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STRATEGIES OF PREDATORS AND THEIR PREY: OPTIMAL FORAGING AND HOME RANGE BEHAVIOR OF HORNED LIZARDS (PHRYNOSOMA SPP.) AND RESPONSE BY HARVESTER ANTS (POGONOMYRMEX DESERTORUM)

by

James Cameron Munger

A Dissertation Submitted to the Faculty of the DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY

In Partial Fulfillment of the Requirements For the Degree of DOCTOR OF PHILOSOPHY

In the Graduate College

THE UNIVERSITY OF ARIZONA

1982
As members of the Final Examination Committee, we certify that we have read the dissertation prepared by James Cameron Munger entitled Strategies of predators and their prey: optimal foraging and home range behavior of horned lizards (Phrynosoma spp.) and response by harvester ants (Pogonomyrmex desertorum).

and recommend that it be accepted as fulfilling the dissertation requirement for the Degree of Doctor of Philosophy.

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Final approval and acceptance of this dissertation is contingent upon the candidate's submission of the final copy of the dissertation to the Graduate College.

I hereby certify that I have read this dissertation prepared under my direction and recommend that it be accepted as fulfilling the dissertation requirement.

James N. Brown 27 May 1982
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ABSTRACT

Tests of optimal foraging theory have shown that many predators are selective about which prey and which patches should be utilized. I hypothesize that prey species "exploit" this choosiness by evolving characteristics that cause predators to choose alternate prey. Specifically, prey should evolve traits that increase the probability of predator death, decrease the per prey or per patch nutritional intake, increase processing time, and advertise (or mimic advertisements of) undesirable traits. Predator choosiness allows prey to divert the predator instead of defeating it.

The evolution of a long-term, prudent foraging strategy requires that three conditions be met: (1) The forager must use resources from a discrete subpopulation; (2) use of that subpopulation must be relatively exclusive; (3) the resource population must respond in such a way that a long-term strategy provides an economic advantage.

For the horned lizard-ant system, conditions (1) and (2) were tested by tagging lizards with transmitters or radioactive tags. Horned lizards occupy home ranges much smaller than would be expected if they moved at random and home range overlap was less than expected by random placement of home ranges, thus conditions (1) and (2) were not rejected. Most techniques of home range study do not distinguish random from non-random movement. Condition (3) was tested by subjecting ant colonies to various levels of artificial predation. In none of five experiments was the result obtained that an increased harvest intensity led to a decrease
in long-term yield; condition (3) is tentatively rejected. Ant colonies shut down in response to predation; this puts a ceiling on their losses.

Short-term foraging models were tested for horned lizards foraging at ant colonies. A prediction of the marginal value theorem was not rejected: Horned lizards tended to leave colonies when their instantaneous rate of harvest at that colony had fallen to their average rate of harvest for the day. Another short-term prediction, however, was rejected: Lizards did not stay longer at the "better" of two colonies. A more liberal version of the same prediction was not rejected. Apparently, horned lizards forage adaptively but not optimally.
CHAPTER 1

EVOLUTION OF DEFENSIVE TRAITS
IN THE PREY OF CHOOSY PREDATORS

Introduction

Prey individuals may possess any of a number of traits that reduce their probability of being killed by predators. For example, some are cryptic to avoid being detected, others run fast to avoid being captured, taste bad or are poisonous to avoid being eaten, or fight back to avoid being killed (Edmunds 1974). How do these traits evolve? Obviously, those prey individuals that possess these traits tend to survive longer than leave more offspring than those that do not possess them. A question with a less obvious answer is: By what mechanism are these traits effective? One way these traits can work is by actually defeating the intentions of the predator: Cryptic coloration works because it prevents detection by predators, running fast works because predators cannot catch fast prey; poison, bad taste, and fighting work because the predator is unable to capture or consume the prey.

A second way in which these traits can be effective has yet to be fully discussed in the literature. The traits listed above (as well as others) can effect defense by diverting the predator, causing it to choose alternate prey. Actual defeat of the predator is not necessary. This mechanism is based on the fact that many predators choose prey individuals and distributions that maximize the predator's survival and reproductive success. Prey individuals can, in an evolutionary sense,
exploit this choosiness. Those prey individuals that possess traits that cause predators to select alternate prey will tend to survive longer, thus reproduce more; such traits will thus be favored by natural selection. For example, all else equal, a predator would choose the slower running of two prey. The faster individual would not have defeated the predator, it would have simply been less desirable.

In general, a defensive trait that would evolve due to benefits of diverting a choosy predator could also evolve due to benefits of defeating a predator; the two effects would simply reinforce each other. The evolution of a number of traits, however, should rely much more heavily on the presence of predator choice; for example, as discussed below, the evolution of the following traits requires predator choice: tannins in leaves, aposematic coloration, and Batesian mimicry. In any case, predator choice should often be a contributing factor in predator-prey coevolution.

Below I first consider the evidence that predators are choosy. I then discuss in general terms the effect that predator choice should have on prey evolution, using parts of the coevolutionary models of Rosenzweig (1973) and Schaffer and Rosenzweig (1978) as a conceptual framework and as a basis for generating simple predictions. Several of the predictions are fairly obvious and some have been stated before; indeed, the importance of predator choice has been implicitly assumed in many discussions of the evolution of defense traits. The purpose of this note is to explicitly spell out the expected impact of predator choice in a manner that ties together as many ideas as possible.
Are Predators Choosy?

If traits that "exploit" the choosiness of predators are to evolve, predators must be predictably choosy. A growing body of theory and empirical work considers the choice by foragers among food items or patches and shows that choice often does occur. Two predictions of this "optimal foraging" theory are important to the following discussion:

(1) A forager should rank classes of food items according to their energy value. Beginning with the most profitable class, the forager should continue to add prey classes to its diet as long as each inclusion increases the average rate of energy intake (MacArthur and Pianka 1966). In more general terms this predicts that foragers should choose items that yield high energy per time over those with lower yield. This pattern has been observed many times and over a broad range of taxa, e.g., birds (Goss-Custard 1977a, Krebs et al. 1977), fish (Werner and Hall 1974), crabs (Elner and Hughes 1978), mammals (Glander 1981); see reviews of Pyke et al. (1977) and Krebs (1978). A major criticism of this prediction is that it does not consider non-energetic needs; other nutritional requirements may be most important (Pulliam 1975, Rapport 1981, Thompson et al. 1982). However, these authors do not question the occurrence of choice but question the assumption that energy is the basis of the choice.

(2) A forager should rank patches (circumscribed areas where food may occur) and feed in a patch if it yields an increase in average rate of energy intake (MacArthur and Pianka 1966). If the forager cannot assess the quality of a patch before foraging, it should leave a patch when the rate of yield in that patch has fallen to the average for the
habitat as a whole (Charnov 1976). In more general terms, a forager should choose to stay or forage for a longer time in patches that yield higher returns. Again, empirical support of this idea is substantial (Royama 1970, Goss-Custard 1977b, Zach and Falls 1979; see reviews, op. cit.).

I am not claiming that all predators choose among prey and patches based on all possible qualities of those prey and patches. It is only necessary that some predators make choices based on some characteristics. This partial selectivity forms the basis of tests of the importance of predator choice: Defensive traits should evolve only if they affect prey characteristics that form the basis of predator choice.

Predictions From a Coevolutionary Perspective: How Should Prey Evolve?

If predator choice occurs as predicted by models of optimal foraging, then prey should evolve to exploit this choosiness to reduce their own chances of being preyed upon. In this section I derive, from this hypothesis, general predictions of the way prey characters should evolve. Although several of these predictions have appeared previously, the importance of predator selectivity is typically not considered. I know of two notable exceptions. Kerfoot (1977a) suggested that if predators are selective in the location, capture, and manipulation of prey, then their prey will evolve to be less easily located, captured, and manipulated (all else equal). As shown below, the same argument should apply to the quality of the prey and of the patch they inhabit, and to the physical danger the prey represent to the predator. Slobodchikoff et al. (1982, discussed below) hypothesized that irritants
released by tenebrionid beetles increase the handling times of their predators, causing them to seek other prey.

The following predictions are derived from consideration of the effects of choosiness in predators on predator-prey coevolution. Rosenzweig (1973) and Schaffer and Rosenzweig (1978) examined evolution of a one predator-one prey system using the following Lotka-Volterra type population dynamics equations:

\[
\frac{1}{V} \frac{dV}{dt} = r(1 - \frac{V}{K}) - \frac{PK}{x + V} \\
\frac{1}{P} \frac{dP}{dt} = \beta k(\frac{V}{x + V}) - d
\]

In these equations, \( r \) is the prey species per capita rate of increase when rate, \( K \) is the maximum prey carrying capacity in the absence of predation, \( k \) is the maximum kill rate of an individual predator, \( x \) is the prey density at which the average kill rate equals \( k/2 \), \( \beta \) is the conversion rate of prey to predators (the number of predators that result from the death of one prey), \( d \) is the death rate in the predator population, and \( P \) and \( V \) are the population densities in the predator and prey populations, respectively (Schaffer and Rosenzweig 1978).

