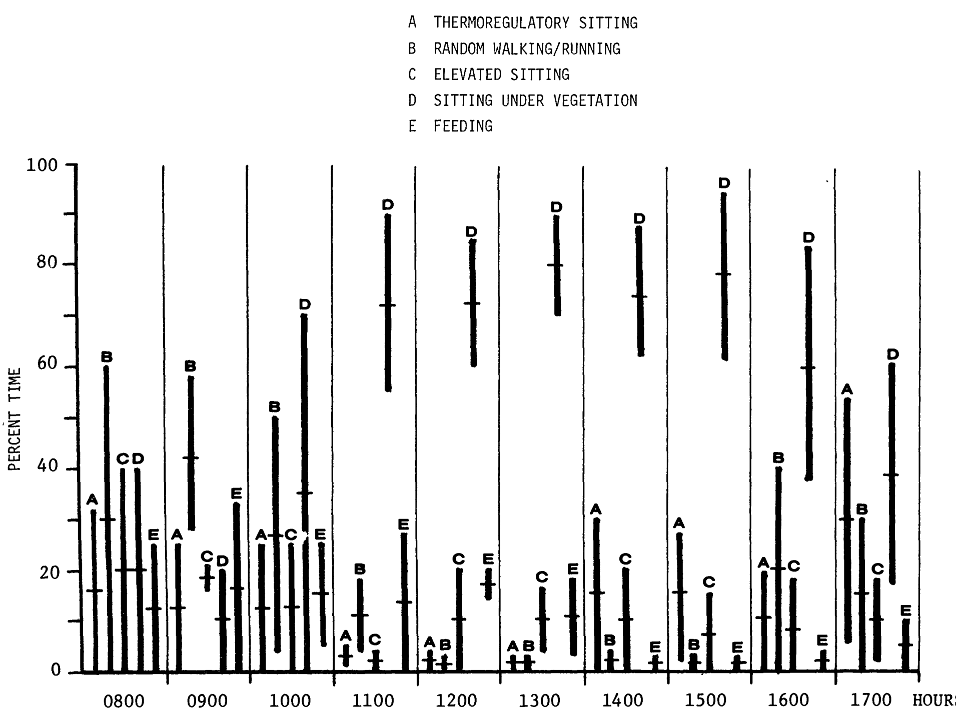

Fig. 1.—The behaviors of 13 *Phrynosoma modestum*. The horizonal line is the mean and vertical bar equals ± 1 SD

Peak feeding times for *Phrynosoma modestum* were between 1000 and 1300 hr, which correspond to the peak activity periods of the *Myrmecocystus* species found on the site (Figs. 1 and 2). *Phrynosoma modestum* fed most often on ants that were coming down out of the foliage where they had been foraging. Ants were rarely taken on nest disks. Overall, *P. modestum* fed at an average rate of 3.9 ± 2.2 ants per bout (range 1-8) with 7.0 ± 1.7 bouts per hr (range 6-9). The *Myrmecocystus* species found on the site (*M. depilis* and *M. mimicus*) occur at an average density of 21 ± 7 nests • ha^{-1} range 10-20). These ants typically forage individually for plant exudates, aphid and scale honey dew and insect prey. Foragers left the nest together in waves of from 200-500 workers during the morning hours (Fig. 2). The workers then dispersed in all directions in search of food. Workers returned to the nest individually throughout the day when temperatures allowed movement across open areas. During the hottest parts of the day the honey pot ants remained in the canopies of mesquite, small shrubs and soaptree yucca, where they feed on exudates. When a passing cloud momentarily lowered the soil temperature in the immediate area, the foragers often retreated out of the canopy, went to another plant or returned to the nest (Fig. 2). When startled or attacked, the *Myrmecocystus* workers exhibited one of two behaviors: they either became motionless or ran away with surprising speed. They usually used a combination of these behaviors which was frequently very effective in avoiding predation.

