BEHAVIOR OF A PREDATOR AND ITS PREY:
THE HORNED LIZARD (*PHRYNOSOMA CORNUTUM*) AND
HARVESTER ANTS (*POGONOMYRMEX* SPP.)[1]

WALTER G. WHITFORD AND MARTHA BRYANT[2]
Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003 USA

Abstract. Horned lizards, *Phrynosoma cornutum*, were observed between sunrise and sunset in order to record the time spent at different behaviors and the prey taken. Two ant species, *Pogonomyrmex desertorum* and *Pogonomyrmex rugosus*, were the most important prey. The behavioral responses of these prey species were studied by subjecting them to varying levels of simulated predation. The lizards fed most often on ants that were not associated with nest discs or foraging columns and took only a few ants at any one place. Lizards moved an average of 46.8 m/d, remaining in the vicinity of any group of ant nests <15 min. In artificial predation experiments, *Pogonomyrmex desertorum* ceased activity for periods of up to 5 d following losses of ≈25% of the forager population when foragers were removed at a rate of 5/d or 10/d. *Pogonomyrmex rugosus* did not respond to loss of 25% of the forager population, ceased activity of losses of 50% of the forager population, and exhibited frenzied activity upon loss of 75% of the forager population. The horned lizards have evolved a foraging strategy that allows maximization of prey availability over weeks or a month rather than per hour or day. Estimates of horned lizard densities, ingestion rates, and numbers of potential prey suggest that horned lizard numbers are regulated by the availability and productivity of *Pogonomyrmex* spp. These estimates also suggest *Pogonomyrmex* spp. colonies are extremely productive, essentially replacing the entire worker population each year.

Key words: behavior; coevolution; foraging; harvester ants; horned lizards; New Mexico; Phrynosoma cornutum; Pogonomyrmex desertorum; Pogonomyrmex rugosus; predation.

INTRODUCTION

There is considerable literature dealing with predation and the behavior of predators, as evidenced in the recent monograph of Curio (1976). Most studies have focused on search behavior, prey switching, and handling time in a predator species, with less attention paid to behavior of the prey. The evolution of predatory behavior is often viewed by ecologists from an energetic point of view: "if predators are to exploit their prey efficiently, they must permit the prey population to maintain a level that maximizes the number of prey the predators can harvest without decreasing the size of the prey population" and conversely, "defense strategies are costly to the prey organism because they require the allocation of time, energy and materials which are in limited supply" (Ricklefs 1973).

There are few predator-prey systems which are sufficiently simple to test these general ideas. However, the horned lizard and harvester ant comprise one such system. The general ecology of the horned lizard, *Phrynosoma cornutum*, is well documented. Heath (1965) and Pianka and Parker (1975) described the behavior of *P. cornutum* in relationship to environmental temperatures. The foraging ecology and activity patterns of harvester ants (*Pogonomyrmex* spp.) have been studied in detail by Whitford and Ettershank

(1975), Whitford et al. (1976), and Whitford (1978). Preliminary studies showed that in the Chihuahuan desert areas of southern New Mexico, *Phrynosoma* preys almost exclusively on *Pogonomyrmex rugosus*, *Pogonomyrmex desertorum*, and *Pogonomyrmex californicus*. Horned lizards are slow moving, easily captured, and can be observed without disturbing the lizard at sufficiently short distances (<10 m) to allow identification of prey with the aid of field glasses. Harvester ants are amenable to simulated predation (Gentry 1974) which allows examination of prey response.

Pogonomyrmex desertorum is an individual forager (foragers move apparently at random for suitable food items), occurs in colonies of 400–600 workers, is strictly diurnal, and is active throughout the summer (Whitford and Ettershank 1975). *Pogonomyrmex rugosus* is a column forager, occurs in colonies of 1000–3000 workers, is diurnal and nocturnal, and may remain inactive for extended periods of time during the growing season (Whitford and Ettershank 1975).

Pogonomyrmex californicus is an individual forager occurring in colonies of ≈1000 workers. Few colonies are active in the summer when horned lizards are active, and hence *P. californicus* is a minor prey species for *Phrynosoma cornutum* (Whitford and Ettershank 1975). The differences in activity patterns and colony size suggested that these species might respond differently to predation. Responses of ant colonies to predation could include: (1) shift in peak foraging time, (2) cessation of foraging for a variable period after predation losses, (3) changes in foraging intensity re-

flecting loss of workers, and (4) no change in activity, etc.

Pyke et al. (1977) state that, in the future, general optimality theories should provide insights into coevolutionary systems such as predators and their prey. The horned lizard–harvester ant system provides a means of examining the foraging strategy of a predator and the coevolved responses of its prey. The studies reported here examine the foraging behavior of the horned lizard, and the responses to simulated predation of the two species of harvester ants, *P. deserto-rum* and *P. rugosus*.