Although Rosenzweig (1973) and Schaffer and Rosenzweig (1978) were primarily concerned with the existence of a coevolutionary steady state, they also considered how six parameters of the above equations (\( r, K, k, x, \beta, \) and \( d \)) should change as a result of evolution in the prey and predator population.

The first two terms, \( r \) and \( K \), are primarily concerned with processes within the prey species (though they may be involved in tradeoffs with other parameters; Rosenzweig 1973). I can see no obvious
way they would affect a predator's choice, therefore I will not consider them further.

Rosenzweig (1973) argued that prey species should undergo selection for characteristics that result in lower $\beta$ (it should require more prey individuals to produce a single predator). He argued that evolution of decreased $\beta$ either relies on kin selection or on a tradeoff between numbers and $\beta$ of young. Kin selection would occur if the production of young with decreased $\beta$ lowered predator density and thereby reduced the predation pressure on kin. Alternatively, it could be advantageous to produce more young with lower $\beta$ each if this would saturate the killing abilities of the predators and cause more young to survive. Both of these arguments require that as the $\beta$ of a prey item is decreased, the time needed to process a prey item does not decrease by the same proportion as does the amount of energy gained from a prey item.

Schaffer and Rosenzweig (1978) argued that characteristics affecting neither $\beta$ nor $d$ should be under selection in the prey, as these parameters occur only in the growth equation of the predator population, not in that of the prey.

However, evolution in the prey will affect $\beta$ and $d$ if predators choose prey individuals on the basis of their contribution to the predator's total reproductive success. All else equal, a predator should choose prey which do not increase its own death rate and which will increase the number of young that can be produced per prey consumed. From these arguments, two general predictions follow:
Prediction 1: Prey should evolve characteristics that will increase the probability of death (or serious injury) to their predator if the prey is attacked, captured, or consumed.

Prediction 2: Prey species should evolve to decrease the amount of energy that can be obtained from consuming them.

Evolution of prey characteristics that affect $k$ and $x$ is also promoted by selectivity in predators. Rosenzweig (1973) and Schaffer and Rosenzweig (1978) argued that prey species should be under selection to decrease $k$ and increase $x$ simply because such evolution would directly decrease their losses to predators. This effect is magnified, however, if predators are choosy. The maximum rate at which prey can be killed, $k$, is achieved when predators are able to spend all of their time handling prey because the prey are so easy to find that no search time is required. Mathematically, then, $k$ is simply the reciprocal of handling time (Royama 1971). $x$, the prey density at which the kill rate is one half of its maximum, will depend on the speed with which predators find and process their prey. $x$ can be reduced to the reciprocal of the rate at which prey are encountered times the reciprocal of the handling time (Royama 1971).

Theories of optimal foraging predict that a predator should choose prey that yield the highest energy per handling time and should spend more time in patches that yield higher rates of encounter with prey individuals. Recasting the predictions of Rosenzweig (1973) and Schaffer and Rosenzweig (1978) concerning $k$ and $x$ leads to two further predictions:

Prediction 3: Prey should evolve characteristics that increase the time necessary to process them.
Prediction 4: Prey should evolve characteristics that decrease the quality, to a predator, of the patch they inhabit.

In those cases where a prey individual must die or be seriously injured before the predator can learn of its quality as a prey item, kin selection or group selection would be required for evolution to occur as indicated by predictions 1-4. However, if the predator can assess quality before attack is consummated, then selection above the level of the individual is not required. Morphological characteristics such as size, thorniness, and possession of teeth or horns or behavioral characteristics such as speed, agility, and willingness to fight are easily assessed before an attack is completed and could therefore evolve at the level of the individual solely because of the effect of those traits on predator choice.

Three further predictions are not based on the arguments and parameters of Rosenzweig (1973) and Schaffer and Rosenzweig (1978). These predictions are not novel; I present them here to allow me to further stress the importance of predator choice. First, the less detectable an organism is, the less likely it is to be chosen, yielding:

Prediction 5: Prey should be under selection to reduce the ability of their predators to detect them.

Second, to allow a predator to choose to avoid an undesirable prey individual without injury to that individual, a prey should "educate" the predator before an attack commences. Prey should advertise that they may cause death if attacked, have a low energy content, have high handling time, or inhabit "poor" patches.
Prediction 6: Prey species should advertise their negative qualities when those qualities may form the basis of predator choice. Finally, as most systems are liable to cheaters:

Prediction 7: Prey should sometimes utilize only the advertisements of negative attributes (which they do not actually possess) to avoid being chosen by a predator.

Discussion of Predictions

In this section I discuss the above predictions in greater detail and present a number of examples, both to translate the terminology of the predictions into specific traits and to show that in many cases the predictions appear to be supported.

Prey Should Evolve Characteristics That Increase the Probability of Death and Serious Injury to a Predator

If a predator has no choice among prey items, but must catch prey to survive, it must press an attack, no matter how formidable the prey may be. With a choice, however, a predator can avoid encounters with those prey individuals which are most likely to cause injury or death. Many morphological traits of prey, such as large body size, antlers, hooves, horns, stingers, and teeth, can increase the probability of death to the predator during an encounter. In addition, a number of chemicals contained in prey can cause harm to predators. For example, alkaloids in plants adversely affect (Rhoades 1979) and can presumably kill many predators. Here, as in later sections, I do not claim that these defensive measures are effective against all predators. It is only necessary that the trait produce a net benefit for the prey against the
whole array of potential or actual predators by causing some predators to choose other prey.

Prey Should Evolve to Decrease the Amount of Energy That Can Be Obtained From Them

A number of plants produce secondary compounds such as tannins which bind with plant proteins and carbohydrates to render those nutrients less available to an herbivore (Rhoades 1979, Swain 1979). If, in a particular system, herbivores were unable to unwilling to make a choice as to which plant to consume, it would be a disadvantage for individual plants in that system to contain digestion inhibitors. In order to maintain a high rate of energy assimilation, non-choosy herbivores would have to eat more of a plant containing inhibitors than they would of a plant without them. Inhibitor-containing plants would therefore receive more damage but would still have to pay the costs of manufacturing the inhibitors. If herbivores are able to make choices and are attempting to maximize energy assimilated, then they should exclude plants with digestion inhibitors from their diets. In this situation, plants with inhibitors would receive less damage from herbivory than plants without them, and could receive a benefit in excess of the cost of manufacturing the inhibitors.

An obvious way for a prey species to decrease the amount of energy each individual contains is to reduce body size. A number of experiments have shown that smaller prey individuals are less likely to be taken by a predator than larger individuals of the same species (e.g., Goss-Custard 1977a, Jaeger and Barnard 1981). Increased liability to predation may be an important cost of increased size.
Prey Should Evolve to Increase the Handling Time Necessary to Process Them

Slobodchikoff (1978) and Slobodchikoff et al. (1982) showed that tenebrionid beetles are able to increase the time it takes a predator to handle them by releasing irritating substances from their abdomen. Before skunks can eat a tenebrionid beetle, they must roll it about on the substrate to cause it to release the irritants (Slobodchikoff 1978). Grasshopper mice force these beetles into the ground, abdomen first, before consuming them. In preference tests, grasshopper mice invariably chose non-irritating crickets over the tenebrionids (Slobodchikoff et al. 1982). Skunks, however, showed no such preference (Slobodchikoff 1978). This latter result would be expected if skunks are relatively immune to their own predators, not limited by handling time, and therefore not selective among prey.

Kerfoot (1975, 1977b) has shown in systems of planktonic Crustacea that in areas where predation by copepods is intense, cladocerans which have long spines and a thick carapace come to predominate over those which lack these defensive structures. Apparently, copepods have a more difficult time handling cladocerans that are well-armed and preferentially consume the less well-armed individuals.

Silica in grass and toughness in any vegetation increases the time necessary for herbivores to process them. This should cause herbivores to choose plants or plant parts that are less tough. Such a pattern has been documented for a number of herbivores (Lamprey 1963, Bell 1970, Baker 1971, Glander 1981).
Prey Should Evolve Ways to Decrease the Apparent Quality of the Patch They Inhabit

In flocks of many bird species and in groups of a number of mammal species, individuals give an alarm signal, typically a call, which warns conspecifics of an approaching predator. As calling potentially attracts the attention of a predator, thereby increasing the danger to the caller (Sherman 1977), explanation of the evolution of this behavior is difficult. Sherman (1977) and Harvey and Greenwood (1978) discussed various hypotheses which have been suggested to explain this behavior. Sherman (1977) and Dunford (1977) presented evidence that alarm calls have evolved through kin selection in ground squirrels. In both studies, it was assumed that the mechanism by which the caller helped its kin was by warning its kin of an attack, thereby helping them to escape.