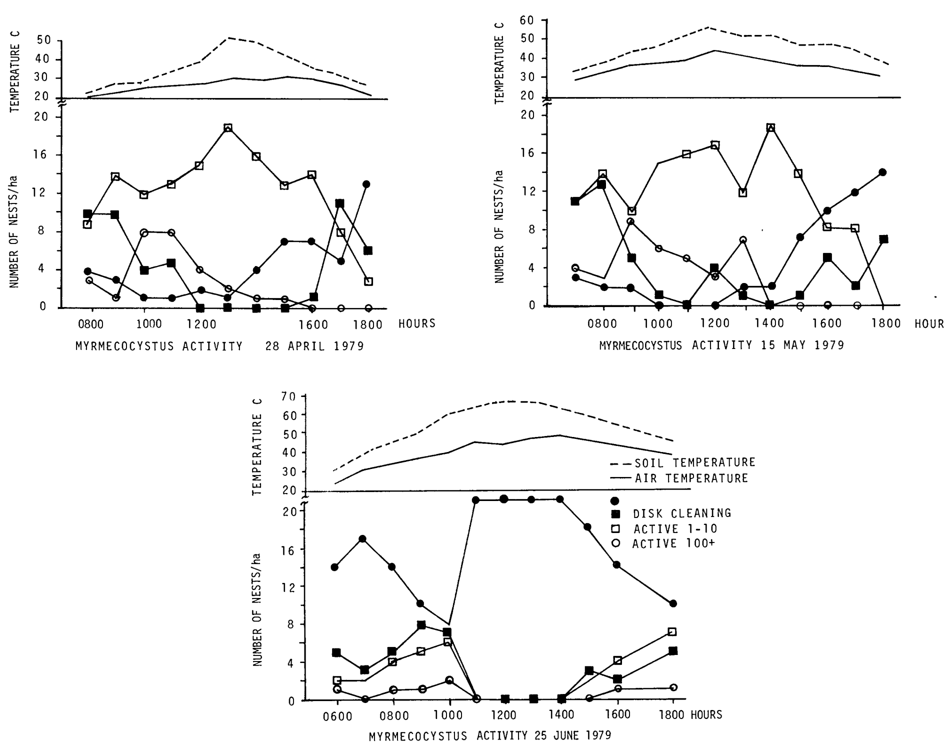

Fig. 2.—Distribution of activity of *Myrmecocystus mimicus/depilis* colonies on representative days from spring to summer. Active 1-10 indicates 1-10 ants returning to/or leaving the colony in 5 min and active 100+ indicates more than 100 ants returning to or leaving the colony in 5 min

The average number of prey individuals ± 1 SD by species in the diet of *Phrynosoma modestum,* estimated from the examination of 42 fecal pellets collected in 1978 and 1979, consisted of *Myrmecocystus depilis/mimicus* 24.7 ± 20.9 (range 1-76); *Pogonomyrmex* spp. 14.6 ± 10.9 (0-25); *Pheidole* spp. 23.4 ± 58.2 (0-421); *Conomyrma* spp. 6.4 ± 14.5 (0-67); *Novomessor cockerelli* 1.8 ± 5.0 (0-20); and various other insects, chiefly beetles of the genus *Ophrystes* 1.6 ± 2.6 (0-11). In 1979, *P. modestum* exhibited periodic prey switching reflected by an increase in the diversity index (H') of its prey (Table 1). This increase in H' was found to be correlated with three factors: average dew point, total rainfall and average maximum daily temperature for the period 3-6 days before pellet collection. A stepwise multiple regression of the diet diversity index on these three factors showed that the average dew point accounted for 60.5% of the variation, total precipitation accounted for 15.75% and average maximum daily temperature accounted for 14.14% ($r^2 = .901$, $p < 0.05$) (Table 2).

The number of ants active before predation and the number of ants which could be taken were used as measures of the effect of simulated predation on ant activity. The results are presented in Table 3. Predation levels of five and 10 ants • nest/day had little effect on activity and no effect on number of ants available to be taken as prey (Table 3). Removal of 20 ants ∘ $nest^{-1}$ ∘ day^{-1} resulted in four of five nests having significantly fewer ants available as prey on days 6 and 7. That level also

TABLE 1.—Species composition of *Phrynosoma modestum* fecal pellets collected from April through June 1979. Numbers listed under each prey category represent totals for the number of pellets given

Lizard number	1	2,3	4	5	6	7	8
Date collected	4/14	4/20	4/27	4/28	5/17	5/28	6/25
Number of pellets	2	7	1	4	4	3	3
Myrmecocystus depilis/mimicus	83	208	11	66	164	47	20
Poponomyrmex desetorum	1	11	6	6	6	7	3
P. californicus	16	82	16	48	20	15	21
Large *Pheidole* spp.	0	27	0	0	0	18	209
Small *Pheidole* spp.	0	0	0	0	0	0	257
Conomyrma spp.	6	19	1	0	2	93	47
Novomessor cockerelli	0	1	5	1	1	5	21
Ophrastes spp.	1	2	0	0	0	0	1
Hemiptera	0	1	0	0	0	2	1
Other Hymenoptera	1	0	0	0	0	0	0
Other insects	0	2	1	1	2	2	12
Shannon Weaver Diversity Index (H)	0.78	1.21	1.47	0.93	0.61	1.43	1.41