METHODS

Studies were conducted on the New Mexico State University Experimental Ranch, 40 km north-north-east of Las Cruces, New Mexico (the United States/International Biological Program Jornada Validation Site). The area is characterized by sandy soils and sparse, shrubby vegetation. Numerous annual plants and the small perennial grass, *Erioneuron pulchellum*, provide a source of seeds for harvester ants (Whitford 1978). Common shrubs include mesquite (*Prosopis glandulosa*), creosotebush (*Larrea tridentata*), mormon tea (*Ephedra trifurca*) and soaptree yucca (*Yucca elata*).

Between May and August 1976, the behavior and feeding of 13 horned lizards, *Phrynosoma cornutum*, were observed for at least one entire day. Additional data were collected on *P. cornutum* in 1975 and 1977 on an irregular basis. We captured the first lizard seen in the morning and marked it with a spot of paint at the base of the tail. That lizard was then observed for an entire day during which the duration of each behavior and each item eaten were recorded. We also noted if the ants that were eaten were taken at a nest, on a trail, or as lone foragers. At the end of the day, when the lizard had remained buried for at least ½ h, it was recaptured and placed in a wire cage (25 cm²) and returned to the place where it had burrowed. That lizard was released for observation only during the morning hours on the following two days and then permanently released. The lizards were watched with binoculars from a distance of 5–8 m. We recorded the total distance including reversals and direction of movement for each hour of observation.

When the lizards defecated, the fecal pellets were collected and examined to verify the observations and counts of prey during feeding. Fresh fecal pellets from other horned lizards were also collected and examined.

Two types of experiments were performed during June–August 1976, to study the behavioral responses of *Pogonomyrmex* spp. to predation. Estimates of numbers of foragers per colony were made by mark-recapture and by application of Lincoln Index (Southwood 1966). We made estimates on six colonies of *P. desertorum* and four colonies of *P. rugosus*. We marked approximately 100 *P. rugosus* per colony and 50 *P. desertorum* per colony by removal of the terminal one-third of the right antenna. Estimated numbers of foragers ±1 SD were 196 ± 42 *P. desertorum* and 596 ± 55 *P. rugosus*. Therefore we took percentages of 200 and 600 for our percent removal of *P. desertorum* and *P. rugosus* respectively.

In one set of experiments, a percentage of the estimated number of foragers in a colony was removed as rapidly as possible and the foraging activities were monitored over the following month. Activity was monitored by counting the numbers of foragers returning to nests at 2-h intervals between sunrise and 2400 h. We removed 25%, 50% and 75% of the estimated number of foragers in *P. rugosus* and 25% and 50% in *P. desertorum*. There were 10 colonies in each treatment and 10 controls.

In late July we initiated studies in which we removed a constant number of returning foragers from a colony each day until foraging ceased. These studies were repeated in June and July 1977. We were unable to obtain reliable data from *P. rugosus* because most of the colonies were inactive during the period of the study. In *P. desertorum* we removed ants at the rate of 5/d and 10/d using 10 colonies in each treatment and an additional 10 colonies as untreated controls.

Estimates of water loss and assimilation efficiency were obtained on five horned lizards confined in field enclosures which contained colonies of all prey ant species. Within the 200-m² enclosures, smaller 4-m² ant-proof enclosures containing a shrub for cover but no ants, were used to obtain post absorptive animals. A lizard was considered post absorptive if no feces were voided in 48 h. These lizards were then fed a known weight of live harvester ants (*P. rugosus*), and the fecal pellets were collected and weighed until the animal was again post absorptive. Post absorptive animals were weighed every 4 h for periods from 8–24 h on a top-loading Mettler balance to obtain estimates of evaporative water loss. Lizards were placed in the large enclosure to obtain feeding rates and species composition of the diet. Water content of ants was obtained gravimetrically.