An additional benefit of alarm calling becomes apparent if predator choice is considered. I propose that the alarm call functions to decrease the quality of the patch that the caller inhabits, causing a predator to move on. Trivers (1971) proposed essentially the same hypothesis in general terms, stating that calling might reduce the probability of future hunting in an area, thereby reducing future danger to the caller. Trivers did not, however, make it explicit that this probability is based on predator choice, which, in turn, is likely to be based on strategies of patch use. The process would be as follows: An alarm call warns the remainder of the group of the approaching threat. If warned group members are immediately harder to catch, then the quality of that patch (measured by the predator's expected rate of return) has fallen. If a predator chooses patches according to their quality, it
should leave that patch; danger to the caller would then decrease. Note that this behavior might evolve even if calling increases the immediate chances of a caller being singled out and attacked. It is only required that the long-term probability of being killed decreases because the probability of the predator moving on increases.

Charnov and Krebs (1975) argued that (assuming the mechanism of evolution discussed above) as the frequency of callers in a population increases, non-callers would often be in groups with callers and would receive as many benefits as callers, but would not pay the cost of increased risk. Therefore, the frequency of callers in populations with groups that have no kin structure (such as wintering bird flocks) would not be expected to approach fixation; instead a frequency dependent polymorphism would be expected.

Charnov and Krebs (1975) proposed an alternative hypothesis that callers are not in increased danger, instead they benefit by manipulating other members of the group into being more susceptible to predation, thereby providing more protection for themselves. It is interesting to note that this scenario also contains elements of predator choice.

In my own studies of foraging by horned lizards (*Phrynosoma cornutum* and *P. modestum*) on colonies of harvester ants (*Pogonomyrmex desertorum*), I have observed that workers rapidly cease leaving a colony on foraging forays when their colony is subjected to loss of workers by horned lizard or artificial predation. The lack of outgoing workers decreases the quality of the patch that the colony represents and the horned lizard moves on to other colonies. In this case, the predator is
not informed (by a call) of a decrease in patch quality; it leaves based on its own assessment of resource levels (Munger 1982, 1983c, d).

Animal-pollinated plants are faced with the problem not of avoiding exploitation but of promoting it (Heinrich 1975). The dynamics of this system may be very similar to those of the other exploitation systems discussed. The exploiter's choice of individuals or patches is based on some quality of those individuals or patches. I have hypothesized that an exploited individual will be under selection to cause a predator to choose other, more exploitable individuals. In pollination systems this is reversed; plants should evolve to increase their exploitation. Pleasants (1980) reported that, in the mountain meadow system he studied, plant species with flowers that produced higher amounts of nectar sugar were visited more often than species with less energetically rewarding flowers. Sutherland (1982) has found that flowers secrete nectar of the concentration that maximized energy harvest per time for pollinators. Furthermore, Sutherland (in prep.) found that hummingbirds preferentially visit plants (in this case Agave parryi) which possess larger proportions of flowers with optimal (for the pollinator) nectar concentrations. A plant may also manipulate within-plant behavior of its pollinators by varying the reward among flowers. Pyke (1978b) has hypothesized such a mechanism for the evolution of certain floral characters. In many species, flowers at the bottom of an inflorescence have more nectar than flowers toward the top. This should cause foraging bumblebees to visit the bottom flowers first, then move up the stalk. As the flowers are protandrous (anthers mature before the stigma) and mature sequentially from the bottom to the top of the inflorescence, this pattern of nectar
availability would promote maximum pollination efficiency by reducing intraplant transfer of pollen and promoting cross pollination (Pyke 1978a).

Prey Should Reduce the Probability That Predators Will Detect Them

This can be achieved by mimicking inanimate objects (Rothschild 1971) or by reducing the ability of a predator to distinguish the prey from the background. The latter can involve mimicking of the background (Kettlewell 1956) or countercoloration and disruptive coloration (Cott 1940). In addition, predators often form search images (Tinbergen 1960) which facilitate their subsequent location of prey similar in appearance to those previously located. Thus, cryptic prey should be under selection to diverge in appearance, leading, for instance, to polymorphisms in color or shape, as has been discussed by a number of authors (Ford 1957, Clarke 1962, Allen and Clarke 1968, Clarke and Murray 1971, Smith 1975).

Prey Should Advertise Their Negative Attributes

Aposematic coloration is a striking example of advertisement of toxicity. It immediately signals a visually hunting predator of the toxicity of the prey item. Convergence of the signal among aposematic colored species (Müllerian mimicry) will increase the chances that a predator will have learned the meaning of the advertisement through encounters with other, similarly colored aposematic species. The rattling of rattlesnakes and the white mouth and hissing of the cottonmouth snakes also serve as warnings of toxicity.

Alarm signals given by a prey individual should be audible or visible to the approaching predator. This would inform a predator of
a sudden decrease in patch quality. Thus a predator could quickly assess patch quality and choose not to attack. This is similar to the pursuit deterrence hypothesis of Woodland et al. (1980) which states that prey individuals signal to inform a predator that it has been detected, and therefore pursuit of the calling individuals would probably be unsuccessful. Woodland et al. (1980) and Tilson and Norton (1981) present evidence that this hypothesis is true in swamphens and klipspringers, respectively.

Smythe (1970) hypothesized that tail flashing (common in ungulates) functions to invite pursuit by the predator. A prey individual in good health may know it can escape from a predator, but unless the predator knows as well, it will continue to stalk or pursue the prey. In order to cut the interaction short so that it can return to other activities, the prey individual invites pursuit. Only when the predator pursues the prey will it come to learn that the prey is uncatchable (Smythe 1970). By inviting the pursuit the prey individual helps the predator assess the "value" of that prey individual and decide to seek other prey.

With regard to pollinator-plant mutualisms, Gori (1983) has argued that a number of plants exhibit floral changes in order to signal to pollinators the location of potentially rewarding flowers. With this information, the pollinator can forage more efficiently within a plant, thereby increasing its harvesting rate at that plant. This leads to longer foraging bouts at plants which signal if pollinators determine the duration of foraging within a patch (here the plant) by the harvesting rate within that patch. This should increase the number of flowers pollinated and the amount of pollen transferred to other plants (Gori 1983). Gori (in prep.) showed experimentally that plants which signal
resource states of their flowers are visited for longer times by pollinators than plants which do not signal. In this case, the "prey" is not manipulating the actual resource quality of the patch if inhabits or represents, it is simply providing a signal that the "predator" can use to assess resource quality within that patch.

Prey Should Evolve Advertisements of Negative Attributes Even in the Absence of the Actual Attributes

I have proposed that prey should exhibit a number of strategies. Other prey species should exploit those strategies. Such exploitation can take two forms: (1) prey can mimic the true advertisements of other species, and (2) prey can appear to have characteristics of less desirable items.

Batesian mimicry has been extensively treated by a number of authors (e.g., Wickler 1968, Turner 1977). Prey individuals falsely advertise undesirable qualities with the result that a predator may decide to avoid the prey. A common example is a palatable butterfly which mimics an unpalatable butterfly, thereby avoiding being eaten by visually hunting predators, such as birds (Brower 1958; Turner 1971, 1977).

There are a number of ways that prey can appear less suitable. First, they can appear less palatable. Prey may feign death and be avoided by predators which thereby decrease the probability of ingesting the parasites or microorganisms that may infect recently dead prey (Janzen 1978). Second, they can appear to be larger and more fearsome. For example, many animals erect the hairs of the back when threatened, thus appearing larger. Eyespots on the wings of butterflies may fool
a predator into thinking they are actually large animals (Edmunds 1974).

**General Discussion**

The importance of predator selectivity in multiple prey species communities has largely been ignored in examinations of the evolution of defensive tactics in prey. In the above discussion I made seven predictions of how prey defenses should evolve. I assert that for each, predator selectivity is important. Though the first five predictions do not require predator selectivity, their probability is greatly increased in situations where predators are selective and can thus be diverted to other prey. In order to decrease losses to a non-selective predator, the prey must actually defeat the predator by preventing location, capture, or consumption. The final two predictions, which concern the evolution of real and deceptive advertisements, require predator selectivity. It is of no advantage for a prey individual to bring attention to itself if the predator has no choice but to take that prey individual or one that looks like it.