TABLE 2.—Environmental factors 3-6 days before collection of pellets. Dew point and maximum daily temperature are averages over the 3-6 day period. Precipitation is the total amount over the 3-6 day period

Lizard number	Date	Number of pellets	Average dew point (C)	Total precipitation (mm)	Average maximum daily temperature (C)	Shannon Weaver Diversity Index (H)
1	4/14	2	− 0.14	0.00	20.4	0.78
2,3	4/20	7	8.19	0.00	30.5	1.20
4	4/27	1	6.81	10.41	26.5	1.47
5	4/28	4	7.92	0.00	26.7	0.93
6	5/17	4	1.48	0.00	23.9	0.61
7	5/28	3	10.28	6.60	31.8	1.43
8	6/25	3	7.06	0.76	34.8	1.41
Proportion of variation of Diversity Index (H) accounted for by each independent variable.			.60	.16	.14	$R^2 = .90$*

*Significant at the $\alpha = 0.05$ level resulted in a significant reduction of activity on days 4-8 (Table 3). Removal of 40 ants • $nest^{-1}$ • day^{-1} resulted in three of five nests having significantly fewer ants available as prey on day 4; and five of five nests on days 6-10 (Table 3). At that rate of removal all colonies reduced their activity on days 4-9. The estimated forager population size for *Myrmecocystus depilis/mimicus* on the site was 1866 ± 1375.

Discussion

Relatively few species of *Phyrnosoma* are sympatric over large areas. Besides *P. cornutum* and *P. modestum,* only *P. platyrhinos* and *P. douglassi* in Utah and *P. solare* in southwestern Arizona are sympatric to any signicant extent (Pianka and Parker, 1975; Stebbins, 1966). Pianka and Parker (1975) suggested that the lack of dietary overlap between *P. platyrhinos* and *P. douglassi* was a possible explanation for this sympatry because they did not find any differences in the thermal preferences of the two species. They also failed to find any significant differences in the thermal preferences of *P. modestum* and *P. cornutum.* Our study and that of Whitford and Bryant (1979) provide evidence that sympatric *Phrynosoma* can coexist because of differences in prey selection and feeding behavior.

Whitford and Bryant (1979) showed that *Phrynosoma cornutum* has evolved behaviors to optimally exploit its most dependable prey species, *Pogonomyrmex desertorum,* but does take other ants larger than 5.0 mm total length. While *P. modestum* takes a limited number of *Pogonomyrmex* spp., its behavior of sitting in the shade of large shrubs makes the probability of encountering prey of species other than *Myrmecocystus* fairly low. Several other ants species forage in and around the large shrubs but these ants normally cease foraging soon after sunrise. This behavior makes such species largely unavailable as prey except for periods imme-

TABLE 3.—The effects of simulated predation on colony activity compared with colonies not subjected to simulated predation (Mann-Whitney U test). NS = Not Significant, *$p < 0.05$, **$p < 0.01$, ***$p < .0001$. The numbers below the significance levels for the 20 and 40 ants/day removal are the percent of colonies from which less than the predetermined number of foragers could be removed (paired t-test). There was no effect on ants available for removal rates of 5 and 10 • day^{-1}

Level of predation simulated	Day of study 1	2	3	4	5	6	7	8	9	10
5 ants • day^{-1}	NS	NS	NS	NS	NS	*	NS	NS	NS	NS
10 ants • day^{-1}	NS	NS	NS	NS	NS	NS	**	NS	*	NS
20	NS	NS	NS	**	*	***	*	*	NS	NS
ants • day^{-1}	0	0	0	20	40	80	60	40	40	20
40	NS	NS	NS	*	*	***	***	***	*	NS
ants • day^{-1}	0	0	0	60	60	100	100	80	80	100

TABLE 4.—Percent colonies from which less than the predetermined number of foragers could be removed (paired t-test). NS = Not Significant, * = $p < .05$, ** = $p < .01$, and *** = $p < .001$. Simulated predation levels of five and 10 ants • day^{-1} resulted in no reduction in the number of foragers taken as prey

Level of predation simulated	Day of study 1	2	3	4	5	6	7	8	9	10
20	0%	0%	0%	20%	40%	80%	60%	40%	40%	20%
ants/day	NS	NS	NS	NS	NS	*	*	NS	NS	NS
40	0%	0%	0%	60%	60%	100%	100%	80%	80%	100%
ants/day	NS	NS	NS	*	NS	**	***	**	**	***

diately after rains when these ants extend their activity through midmorning hours. Thus this study and Whitford and Bryant (1979) demonstrate that *P. cornutum* and *P. modestum* avoid competition by focusing their feeding behavior on different but predictably active ant species as their primary prey.