RESULTS

Behaviors

The distinct behaviors of the horned lizard as recorded in this study were: sitting (sitting-basking), walking-running, elevated sitting-feeding, encounter, and sitting in vegetation. When sitting, the lizard remained immobile with its front legs slightly extended. The posterior half of the body was in contact with the soil, and was positioned to provide nearly perpendicular orientation of the back to the sun. Walking is the slow deliberate gait of horned lizards employed in changing locations. In elevated sitting the horned lizard extended its front legs, elevating the body so that
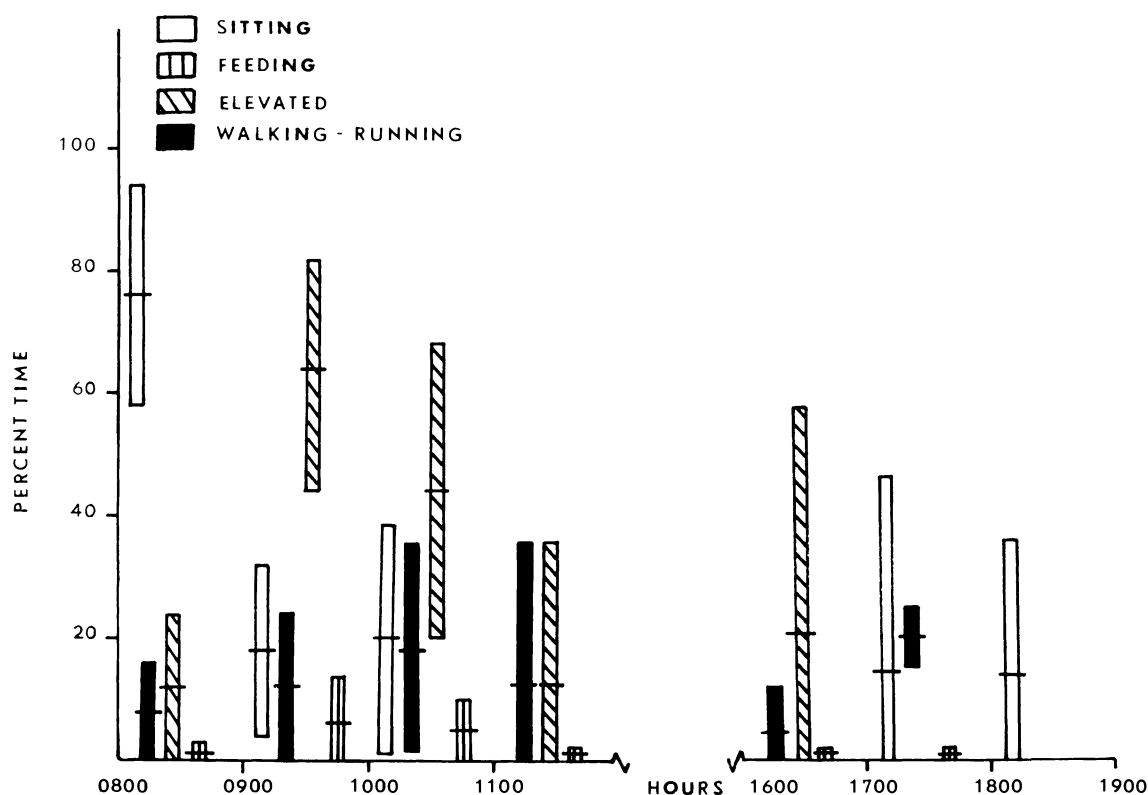
FIG. 1. The behaviors of 13 adult horned lizards, *Phrynosoma cornutum*. Horizontal lines represent the mean and the vertical bars designate ±1 SD. Between 1130 and 1600, the lizards climbed into, and remained in the canopy of small shrubs.

only the feet were in contact with the substrate. Often the lizard would assume this position with its front feet on a clump of fluff grass or other object that further elevated the animal above the substrate. Feeding occurred most often from the elevated position. When an ant was moving in the vicinity of a horned lizard, the lizard would often take one to two steps, tilt its head to the side, and rapidly ingest the ant with its tongue. Head-tilting preceded ingestion when feeding occurred from the stationary position or after movement of the lizard to the prey.

Encounters occurred when two horned lizards approached each other to within a meter or less. In these instances, both lizards would initiate head-bobbing and push-ups (typical of iguanid encounters, Carpenter 1975) and generally licking, biting, and chasing would occur.

During the hottest part of the day, horned lizards climbed into a low shrub (usually *Yucca elata* or *Ephedra trifurca*) of ≈0.5 m height. Long periods of inactivity were broken by movement between the shaded and sunny portion of the shrub canopy.

Although we were in the field starting at sunrise, we did not observe activity in horned lizards before 0800 (approximately 2 h after sunrise) and most feeding and other activity was confined to the morning hours (Fig.

1). Typical midmorning activity was as follows: sitting for 30 s to several minutes, walking followed by elevated sitting, lasting from a few seconds to several minutes, terminated by a feeding bout or further walking, then resumption of elevated sitting (Fig. 1). At midday, 1200–1600, the horned lizards were in a shrub canopy where the ambient temperatures ranged between 35°–40°C. They fed between 0900 and 1100 which corresponds to the peak activity periods of harvester ants (Whitford and Ettershank 1975, Whitford et al. 1976). Thermoregulatory basking was greatest in the early morning and late afternoon (Fig. 1).

We observed no disruption of the typical foraging behavior of *Pogonomyrmex desertorum* when the ants were in proximity to a horned lizard. On a *P. rugosus* foraging column, one of us (WGW) twice observed an avoidance response by ants in the column. In both instances the lizard made several moves to capture an ant. Other ants in the column quickly became immobile, assuming a vertical position either on the soil surface or while clinging to a grass blade. This resulted in rapid cessation of activity in the column of foragers. This immobile vertical position was held for 10–15 min. While aspirating *P. rugosus* during the experiments, we were able to elicit this responsy by moving a hand near the column at the soil surface but did not

TABLE 1. Characteristics of feeding bouts by the horned lizard, *Phrynosoma cornutum*, preying upon *Pogonomyrmex* spp. Each bout: stops when a lizard fed.