A single prey species would not be expected to evolve according to all seven predictions, because in some cases alternative tactics are mutually inconsistent or contradictory. For example, I have predicted both decreased and increased body size in prey. These predictions, however, apply to very different situations. A prey species should evolve smaller body size when its predators tend to choose prey individuals which yield higher energetic return. A prey should evolve a larger body size when its predators tend to avoid large prey because
those individuals are more likely to kill or injure them or are more
difficult to handle. Furthermore, the evolution of defensive tactics
will often be constrained by other factors. Kerfoot (1977a), for
example, showed a direct tradeoff between fecundity and the possession
of defensive traits.

Rosenzweig (1973) and Schaffer and Rosenzweig (1978) considered
coevolution in the special case of one predator species with a single,
homogeneous prey species, representing the interaction as a coevolutionary
race. In the case of a predator and a cryptic prey, this approach
produces a predator that must constantly evolve improved detection
abilities to counter increased crypsis in the prey. The only evolutionary
strategy open to the prey is actual defeat of the predator. A very
different situation exists when predators have a choice. As a predator
could then choose prey that were less cryptic, a prey species could
divert the predator to other prey species by becoming more cryptic than
they. In this situation, the population dynamics of the predator would
be less tightly tied to any particular prey species. In his study of an
ecological analog of this problem, Inouye (1980) showed theoretically that
the introduction of a second prey species could stabilize an ecologically
unstable predator-prey interaction, if the predator is less efficient at
harvesting a mix of prey than either species alone. Such an introduction
might have similar effects on the evolutionary interaction. The
coevolutionary race might not be so "tightly run" and a coevolutionary
steady-state might be easier to attain. Complete assessment of the
effects of predator selectivity on coevolutionary dynamics must await
further analysis.
Summary

Many predators choose to consume prey individuals which yield a relatively high rate of energy (or other nutrient) intake over individuals or distributions that yield a relatively low intake. In addition, predators should avoid prey which may decrease their survival.

Prey species are predicted to evolve to "exploit" this choosiness; they should exhibit characteristics that make them less desirable as prey, thereby causing the predator to select alternate prey. Specifically, selection should lead to evolution of prey that:

1. Increase the probability of death of their predators;
2. Decrease the nutrition that can be gained per prey;
3. Increase the time required to handle them;
4. Decrease the quality of the patch they inhabit;
5. Reduce the ability of predators to detect them;
6. Advertise their negative qualities; and
7. Cheat by falsely advertising negative qualities.

In situations where predators are selective, prey have the evolutionary option of employing tactics which divert the predators to different prey. Though the first five predictions may hold in situations where predators are not selective, they are much more likely where predators are selective and prey can divert predators to alternate prey. The final two predictions can only be true in situations where predators are selective.
CHAPTER 2

LONG-TERM YIELD FROM HARVESTER ANT COLONIES: IMPLICATIONS FOR HORNED LIZARD FORAGING STRATEGY

Introduction

Do any organisms harvest their resources in a prudent manner, when that prudence requires that the resource be harvested in such a way that the long-term yield is maximized at the expense of short-term yield? Slobodkin (1961) first discussed this concept as it applies to predators, stating that predators would act in a prudent manner if they harvested prey in such a way as to maximize the harvest while also maximizing the probability that the prey population will be able to maintain itself as a resource in the future. This concept was criticized by Maynard Smith and Slatkin (1973) who believed that group selection would be required for prudence to evolve. Slobodkin's (1974) reply, as well as subsequent discussion by Mertz and Wade (1976), and Michod (1979), essentially ignored the evolution of true prudence in predators. Instead they discussed the mechanisms by which prey might evolve reduced reproductive value in age classes subject to predation (Slobodkin 1974, Michod 1979; though see Mertz and Wade 1976). Such evolution in the prey lends the behavior of predators a false appearance of prudence (i.e., predators appear to actually choose to attack individuals of low reproductive value). This has been termed apparent prudence (Slobodkin 1968) or prey prudence (Mertz and Wade 1976).
But what of the evolution of true prudence in predators? Mairorana (1976) recognized that predator prudence requires mechanisms for controlling the quantity of prey taken. This sort of "management" has been well studied in fisheries and forestry biology (Clark 1976, Beddington 1979) where it has been recognized that ever-increasing harvesting intensities will often lead to a decrease in long-term yield from a harvested resource. A model that results in this relationship is illustrated in Fig. 1a. As harvest intensity increases (increased slope in the YENJ line) the yield sustainable by a resource population first increases, then decreases as increased harvesting reduces the resource population to a point below the level where its productivity is maximal (N₂ to N₃; Fig. 1a), resulting in a decreased yield (Y₃). This model can be contrasted with another model, in which long-term yield is a simple increasing function of harvesting effort (Fig. 1b).

I maintain that there are certain circumstances under which group selection is not required for the evolution of true prudence in predators. Although these circumstances are somewhat restrictive, it is by no means unrealistic to expect to find them to be met in some systems. For prudence to evolve by natural selection at the level of the individual, the following conditions must be met in a predator-prey system:

(1) The predator must use prey from a discrete subpopulation so that it will benefit from its past acts of husbandry. This can most easily be achieved if the prey individuals are spatially static and the predator maintains a constant home range.

(2) An individual predator must have relatively exclusive use of the prey within its subpopulation so that if the predator exhibits
Fig. 1. Two alternate models of exploitation.--(a) Model after Clark (1976), showing the components of the equation $\frac{dN}{dt} = G(N) - Y(N)$. The hump-shaped curve represents $G(N)$, the growth function of the resource population in the absence of exploitation, based here on a logistic function. The functions $Y_1$, $Y_2$, and $Y_3$ represent yield from exploitation of the population as a function of $N$ (population density). Increased slope of the yield function represents increased harvesting effort, e.g., $Y_3$ represents greater harvesting effort than $Y_2$. Where the yield function crosses the growth function, the net population growth is zero: $\frac{dN}{dt} = 0$. Continued harvesting at that level will keep the population at the corresponding $N_i$, with a yield of $Y_i$. The yield functions are depicted as linear; they do not show a saturation at higher $N$ or $Y$. This is probably reasonable for the Phrynosoma cornutum-Pogonomyrmex desertorum colony system. (b) Model which leads to an increased harvested yield ($\bar{Y}_i$) with increased harvest intensity (increased slope of $Y_i[N]$ function) over all values of $N$. 
behavior that promotes long-term yield of prey from the subpopulation, that individual (and not other, nonprudent individuals) will benefit.

(3) The prey population must be responsive to variations in the foraging strategy of the predator. For example, it should be possible, at some prey density, to increase the long-term productivity of the prey population by decreasing foraging effort (Fig. 1a). If this was not true, a strategy to maximize long-term yield would be the same as a strategy that maximizes short-term yield and the question of the possibility of the evolution of a prudent, long-term strategy would cease to be important.

The purpose of this study and a companion study (Munger 1983a) is to test these conditions in a system in which it has been hypothesized that the predator behaves in a manner that maximizes the long-term yield at the expense of short-term yield. Whitford and Bryant (1979) hypothesized that individual horned lizards (Phrynosoma cornutum) forage in such a way as to increase long-term yield from colonies of Pogonomyrmex desertorum, a seed-eating ant which is an important prey item of these lizards. Colonies that experience substantial loss of workers (as to a foraging horned lizard) often cease surface activity for extended periods of time, thereby becoming unavailable for subsequent harvesting by horned lizards. Whitford and Bryant (1979) observed that horned lizards appear to avoid prolonged harvesting bouts at any one ant colony; it was suggested that this behavior keeps the colonies active and available for subsequent harvesting.
The three general conditions listed above can be translated into specific conditions that must be met for a long-term strategy to have evolved in the *Phrynosoma-Pogonomyrmex* system:

(1) Is an individual predator spatially congruent with a discrete subpopulation of the prey species? *P. desertorum* colonies are spatially static. Therefore this condition requires that individual horned lizards maintain home ranges within which they are able to harvest from colonies to *P. desertorum* a number of times. This condition was tested in a companion study (Munger 1983a; see also Munger 1982) and appears to be met.

(2) Do individual predators have exclusive use of their prey subpopulation? If horned lizards maintain home ranges, are they exclusive home ranges? This condition also appears to be met (Munger 1982, 1983a).

(3) Is the resource responsive to foraging intensity? Does a foraging strategy in which a horned lizard reduces harvest intensity to prolong availability of workers actually produce a higher yield in the long run? Whitford and Bryant (1979) showed that an increased loss of workers to artificial predation caused an increase in the amount of time *P. desertorum* colonies were inactive. However, they did not attempt to show if this decreased activity led to a decrease in long-term yield from those colonies. I present a test of this condition in this paper.