Our study provides data which can be used to test optimal foraging theory. Optimal foraging theory states that natural selection will operate on the heritable variation in behavior such that the foraging efficiency of an animal is maximized within the constraints of the system (Pyke *et al.,* 1977). Lizards could maximize energy intake, nutrients or time spent foraging. *Phrynosoma modestum* is not affected by the time constraints imposed on *Phrynosoma cornutum* by temperatures which cause cessation of activity of prey and force the lizards to seek a thermal refuge (Whitford and Bryant, 1979). *Phrynosoma modestum* can sit and wait at the base of a large shrub where the thermal microclimate remains within the tolerance range of the lizard throughout the day. Thus *P. modestum,* the round-tailed horned lizard, spends little energy in search of prey. The extended duration of feeding allows the round-tailed horned lizard to use prey that are available at a relatively low frequency, thus maximizing the ratio of energy intake to energy spent. Prey switching when species other than *Myrmecocystus* are available further maximizes energy in to energy spent. Since energy values of ants and handling times differ little, *P. modestum* can be indiscriminant, taking any ants perceived as suitable prey. For ant specialists like *Phrynosoma,* optimal foraging behavior is shaped by the constraints of prey predictability in time and space.

From April to June 1979, 10 rains were recorded, one in April totaling 10.41 mm, six in May totaling 12.7 mm and three in June totaling 4.83 mm for a total of 27.9 mm of rain for the entire 3 months. These rains affected only 11% of the days during that period. Thus, while prey switching is important, the primary prey, *Myrmecocystus mimicus/depilis,* which account for most of the ants eaten the other 89% of the time, are obviously most important to *Phrynosoma modestum.*

When other ants are relatively unavailable, *Phrynosoma modestum* took 40-45 *Myrmecocystus* • day^{-1}. Since *P. modestum* feeds primarily on the base of shrubs in which *Myrmecocystus* forage, the lizards are taking prey from the total nest population 21 ± 7 nests • ha^{-1}. At a density of 2 • ha^{-1} *P. modestum* would only take 80 *Myrmecocystus* • day^{-1} or an average of 4-5 ants • $nest^{-1}$ • day^{-1}. Based on our simulated predation studies, *P. modestum* could remove 210 ants • day^{-1} without adversely affecting the long-term activity of *Myrmecocystus.* We conclude that in our study area *P. modestum* is not food-limited nor are these lizards adversely affecting the honey pot ants.

Myrmecocystus foragers (body size 3-5 mm) actively forage for plant exudates and insect prey at ambient temperatures of 13-46 C and soil temperatures of 13-60C (Kay and Whitford, 1977). At soil temperatures above 50 C foragers remain on the soil surface only a short time, climbing onto every rock or shrub they encounter between the nest and plants on which they have been foraging (pers. observ.; Kay and Whitford, 1977). Also, at temperatures approaching the upper limit of activity, general foraging activity decreases, with the foragers either returning to the nest or remaining in the foliage until temperatures permit their return (Kay and Whitford, 1977). By remaining in the plant canopy during the hottest portions of the day, *Myrmecocystus* spp. can remain active at midday in the summer when no other ants are active. Thus, *Phrynosoma modestum* which sits under vegetation has a high probability of encountering only *Myrmecocystus* foragers during the hot part of the day.

Using the mean ingestion rate of 24.7 ants per day, approximately 50 *Myrmecocystus* • ha^{-1} • day^{-1} were consumed by *Phrynosoma modestum.* Thus *P. modestum* is taking 0.5-1.0% of the total available forager population, *M. depilis/mimicus*. If this 0.5-1.0% of the total available forager population were taken on each hectare each day over the entire warm season, mid-April to mid-October (50 ants^{-1} • day^{-1} x 200 days), then approximately 10,000 ants or one-half of the midsummer standing crop of *Myrmecocystus depilis/mimicus* would have been taken by *P. modestum* during the active season. Although we have no data on annual production by *Myrmecocystus* spp., other species of ants have annual productions ranging from 20% to 100% of the average worker population (Neilsen and Josens, 1978). The horned lizards are obviously removing a significant fraction of the annual *Myrmecocystus* spp. production, but this loss probably has little if any adverse effects on the colonies. Foragers are probably the older, most expendable workers in a colony (Oster and Wilson, 1978) and should have a short life span. Since *Myrmecocystus depilis/mimicus* colonies did not respond to losses up to 40 workers • day^{-1} for 3 days, we suggest that such losses are not unusual and are compensated for by production of new workers.

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