Number of bouts per nest disc or column	$\bar{x}$ Number of ants per bout (range)	$\bar{x}$ Time between captures in seconds ± SD	Number of bouts open	$\bar{x}$ Number of ants per bout (range)	$\bar{x}$ Time between captures in seconds ± SD
Pogonomyrmex californicus					
2	17.0 (7–18)	3.1 ± 1.3	5	4.0 (2–5)	3.4 ± 1.1
Pogonomyrmex rugosus					
6	16.5 (4–29)	7.8 ± 8.0	15	4.5 (1–14)	2.9 ± 1.3
Pogonomyrmex desertorum					
6	12.3 (3–24)	9.2 ± 8.5	26	5.7 (1–17)	11.6 ± 16.4

obtain responses by aspirating from above the returning column.

The horned lizards moved an average of 46.8 m/d (range: 9–91 m). In all but two of the lizards this resulted in movement out of the foraging area of a given set of ant colonies in <0.5 h. The movements between feeding bouts were random in direction, thus an individual horned lizard moved over a zigzag course during a day but rarely crossed its own trail. The maximum number ants of a species taken at one stop was: 18 *P. californicus*, 29 *P. rugosus*, and 25 *P. desertorum*.

The total number of ants ingested in a day varied from ≈30 to >100/d and the species composition varied from one species to four species as shown in the following examples: 111 *P. desertorum*; 8 *P. desertorum*, 52 *P. rugosus*, 42 *P. californicus*, and 27 *Myrmecocystus* spp.; 16 *P. desertorum*, 15 *P. rugosus*, 3 *P. californicus*, and 4 *Myrmecocystus* spp.; 35 *P. desertorum*; and 27 *P. rugosus*. The diet of horned lizards was estimated from counts of 34 freshly collected fecal pellets of which (mean ± 1 SD) 10.7 ± 7.3 were *P. californicus* (range: 0–26), 51 ± 36 were *P. desertorum* (14–137), 17 ± 8 were *P. rugosus* (7–36), and 10 ± 7 were other species, principally *Myrmecocystus* spp. (0–21).

When we compared feeding bouts at a nest disc next to a foraging trail or at some distance from a nest disc or trail, there were differences in numbers taken per bout and an average time between ants (capture and handling time plus time required for an ant to move into the visual range of the lizard) (Table 1).

When *P. rugosus* and *P. californicus* were active, the average time between captures was low and for *P. rugosus* was lower in the open than at a nest disc or column, possibly due to the predation-avoidance behavior of *P. rugosus*. The greatest variation in time between captures and numbers of ants taken per bout resulted from feeding on *P. desertorum* which was the most consistently available prey species (Table 1).

We made limited observations (a total of 26 h) on five hatchling horned lizards. The hatchlings fed exclusively on *P. rugosus* or *P. desertorum*, taking an average of three harvester ants per bout and retreating to the shelter of a low shrub or grass where they remained for 20–30 min before feeding again.

Effects of simulated predation

There were no differences (shifts) in foraging time between controls and experimentals in either species of harvester ants. Simulated predation at a level of 25% of the estimated foragers had no observable effect on *P. rugosus*. Simulated predation had no effect on the numbers of colonies of *P. rugosus* active and foraging at night (Fig. 2) but did affect those active during the day. In the 10 d following simulated predation, seven of the 10 colonies subjected to loss of 50% of the workers remained closed during the normal activity period while half of those subjected to loss of 75% of the estimated number of foragers remained active; all colonies returned to activity in 10 d after simulated predation (Fig. 2). The response of the individual-foraging, small colony *P. desertorum* differed from *P. rugosus* in that colonies experiencing 25% reduction in numbers of foragers remained active or the number of active colonies was not significantly different from the control (Fig. 2). Colonies of *P. desertorum* experiencing loss of 50% of their foragers largely ceased activity during the first 5 d after forager removal and half of these remained closed up to 10 d after the simulated predation (Fig. 2). These experiments were repeated in mid-July with essentially the same results except that all activity, including controls, was lower in July and August (Fig. 3). However, from late July through August, <20% of the colonies of *P. rugosus* were active during the day and there was a significant reduction in *P. desertorum* colonies active after being subjected to loss of 25% of the estimated worker force.