I performed five experiments in which I varied the intensity of artificial harvesting of colonies of *P. desertorum*. If an increased harvesting intensity caused a decreased long-term yield, then colonies of *P. desertorum* are a resource that conforms to the dynamics depicted
in Fig. 1a, not those depicted in Fig. 1b. The third condition necessary for the evolution of a long-term foraging strategy in the *Phrynosoma-Pogonomyrmex* system would therefore be met.

I concentrated my efforts on *P. desertorum* because it is the prey in the study of Whitford and Bryant (1979), because it is the most common prey item of the horned lizards at my study site (Munger 1982, 1983b), and because colonies are abundant enough (approx. 10-20 per ha; Munger, pers. obs.) and small enough (200 to 400 individuals per colony; Whitford and Ettershank 1975) to be manipulated easily.

**Methods**

**Study Site**

This work was carried out 6.5 km E, 2 km N of Portal, Cochise Co., Arizona, in an area of superficially homogeneous Chihuahuan deserts up habitat, at an elevation of 1,330 m. The study site lies on a gently sloping bajada, roughly halfway between the base of the Chiricahua Mountains and the center of the San Simon Valley. The substratum is generally a sandy loam with occasional rocky areas, especially near washes. The principal perennial vegetation consists of *Flourensia cernua*, *Gutierrezia* sp., *Ephedra trifurca*, and *Prosopis juliflora*. The spaces between these perennials are generally bare, except during both the winter and summer rainy seasons when a rich community of annual plants may develop. Winter storms are cyclonics from the west coast or cold fronts from the north or northwest. During the period of April through June, there is generally little rainfall. By the end of June, ant activity, which is dependent on humidity (Whitford and Ettershank
1975) is generally reduced. Beginning in early July and extending into September, thunderstorms, originating from the Gulf of Mexico, rake the area. The resulting increased humidity leads to greatly increased ant activity.

Harvesting Experiments

In each of the five experiments, colonies of *P. desertorum* were first located and marked with stakes. Colonies were included in the experiments only if they appeared healthy and fully active, had a single nest entrance, and were separated from other *P. desertorum* colonies by at least 2 m. Acceptable colonies were assigned at random to the various experimental treatments. During each artificial foraging bout, worker ants were aspirated within approximately 30 cm of the nest entrance for the times required by the various experimental treatments, then killed and counted. The resulting number constitutes the harvested yield from that colony for that foraging bout. Colonies were harvested during the period of daily colony activity, typically between 0700 and 1100, depending on temperature and humidity. Detailed descriptions of the methods particular to each experiment follow.

Experiment 1. This experiment involved 24 colonies subjected to three different experimental factors in a three-way design. The first factor was "giving-up time," which is based on a decision rule in which the predator leaves a patch when the time between encounters of prey items increases to some threshold (Krebs et al. 1974). For the low intensity treatment, I terminated my artificial foraging bout when I had not harvested an ant for 15 sec. For the high intensity treatment, I
terminated the bout when I had not harvested an ant for a full 2 min. In practice, this led to bouts averaging 1.5 and 9 min for the low and high intensity treatments, respectively. The second factor was the number of bouts per day. I harvested the colonies twice a day, once a day, and every other day for the high, medium, and low intensity treatments, respectively. For the third experimental factor, I took only outgoing ants (low intensity) or I took both incoming and outgoing ants (high intensity). It appears (Munger, pers. obs.) that ants within a colony are sensitive to the rate at which foraging workers arrive at the colony. This rate declines precipitously if both incoming and outgoing ants are harvested; it declines gradually if only outgoing ants are harvested. Therefore, I reasoned that if only outgoing ants were taken, the colony would be less likely to become aware of their losses and consequently cease surface activity for long periods. This experiment was conducted over a 12-day period, August 14 to August 25, 1979. Not all colonies were harvested during the entire time period. However, statistical analysis was based on the average harvest per day, not the total harvest from each colony. Two colonies were dropped from the experiment when they opened secondary entrances.

Experiment 2. Twenty-five colonies were subjected to five different treatments of foraging duration (min per bout): ½, 1, 2, 4, and 8. All colonies were harvested 22 times, an average of .23 bouts per day, over a period of 96 days, May 25 to September 1, 1980. One colony was dropped from the experiment because its marker stake was lost.

Experiment 3. Twelve colonies were subjected to three treatments of foraging frequency, which in practice were .59, .28, and .16 4-min
bouts per day. For the most intense treatment, colonies were harvested twice on those days harvested; the average for this treatment is lower than two bouts per day because one to several intervening days were typically skipped. Colonies were harvested over a period of 61 days, from July 20 to September 19, 1980. One colony was dropped because its marker stake was lost.

Experiment 4. During two consecutive years a total of 32 colonies were subjected to two frequencies of artificial harvesting as well as to various levels of seed and insect matter addition. I will subsequently ignore factors other than harvesting intensity. From August 24 to September 15, 1980, 12 high intensity colonies were harvested seven times and 12 low intensity colonies were harvested five times. From September 26 to September 29, 1980, four new colonies were added to each treatments and harvested six or three times for the high and low intensity treatments, respectively. On October 10, all 16 high intensity colonies were harvested once. From May 5 to June 27, 1981, all 16 high intensity colonies were harvested 26 times and all low intensity colonies 13 times. Overall, the 16 colonies which were harvested at high intensity were subjected to an average of 32.7 4-min bouts, while the 16 colonies harvested at a lower intensity were subjected to an average of 17.5 4-min bouts.

Experiment 5. Sixteen colonies were subjected to two treatments, 20 min vs. 40 min per bout. Five colonies from each treatment were harvested on July 11, 1981. Those colonies and three additional colonies were harvested eight times, from July 17 to August 1, 1981. At the onset of a foraging bout, I aspirated any ants near the colony
entrance, then sealed the colony entrance with tanglefoot. At the end of the bout, I returned to the colony and aspirated the workers that had returned from foraging forays and were milling about the colony entrance attempting to re-enter.

Statistical Analysis

Data from the harvesting experiments were analyzed using a BMDP2V repeated measures analysis of variance (Winer 1971, Dixon and Brown 1979). This program essentially tests for treatment effects using the means for each colony in a standard analysis of variance. It also allows testing for time by treatment interactions. In experiments where the number of bouts per day was varied, data were grouped into appropriate blocks of time. For example, in Experiment 1, the data were grouped into four blocks each containing four 2-per-day bouts, two 1-per day bouts, and one every-other-day bout.

In a small number of cases, I failed to label samples or samples were lost before recording. As the procedure used for analysis of variance requires data in all cells, an estimate was made for each missing value, based on colony censuses, harvests from other colonies that day (which are an indication of overall activity levels on that day) and previous and later harvests from the colony with the missing datum. This estimated value was then included in the analysis. Out of a total of 2,055 values analyzed for all five experiments, only 15 were missing.
Results and Discussion

A necessary condition for the evolution of a long-term strategy is that it must provide some economic advantage over a strictly short-term strategy. Whitford and Bryant (1979) hypothesized that horned lizards employ a long-term strategy in which they limit their harvesting intensity at ant colonies in order to increase the long-term availability of workers from those colonies. It is a necessary condition that, over some range of harvesting intensities, colonies that are harvested at a lower intensity must yield a larger long-term return than colonies subjected to a higher intensity of harvest. However, no such result occurred in any of the five experiments described here (Table 1, Figs. 2-6). In all cases where total yield was significantly affected by harvest intensity, the higher harvest intensity led to a higher long-term yield, a result opposite that required for a long-term strategy to evolve.