Simulated predation affected not only the relative number of colonies that were active, but also the intensity of foraging activity (as estimated by the number of workers returning to the colony per min). In *P. rugosus*, removal of 50% of the estimated number of foragers resulted in a proportional reduction in foraging intensity in June (Fig. 4). Reduction of the estimated forager pool by 75% resulted in frenzied for-
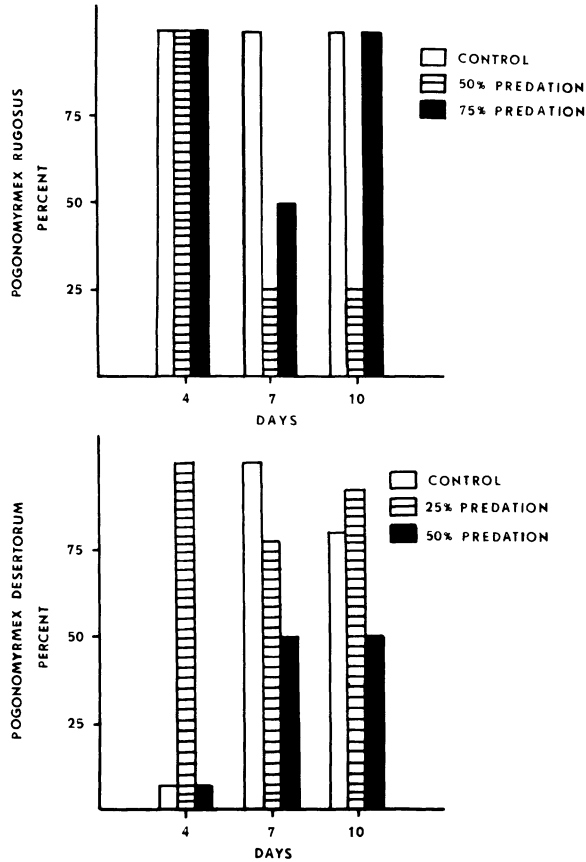
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FIG. 2. Effects of simulated predation (catastrophic removal at one time of a percentage of the estimated forager population) on the activity of *Pogonomyrmex rugosus* and *Pogonomyrmex desertorum*. Ordinate is percentage of active colonies. In *P. rugosus* the data for Day 4 represents nocturnal foraging. These experiments were conducted in June.

FIG. 3. Effects of simulated predation (catastrophic) on *P. rugosus* and *P. desertorum* conducted in mid-July.

aging with intensity higher than controls (Fig. 4). In *P. desertorum*, depletion of the foragers resulted in reduction in foraging intensity proportional to the number of foragers removed (Fig. 5).

Applying predation at a constant rate resulted in cessation of activity in *P. desertorum* at much lower total losses than when a fixed percentage of the workers was removed at one time (Fig. 6). Even when rainfall stimulated activity of the controls, only 60% of the colonies which had been subjected to simulated predation responded, and although all of the controls remained active, most of the colonies which had experienced predation remained closed. Removal of 10 foragers per colony per day had an immediate effect. Two of the 10 nests closed and remained closed for the 20-d duration of the study after losing only 20 foragers. Other colonies losing 10/d were active sporadically during the following 6 d, experiencing total losses of 30–60 foragers. The maximum number of foragers removed in this experiment was 60, or ≈25%

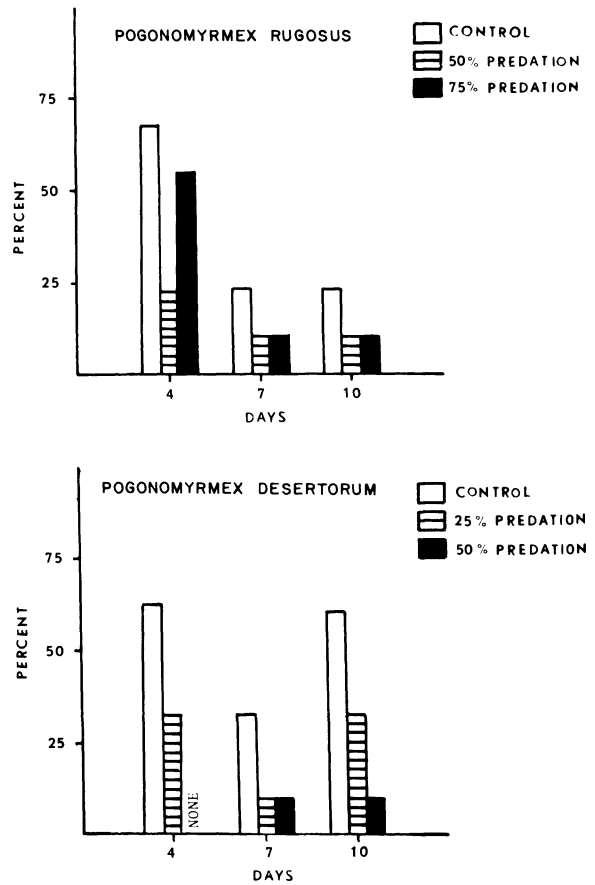of the estimated forager population. In the 1977 experiments between June 7 and June 13, there were marked reductions in numbers of active colonies of *P. desertorum*. Within 3 d after only one removal, two colonies had such reduced activity that only six and four ants could be taken on the following day. There was no reduction in numbers of active *P. desertorum* colonies at the five-per-day removal rate until the fifth day (a total of 20 foragers had been removed). However, in the experiments conducted between July 11 and July 15, 1977, there were no reductions in numbers of active colonies at any level of simulated predation until the fifth day when 30% of the five-per-day and 40% of the 10-per-day colonies were closed.

The average water content of *P. rugosus* and *P. desertorum* was 63.3% and 64.9%, respectively. The average assimilation efficiency of the lizards in field enclosures was 37.1% [(ingestion − egestion)/ingestion]. In the horned lizards estimated water losses ±1 SE were: fecal/urinary, 1.88 ± 0.18 mg·g^{-1}·d^{-1}; evaporative, 4.6 ± 0.56 mg·g^{-1}·d^{-1}; and total, 6.5 ± 0.56 mg·g^{-1}·d^{-1}.

POGONOMYRMEX RUGOSUS
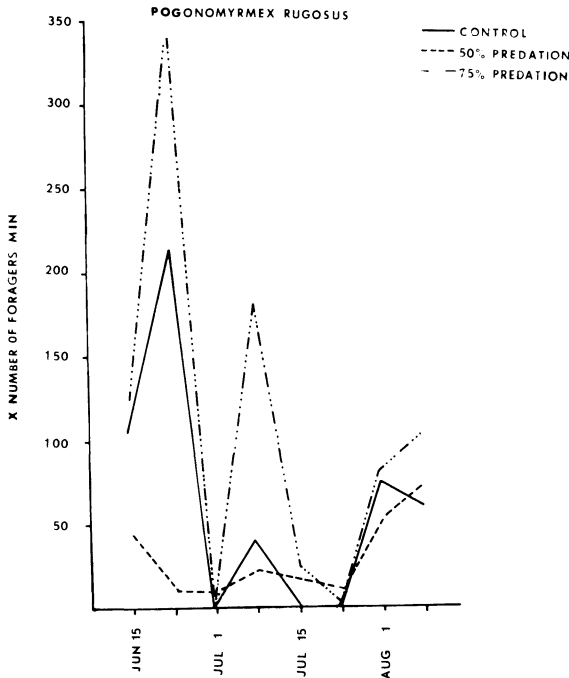
CONTROL
50% PREDATION
75% PREDATION

FIG. 4. Effects of simulated predation on the foraging intensity of 10 colonies of *Pogonomyrmex rugosus*: data are for peak period of foraging activity 0900–1000.

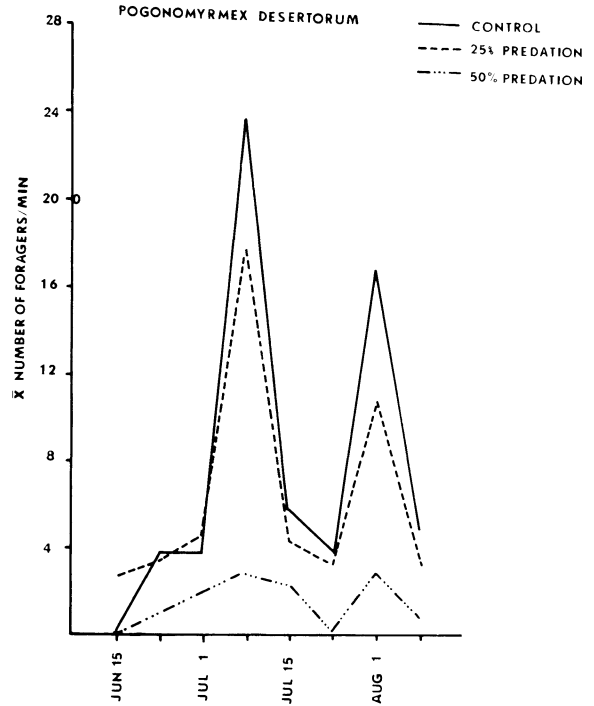POGONOMYRMEX DESERTORUM

CONTROL
25% PREDATION
50% PREDATION

FIG. 5. Effects of simulated predation on foraging intensity of 10 colonies of *Pogonomyrmex desertorum*: data are for peak period of foraging activity 0900–1000.

DISCUSSION

Our study adds considerably to the known behaviors of *Phrynosoma cornutum*. Milne and Milne (1950) described sand-burrowing behavior and head-cocking when approaching prey prior to feeding. Heath (1965) described thermoregulatory behavior and Whitford and Whitford (1973) described combat in *P. cornutum*. However, none of these studies mentions the shrub-climbing behavior and movement in a shrub canopy which represents a significant portion of the diel activity of the species. Sitting in a shrub canopy places the lizard in a thermal environment where it can maintain its body temperature between 35°–40°C, which may be important in digesting the heavily sclerotized ants. Use of burrows to avoid high midday temperatures may be dangerous for a nonterritorial species since available burrows could contain predators. Burrowing by sand-swimming would require high energy expenditure to reach sufficient depth to avoid lethal temperatures.