In discussing the significance of these results, I will entertain three possible reasons for this outcome: (1) *Pogonomyrmex desertorum* is not a resource that can give a higher yield when harvesting intensity is decreased. Therefore a condition necessary for the evolution of a long-term foraging strategy in horned lizards (a strategy based on decreased harvest intensity to increase the yield from subsequent harvests) is not met. (2) My experiments were not performed over a long enough period to show the necessary result. (3) My experiments were not intense enough to cause a decline in long-term yield. In the following section, I argue that the latter two of these reasons are not true and that the first reason is correct.
<table>
<thead>
<tr>
<th>Experiment</th>
<th>Harvest Intensity Criterion*</th>
<th>Overall Duration (Days)</th>
<th>Treatment Intensity</th>
<th>Overall Harvest</th>
<th>Time Period</th>
<th>Treatment Effects</th>
<th>Time X Treatment Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a</td>
<td>giving up time</td>
<td>12</td>
<td>Low</td>
<td>14.6</td>
<td>17.3</td>
<td>.242</td>
<td>.015§</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>High</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1b</td>
<td>X bouts/day</td>
<td>12</td>
<td>Low</td>
<td>6.8</td>
<td>18.9</td>
<td>.004</td>
<td>.008§</td>
</tr>
<tr>
<td>1c</td>
<td>take outgoing only, take all</td>
<td>12</td>
<td>Low</td>
<td>13.6</td>
<td>19.1</td>
<td>.165</td>
<td>.034§</td>
</tr>
<tr>
<td>2</td>
<td>min/bout</td>
<td>96</td>
<td>Low</td>
<td>4.4</td>
<td>4.3</td>
<td>.0265</td>
<td>.793</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>High</td>
<td>6.7</td>
<td>11.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>11.5</td>
<td>per bout</td>
<td>.0265</td>
<td>.793</td>
</tr>
<tr>
<td>3</td>
<td>X bouts/day</td>
<td>43</td>
<td>Low</td>
<td>23.9</td>
<td>30.3</td>
<td>.0032</td>
<td>.0015</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>High</td>
<td>63.8</td>
<td>per time block</td>
<td>.0032</td>
<td>.0015</td>
</tr>
<tr>
<td>4</td>
<td>X bouts/day</td>
<td>47+53</td>
<td>Low</td>
<td>137.3</td>
<td>233.2</td>
<td>.0041</td>
<td>.0018§</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>High</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>min/bout</td>
<td>21</td>
<td>Low</td>
<td>22.6</td>
<td>26.0</td>
<td>.517</td>
<td>.797§</td>
</tr>
</tbody>
</table>

*See text for a description of the measures used for each harvest intensity criterion.
†X = average number of workers harvested per colony, per time period, calculated for the entire duration of the experiment.
‡Probability that treatment or interaction effects are due to chance alone.
§Analysis for time X treatment interaction performed for the first 8 days of treatments for each colony.
¶Before summer rains began.
∥After summer rains began.
*Analysis for time X treatment interaction performed for the 12 colonies that began the experiment, not the 4 later added.
††Analysis for time X treatment interaction performed for the 5 colonies that began the experiment, not the 3 later added.
Fig. 2. Results from Experiment 1.--(a) For the high intensity treatment, the harvesting bout at a colony was terminated if no ant had been harvested for 2 min. The low intensity treatment bout was terminated if no ant was taken for 15 sec. (b) Treatments are as presented. (c) For the high intensity treatment, ants entering and leaving were harvested. For the low intensity treatment, only ants leaving the colony were harvested. --Bars represent ± one standard error.
Fig. 3. Results from Experiment 2, showing harvest yield from the two most intense treatments only. Bars represent ± one standard error.
Fig. 4. Results from Experiment 3.---All bouts were 4 min long. The average frequencies of harvesting (in bouts per day) were 0.59, 0.28, and 0.26 for the high, medium, and low intensity harvesting treatments, respectively. To compensate for the increased number of bouts in the second and third time blocks, the means presented for the high intensity treatment have been reduced by 1/5 and 1/3, respectively.
Fig. 5. Results from Experiment 4.--Bars represent ± one standard error.
Fig. 6. Results from Experiment 5.—Bars represent ± one standard error.
As, to my knowledge, no one has ever measured the $G(N)$ vs. $N$ curve of an ant colony of any species, it is impossible to know if the dynamics of *P. desertorum* colonies are accurately reflected in a model such as that depicted in Fig. 1a. That model was designed for population level phenomena. The growth function of the population is zero when the population level is zero, and initially rises as the population increases in size. Above a certain point (the hump on Fig. 1a), $G(N)$ begins to fall as intraspecific competition becomes important. If exploitation is too intense, the size of the population is decreased to a point (to the left of the hump) where $G(N)$, and thus harvested yield, are reduced.

The dynamics of the exploitation of ant colonies appear to differ from the dynamics of the model depicted in Fig. 1a in at least three ways, any one of which could have led to the result of this study that decreased harvest intensity did not lead to an increased long-term yield. These differences (and their implications) are as follows:

1. Above some threshold, increased foraging effort by a horned lizard may fail to increase the harvesting intensity on the colony. Colonies cease above-ground activity in response to substantial loss of workers to horned lizards. This prevents further losses, no matter how much effort the lizard exerts in foraging. This can be viewed as a constraint, imposed by the colony, on the maximum slope of the harvesting line. The results of Experiment 2, with five levels of harvest intensity, are consistent with this idea (Fig. 7). At high harvest intensity, the yield levels off. In addition, the yields for the various treatments were surprisingly similar in several of the experiments, especially following the initial part of the experiment (Figs. 2-6, Table 2).
Fig. 7. Results of all five treatments of Experiment 2, showing a leveling off of yield with increased harvesting intensity.
(2) Intense harvesting of workers by horned lizards may reduce the production of new workers in a colony by decreasing the amount of forage brought into the colony. This can be caused by a simple reduction in the number of workers foraging and by a reduction in the time the colony spends foraging. This mechanism of overexploitation is very similar to the population level model depicted in Fig. 1a, in which reproducing members of the resource population are harvested, but it differs from that model in an important way. Only workers that are active on the ground surface can be harvested by a horned lizard and these are only a portion of the total colony population. The X-axis becomes "number of surface-active workers" (Fig. 8) and is similar to the model presented by Noy Meir (1975, Fig. 5c) for a resource with an unharvestable reserve. Because the queen, nurse workers, and nest workers can continue to produce new foragers in the absence of foraging workers (although only for a limited period, depending on colony food stores), the G(N) of new foragers (the resource of horned lizards) would be greater than zero when the population size of foragers is zero (Fig. 8). Therefore, the decrease in yield caused by an increase in foraging effort ($\bar{Y}_2$ to $\bar{Y}_3$, Fig. 8) would be less substantial than for the population depicted in Fig. 1a. Such a reduction in the effect of overexploitation could have caused the results reported here, as smaller differences in long-term yield would be more difficult to detect. For the same reason, a reduction in the negative effects of overexploitation would reduce the selective advantage of avoiding overexploitation. Such a behavior would thus be less likely to have evolved in horned lizards.
Fig. 8. Exploitation model for the situation where the resource has an unharvestable reserve, e.g., an ant colony with its queen, nest workers, and stored food. Only surface-active workers can be harvested by a horned lizard. Note that $Y_3$ is much closer to $Y_2$ in this model than in the model depicted in Fig. 1a.
Intense harvesting by horned lizards can cause reduced surface activity by the colony workers and thereby a reduced availability of workers for subsequent harvest. This is based on a behavioral response rather than numerical losses from the resource population and is the mechanism proposed by Whitford and Bryant (1979). While this behavior by ant colonies may well lead to a temporary fall in the rate of intake following an initial intense harvesting bout, it is difficult to see how such a behavior would lead to a decrease in long-term yield when that total includes the initial bout. The lizard should be faced with the simple problem that there are a certain number of ants in the colony; should it take them in several less intense bouts or in fewer, more intense bouts? It is not clear that either strategy should result in a higher yield.

Two factors in the experimental design could have led to my failure to obtain the result that an increase in harvest intensity can lead to a decrease in long-term yield: The harvesting treatments used may not have been intense enough to cause a reduced harvest or my experiments may have been too short in duration.

It is possible to gain some knowledge of whether or not my harvesting experiments were intense enough by examining their effect on colony activity. The mechanism put forth by Whitford and Bryant (1979) as the cause of decreased yield with increased harvest intensity is that colonies subjected to intense harvesting cease activity and become unavailable for subsequent harvesting. As can be seen in Table 2, colonies subjected to more intense harvesting treatments did show a greater tendency to cease activity (as measured by the probability of
TABLE 2
Proportion of Visits to Experimental Colonies That Yielded a Harvest of Zero

<table>
<thead>
<tr>
<th>Treatment Intensity</th>
<th>Experiment</th>
<th>Proportion of Harvesting Bouts in Which No Ants Were Harvested*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Low</td>
</tr>
<tr>
<td></td>
<td>1a</td>
<td>.18</td>
</tr>
<tr>
<td></td>
<td>1b‡</td>
<td>.14</td>
</tr>
<tr>
<td></td>
<td>1c</td>
<td>.19</td>
</tr>
<tr>
<td>(overall)</td>
<td>2‡</td>
<td>.24</td>
</tr>
<tr>
<td>(before rains)</td>
<td>2‡</td>
<td>.11</td>
</tr>
<tr>
<td>(after rains)</td>
<td>2‡</td>
<td>.32</td>
</tr>
<tr>
<td>3‡</td>
<td>3‡</td>
<td>.13</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>.41</td>
</tr>
<tr>
<td>5</td>
<td>5</td>
<td>.20</td>
</tr>
</tbody>
</table>

*A higher proportion of zeros indicates a greater likelihood that the colony was shut down at the time of harvesting.