The diet of *Phrynosoma cornutum* has been discussed in general terms as being composed largely of ants and, on occasion, beetles (Pianka and Parker 1975) but there are no data on the species composition of horned lizard diets. On the Jornada site, this lizard takes ants that are >5.0 mm total length. Of the diurnal species >5.0 mm long (Whitford 1978), *Novomessor cockerelli* and *Trachymyrmex smithii neomexicanus* cease activity early in the morning prior to the feeding

period of *Phrynosoma* (Schumacher and Whitford 1974, Whitford and Ettershank 1975) and only a small fraction of the *Myrmecocystus depilis* workers are ⩾5.0 mm, leaving only the *Pogonomyrmex* spp. as a suitable prey. Our data show that *Phrynosoma cornutum* preys almost exclusively on large *Pogonomyrmex*. The peak feeding of the lizards coincides with
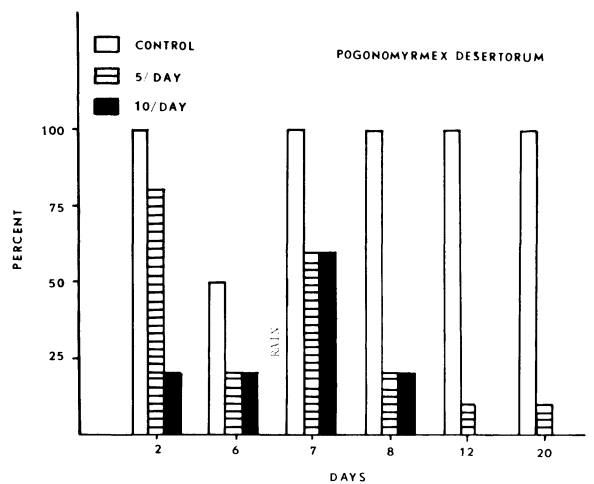
CONTROL
5/DAY
10/DAY

POGONOMYRMEX DESERTORUM

FIG. 6. Effects of simulated predation at constant rates on the activity of *Pogonomyrmex desertorum*. Ordinate is percent removed daily. See text for a discussion of numbers removed resulting in cessation of activity.

the peak activity of *P. rugosus*, *P. desertorum*, and *P. californicus* (Whitford and Ettershank 1975).

Our studies of horned lizards and harvester ants provide data useful in examining optimality theory predictions (Pyke et al. 1977) about the behavior and coevolution of a predator and its prey. If a horned lizard were to maximize the energy obtained in a day or a week, it would sit by a nest disc or foraging trail and take ants as they emerged or returned to the nest until the lizard was satiated or until ants were virtually absent. Indeed, this behavior would be feasible if *P. rugosus*, the column forager, were active every day throughout the growing season, because heavy predation imposed on that species would not eliminate it as a food source, as demonstrated by the predation-simulation experiments. However, since *P. rugosus* activity is unreliable, alternate prey must be utilized. When *P. rugosus* was active, the horned lizards took larger numbers of *P. rugosus* than of *P. desertorum*, but did not completely switch to *P. rugosus*.

The foraging behavior of the horned lizard insures continued activity of its most reliable source of food (*P. desertorum*). The random movement over relatively long distances and the short but intensive feeding bouts reduces the losses to any single colony of *P. desertorum* below that which would stimulate cessation of activity in that colony. Moving over long distances with little or no backtracking on successive days also reduces the possibility that losses due to predation imposed on *P. desertorum* will be sufficient to stimulate a colony to close. As discussed by Pyke et al. (1977), *Phrynosoma cornutum* has evolved an optimal foraging strategy in which the appropriate currency is the amount of energy obtained over a week or month, and not behavior that maximizes the amount obtained in an hour or day.

In his review of the ethology of predation, Curio (1976) makes scant reference to the behaviors of prey in response to predators. Wilson (1971) also makes little reference to the behaviors of ants used in predator avoidance. Our study documents two mechanisms of predator avoidance. Probably in response to alarm pheromones emitted by a worker which is just missed by or "sees" a predator, the column forager, *Pogonomyrmex rugosus*, assumes an immobile, erect posture to avoid detection by horned lizards which depend on movement of prey (Milne and Milne, 1950, and *personal observation*). In *P. desertorum* the colony responds like an individual animal which has been nipped at by a potential predator and assumes a defensive posture to avoid being eaten. Loss of a certain portion of the worker population somehow signals the remaining workers to cease activity for a period of time. Such a defense is expensive for a species that stores few seeds in granaries and must be active throughout most of the growing season to provide energy and nutrients for the developing brood. Also, small losses over successive days result in cessation

of activity at lower total loss than a single removal, indicating a further complication in the predation response of the species. These experiments suggest coevolved behaviors of both the predator *Phrynosoma cornutum* and its prey, *Pogonomyrmex desertorum*.

When interpreting the response of *Pogonomyrmex* spp. colonies by comparing treatments, it is important to remember that harvester ant activity varies not only with time, temperature, and humidity but also with the physiological status of individual colonies i.e., quantity of stored seeds, seed concentrations near the colony etc. (Whitford and Ettershank 1975). In this study, although responses were slightly different in experiments performed at different times during the year, the general response pattern was consistent.

The responses of *P. rugosus* to simulated predation are related to the biology of the species (Whitford and Ettershank 1975, Whitford et al. 1976, Whitford 1978). Simulated predation had no effect on nocturnal activity; this is not surprising since horned lizards are diurnal. Although we had expected this species to respond in a fashion similar to that reported by Gentry (1974), the behavioral response differed considerably. Extremely heavy predation (removal of 75% of total estimated foragers) resulted in frenzied activity to provide food for the developing brood and to fill granaries. Removal of 25% of the estimated worker population of *P. rugosus* had no effect on activity while removal of 50% of the estimated workers resulted in closure of some colonies and in decreased activity in those colonies that remained active. This suggests that a horned lizard could feed at a single colony of *P. rugosus* for up to five consecutive days before there was any measurable change in behavior. As stated previously, because of the great seasonal variation in activity of *P. rugosus*, this does not occur.

Pogonomyrmex desertorum exhibited a similar compensatory activity when subjected to removal of 25% of the foragers at one time, but ceased activity when higher losses at one time were imposed. In a species with small colony size, compensatory activity may be worth the risk of slight additional loss in order to maintain the brood, but when losses are excessive at one time, cessation of activity protects the nucleus of workers necessary to maintain the colony. The response to gradual removal of workers is more pronounced and occurs at lower total losses than single-episode predation, indicating differences in colony "sensitivity" to gradual vs. catastrophic loss.

The data obtained on water turnover and assimilation efficiency in horned lizards allow estimation of the number of ants required to meet water and energy requirements, for comparison with observed ingestion rates. These data can then be used to estimate the effect of the predator on the prey population and conversely the effect of the prey on the predator. A horned lizard has a water requirement of at least 6.5 $mg \cdot g^{-1} \cdot d^{-1}$. The horned lizards in this study ingested

an average of 71 ants/d. For ants with a mean live weight of 8.26 mg, this represents an intake of 372 mg of water per day or 10.6 mg·gm^{-1}·d^{-1} for an average-sized horned lizard of 35 gms. Thus, intake by horned lizards exceeds the estimated water losses.

Using the data in Prieto and Whitford (1971) and assuming 14 h at 25°C and 10 h at 35° C, a horned lizard requires 61.1 J·g^{-1}·d^{-1} for maintenance. At an assimilation efficiency of 37.1%, this represents approximately 35 harvester ants per day to meet maintenance costs. These data suggest that water and energy requirements based on laboratory and/or field and laboratory measurements may be greatly underestimated. Also, field ingestion rates reflect energy accumulation in fat reserves necessary for overwinter survival. This has been documented in studies using double-labeled water on free-living populations of lizards (Nagy 1975, Nagy *personal communication*).

Using the estimates of Whitford and Ettershank (1975) and Whitford (1978), *P. desertorum* occurs at colony densities of ≈115 colonies/ha, *P. rugosus* at ≈20 colonies/ha, and *P. californicus* (summer density) at ≈10 colonies/ha. Multiplying colony densities by the July (peak) estimates of average number of workers per colony yields the following as the standing crop of harvester ants per hectare: *P. rugosus*, 46 000; *P. desertorum*, 57 000; *P. californicus*, 14 000. Whitford and Creusere (1977) reported an average of 10 adult *Phrynosoma cornutum*/ha on the Jornada site. If these lizards ingested 71 harvester ants/d during the months of May–August, they would consume 85 200 ants or 72% of the estimated midsummer standing crop of harvester ant workers. Even allowing for large errors in these estimates, it is apparent that the horned lizard population is utilizing the harvester ants at or close to the maximum exploitation level. Since our data indicate that hatchling and juvenile lizards also prey on the same harvester ant species, *Pogonomyrmex* spp. may support an even larger biomass of horned lizards late in the growing season. However, Whitford and Creusere (1977) have shown that adult lizards largely disappear at that time of year. This feeding behavior of small *Phrynosoma cornutum* was unexpected since many authors suggest a direct relationship between predator body size and prey size. Since juvenile *Phrynosoma cornutum* took only large *Pogonomyrmex*, the lizards may have an innate preference for harvester ants of the genus *Pogonomyrmex*.

In order for *Pogonomyrmex* spp. to survive such losses from year to year, these species must have an extremely high productivity, nearly equal to the standing crop biomass estimated by Whitford and Ettershank (1975). Estimates of harvester ant production similar to those of Golley and Gentry (1964) would be a valuable and independent test of the hypothesis.

These estimates also suggest that no other lizards or other potential predators should utilize these harvester ants. In over six consecutive years of observing and studying these ants we have seen only two incidents of predation by species other than *Phrynosoma cornutum*: one by a robber fly (Ascilidae) and one by a sun spider (Solpugidae). The other horned lizard in the area, *Phrynosoma modestum*, is approximately half the size of *Phrynosoma cornutum* and feeds on other ant species. *Uta stansburiana* also preys on ants but not these *Pogonomyrmex* species. These observations support the above conclusion.

Although Swainson's Hawks prey on adult *Phrynosoma cornutum* (W. Pilz, *personal communication*), the low density of the hawks and the heavy exploitation of harvester ants by *Phrynosoma cornutum* suggest that this lizard is food-limited and not limited by predation.

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