†The values per colony were analyzed by ANOVA or Mann-Whitney U-test (Siegel 1956). P values indicate the probability that the differences in proportions are due to chance.

‡For experiments 1b, 2, and 3 only the two most intense treatments were analyzed.
obtaining nothing during a foraging bout) in several of the experiments (and before the summer rains began in Experiment 2). In these cases the mechanism proposed was operational, indicating that the experimental treatments were intense enough, but a drop in overall yield was still not obtained.

The duration of harvesting is important if harvesting begins when the resource level is above the equilibrium value for the steady-state model depicted in Fig. 1a. In such a situation, an exploiter would benefit from the resources harvested while reducing the population to the steady-state level. A higher intensity of harvesting would lead to a higher initial yield. Both this initial, pre-steady-state harvest and subsequent harvests at the steady-state level would contribute to the total harvest from that resource. Therefore, even though the steady-state harvest might be lower for a more intense harvesting strategy, the greater pre-steady-state harvest could cause the total harvest to be greater for a more intense harvesting strategy. However, the contribution of this pre-steady-state harvest to the total harvest becomes relatively less as the steady-state harvest continues. Therefore, while in the short run the increased pre-steady state harvest may cause a strategy of harvesting at higher intensity to yield a higher total harvest, increasing the length of time over which the harvesting occurs would eventually lead to a higher long-term yield for the lower intensity harvest, if the steady-state dynamics are as depicted in Fig. 1a.

How do the lengths of my experiments compare with the time spans of the natural horned lizard-ant system? Experiment 2 was of the longest duration; harvesting occurred over 96 days. I have observed
horned lizards active from April through October, a span of over 200 days, and have observed that an individual Phrynosoma cornutum may occupy a particular area for at least the four summers that I have been marking lizards at the study site (Munger, unpubl. data). Thus, the time scale of a long-term strategy could potentially be a good deal greater than that of my experiments.

However, even if my experimental harvesting did not persist over a long enough period to cause a decrease in total yield, the trends that would lead to a decreased yield should be apparent in a short-term experiment. That is, the yield per bout from intensely harvested colonies should show a greater decrease over time than the yield from moderately harvested colonies, and, if a steady state is reached, the steady-state yield from a colony harvested at high intensity should be below that of a colony harvested at low intensity. The predicted difference in the degree to which yields have diminished has two necessary consequences (Fig. 9a). First, the difference should appear in a repeated measures analysis of variance (Winer 1971) as a significant interaction between treatment and time factors. Second, a difference in the steady-state values should be detectable by first examining graphs of the harvests over time (Figs. 2-6) to see when the yields appear to have reached a steady state, then performing an analysis of variance on the "steady-state" span. Although a significant interaction of treatment and time factors did occur in several experiments (calculated for the entire duration of the experiments; Table 1), in no case was the "steady-state" yield from the colonies harvested at the lower intensity higher than the yield from the colonies harvested at the higher intensity (Table 3). In most cases
Fig. 9. Two possible idealized interactions of treatment effect with time.---(a) Though initial pre-steady-state harvest is higher for the high intensity treatment, the steady-state yield is lower. This pattern will eventually lead to a higher total yield from the low intensity harvest than from the high intensity harvest. A significant term for interaction between time and treatment effects should appear in a repeated measured analysis of variance. In addition, the steady-state yield from the low intensity harvest should be higher than that from the high intensity harvest. (b) Initial pre-steady-state harvests are similar to those in (a), again leading to an interaction of time with treatment effects. In this case, however, the steady-state yield from the high intensity harvest is not lower than that from the low intensity harvest. Therefore the overall yield from the high intensity harvest will remain higher than that from the low intensity harvest.
a. High intensity harvest decreases over time, while low intensity harvest remains constant.

b. High intensity harvest decreases over time, while low intensity harvest remains constant.
# TABLE 3

**Analysis of Treatment Effects for Period After Harvesting at Colonies had Reached "Steady-state"**

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Period Tested</th>
<th>X Ants Harvested*</th>
<th>Treatment Intensity</th>
<th>Time X Treatment Interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Low</td>
<td>High</td>
<td>P</td>
</tr>
<tr>
<td>1a</td>
<td>days 3-8</td>
<td>10.93</td>
<td>9.7</td>
<td>.761</td>
</tr>
<tr>
<td>1b†</td>
<td>days 3-8</td>
<td>11.2</td>
<td>14.02</td>
<td>.011</td>
</tr>
<tr>
<td>1c</td>
<td>days 3-8</td>
<td>10.44</td>
<td>10.1</td>
<td>.697</td>
</tr>
<tr>
<td>2†</td>
<td>Jul 23 - Sep 1, 1980</td>
<td>9.47</td>
<td>9.24</td>
<td>.954</td>
</tr>
<tr>
<td>3†</td>
<td>Aug 15 - Sep 15, 1980</td>
<td>30.20</td>
<td>51.50</td>
<td>.0824</td>
</tr>
<tr>
<td>5</td>
<td>Jul 20 - Aug 1, 1981</td>
<td>18.8</td>
<td>20.5</td>
<td>.725</td>
</tr>
</tbody>
</table>

Note.—Harvesting at a colony is considered to have reached steady-state if there was a lack of systematic convergence or divergence between treatments in later harvested yield values.

*X* = average number of ants harvested per colony per time period (as in Table 1), calculated over the entire steady-state period.

†For experiments 1b, 2, and 3, only the two most intense treatments were analyzed.
the yields were remarkably similar (Figs. 2-6). Therefore, Fig. 9b provides a better representation of the data than does Fig. 9a. It appears that the yield from colonies subjected to the high intensity treatment does drop, but the steady-state harvest from those colonies is not lower than the steady-state yield from colonies subjected to the low intensity treatments. Therefore, it is unlikely that increasing the duration of the experiments would have changed the results.

The results presented here cast considerable doubt on the possibility that horned lizards could have evolved a long-term strategy that increases long-term yield at the expense of short-term harvest. Horned lizards should be a likely candidate for showing such a strategy. They occupy relatively circumscribed home ranges (Munger 1982, 1983a). Their primary resource is spatially static and long-lived. However, two characteristics of *Pogonomyrmex desertorum* colonies may prevent them from responding to exploitation in such a way that makes it advantageous for *Phrynosoma cornutum* to reduce harvesting intensity to increase long-term yield at colonies of *P. desertorum*. First, ant colonies are able to produce new surface-foraging workers (the resource utilized by horned lizards) even if the population size of surface workers has dropped to zero. Second, by ceasing above-ground activity in response to worker loss, colonies of *P. desertorum* appear to put an upper limit on the intensity with which they can be harvested.

This latter characteristic is potentially an evolved tactic for reducing losses to predators. By ceasing activity, immediate losses are reduced. In addition, if the lizard forages using a strategy in which the time spent foraging in an area is dependent on the rate of feeding
in that area (Charnov 1976, Munger 1983b), cessation of surface activity will serve to reduce subsequent losses from the colony as well. By ceasing activity, the colony reduces the quality of the area it inhabits, potentially causing a choosy horned lizard to move on to a different part of its home range (Munger 1982, 1983c).

Not only is *P. desertorum* a resource that appears to not respond to a prudent foraging strategy, but the behavior of horned lizards that was hypothesized to form the basis of a long-term strategy has been shown to be compatible instead with a short-term foraging strategy. As noted earlier, Whitford and Bryant (1979) observed that *P. cornutum* appears to avoid prolonged foraging bouts at any one ant colony, a behavior that they hypothesized would lead to an increased long-term availability of ants. In a detailed analysis of horned lizard foraging behavior, Munger (1982, 1983b) showed that horned lizards terminate their foraging bouts at ant colonies at a time that roughly corresponds to that predicted by a model that maximizes short-term yield (the marginal value theorem; Charnov 1976).

In conclusion, it appears that if one tries to study "prudence" in exploitation, one will probably end up looking at the prey and studying apparent prudence (Slobodkin 1968) or prey prudence (Mertz and Wade 1976). This may well be a result of what Dawkins and Krebs (1979) term the dinner-life phenomenon. While in an encounter the prey is fighting for its life, the predator is only fighting for its dinner. The selective pressures on prey to prevent their own death are probably higher than those on a predator to avoid killing too many individuals of high reproductive value so that there might be more young prey next year.
In terms of the present study, it is probably a good deal more important for ants to prevent overexploitation of their colony (thereby abetting their survival and reproduction) than for a horned lizard to avoid overexploiting a colony (to increase long-term yield) when it could simply harvest other colonies.

It seems much more likely that prudent behavior will evolve in a predator when the interaction with its prey verges on mutualistic. For example, Stimson (1973) showed that the limpet *Lottia gigantea* keeps space on rocks clear of encrusting algae, barnacles, and other limpets, an action that appears to provide more space for a favored algae to grow. Such a relationship benefits the algae (more space to grow) as well as the limpet; therefore it is not completely advantageous for the algae to prevent exploitation by the limpet.

**Summary**

In order for a long-term, prudent foraging strategy to evolve via natural selection at the level of the individual, three conditions must be met: (1) The forager must use resources from a discrete subpopulation, (2) use of that subpopulation must be relatively exclusive, and (3) the resource population must respond in such a way that a long-term strategy actually provides a greater economic benefit to the forager than does a short-term strategy. In this study, the third condition is tested for a predator (horned lizards: *Phrynosoma cornutum*) that has been hypothesized to employ a long-term strategy when harvesting worker ants from colonies of the ant *Pogonomyrmex desertorum*. Five artificial harvesting experiments were undertaken to determine if,
at some point, an increased harvesting intensity will lead to a decreased long-term yield. Such a result would indicate that it is economically advantageous for horned lizards to employ a strategy in which harvest intensity is reduced in order to promote the long-term availability of ants. However, in none of the five experiments was this result obtained. It is therefore concluded that evolution of a long-term strategy in horned lizards is unlikely. Failure to obtain the required result is attributed to three characteristics of *P. desertorum* colonies. (1) Because colonies cease surface activity in response to depredation of surface-active workers, an increase in foraging effort (above some threshold) by horned lizards will not lead to an increase in losses from preyed-upon colonies. (2) Because colonies have an unharvestable reserve consisting of queen, immature workers, and colony stores, they can, for a limited time, continue to produce surface-active workers (the resource used by horned lizards) even if all surface-active workers have been previously harvested. (3) In the short term, colonies are a finite resource; it should matter little whether the resource is harvested in one intense bout or in a series of less intense bouts.
CHAPTER 3

HOME RANGE BEHAVIOR OF HORNED LIZARDS: IMPLICATIONS FOR FORAGING STRATEGY

Introduction

The manner in which an animal uses space can be considered on the following two levels. First, does it use space in a nonrandom fashion, that is, does it have a home range? Second, does it have exclusive use of an area? Both of these questions have an important impact on the way in which resources are utilized. If a home range is maintained, an individual will have repeated contacts with a subpopulation of its resource and will be able to learn the locations of resource concentrations, as well as of nest sites and escape routes. An individual will tend to have exclusive use of an area (and the resources contained therein) if it defends that area as a territory (which in turn depends on the economics of defense; Brown 1964) or if there is an advantage of reducing the overlap of its home range with the home ranges of others. One such advantage is the avoidance of areas in which the resource has been depleted by other individuals.

The present study attempts to determine if two species of horned lizard (Phrynosoma cornutum and P. modestum) maintain home ranges and if those home ranges are exclusive. This is done by comparing observed movements of radiotransmitter- and radioactively-tagged Phrynosoma individuals to computer generated random models of those movements.
In addition to considering general questions about the use of space, this study was designed to answer specific questions about the long-term foraging strategy of horned lizards. In particular, the strategy of spatial utilization is important in determining whether or not a foraging strategy involving the husbandry of a resource—in order to increase the long-term yield—benefits the forager and can therefore evolve through natural selection. In a companion study (Munger 1983a) I presented three conditions which must be met for such a prudent strategy to evolve:

1. The forager must benefit from its past acts of husbandry through repeated contacts with a discrete subpopulation of its resource. For example, a strategy that includes a reduction in foraging effort could potentially lead to a higher standing crop and thereby a higher production of young in that resource subpopulation than a strategy of higher harvesting effort. In order for this increased production of young to lead to increased harvesting success by the forager, the forager must have repeated contact with that subpopulation.

2. In order that the benefits of prudent tactics not be wasted on non-prudent foragers, prudent foragers must have relatively exclusive use of a resource subpopulation. This could result from active territorial defense or from mutual avoidance.

3. Yield from the resource population must be responsive to the foraging strategy of the predator such that a long-term strategy is economically advantageous.

Whitford and Bryant (1979) hypothesized that horned lizards (specifically *Phrynosoma cornutum*) preying on workers of the desert
harvester ant *Pogonomyrmex desertorum* act in such a way as to increase the long-term yield from those ant colonies. This hypothesized prudence is based on a simple behavioral response of *P. desertorum* colonies to the loss of surface active workers: They cease surface activity for extended periods, thereby making the workers unavailable for subsequent harvesting by horned lizards. Whitford and Bryant (1979) observed that *P. cornutum* individuals feeding on *P. desertorum* do not harvest workers from a colony over an extended period of time, but appear to move on before they would cause a colony to cease activity.

In the present study I attempt to determine whether the first and second conditions are met in the *Phrynosoma-Pogonomyrmex desertorum* system. Munger (1983a) examined the third condition, that colonies of *Pogonomyrmex desertorum* are a resource which responds favorably to foraging strategy, by examining the effect of experimental variation in harvest intensity on long-term yield from *P. desertorum* colonies.

Because colonies of *P. desertorum* are spatially static, meeting the first condition requires that each individual horned lizard occupy a limited area. As a test I compared observed movements of individuals with a random model of those movements. If observed patterns of movement do not lead to use of much smaller areas (and therefore to use of smaller subpopulations of *P. desertorum* colonies) than do patterns resulting from random movement, then the first condition is not satisfied in this system.

As a test of the second condition I compared observed overlaps of home ranges with a random expectation of overlaps generated from observed home ranges. If horned lizard home ranges were observed to overlap as much as they would if they were placed at random, then the
second condition is not satisfied and it is unlikely that a prudent strategy could evolve.

**Materials and Methods**

**Study Site**

This work was carried out 6.5 km E, 2 km N of Portal, Cochise Co., Arizona, in an area of superficially homogeneous Chihuahuan desert-scrub habitat, at an elevation of 1,330 m. The study site lies on a gently sloping bajada, roughly halfway between the base of the Chiricahua Mountains and the center of the San Simon Valley. The substratum is generally a sandy loam with occasional areas of gravel and cobble, especially near washes. The principal perennial vegetation consists of *Flourensia cernua*, *Gutierrezia* sp., *Ephedra trifurca*, and *Prosopis juliflora*. The spaces between these perennials are generally bare, except during both the winter and summer rainy seasons (when a rich community of annual plants may develop). Winter storms are cyclonics from the west coast or cold fronts from the north or northwest. During the period of April through June, there is generally very little rainfall. By the end of June, ant activity, which is dependent on humidity (Whitford and Ettershank 1975) is generally reduced. Beginning in early July and extending into September, thunderstorms, originating from the Gulf of Mexico, rake the area. The resulting increased humidity leads to greatly increased ant activity.

In August 1977, 24 pens were erected at the study site as part of a broader study of the interactions of ants, rodents, and plants (see Munger and Brown 1981). In addition, a barbed wire fence was built
around the entire 20 ha site to exclude cattle. Because the observations in this study were made primarily in and around these pens, I will describe them in detail (see Fig. 1). Each pen is square, measuring 50 m x 50 m, is no closer than 25 m to the nearest other pen, and is fenced with 0.64 cm wire mesh. Sixteen of the pens have four openings (each measuring 7.5 cm wide x 9 cm high) at ground level on each of the four sides, allowing the passage of rodents, lizards, etc., into and out of the plots. During the summer of 1981, the number of holes was doubled to facilitate movements by horned lizards; their size was also reduced to 2 cm high x 3.5 cm wide. The remaining eight pens have very small holes or no holes at all; adult horned lizards are therefore excluded from a total of 2 ha of the site. Within each pen is a grid of 49 stakes at 6.25 m centers. These stakes, as well as the pens themselves, were used extensively as reference locations.

The Organisms

Pianka and Parker (1975) present an excellent review of the literature concerning the genus Phrynosoma. These lizards stand apart from other members of the family Iguanidae in several ways. They have a flat, wide body form, are slow moving, and are easily caught by hand. Instead of always fleeing from potential predators, they rely primarily on their cryptic coloration to prevent detection and their spines to deter attackers. Their food consists primarily of ants. Although this diet has been referred to as a preference on the part of horned lizards (e.g., Pianka and Parker 1975), ants are probably the most common potential
prey item for horned lizards in many areas; it is unknown if ants form a
greater share of their diet than would be expected based on availability.

Horned lizards typically forage during mid-morning and late
afternoon, the times of highest ant activity. Individual lizards often
visit several ant colonies during a day, and also harvest ants encountered
while basking or moving or while stationed near a pathway used by ants

*Phrynosoma modestum*, the round-tailed horned lizard, and *P.
cornutum*, the Texas horned lizard, overlap extensively in their geographic
ranges, which extend from southeastern Arizona into Texas (*P. cornutum*
extends north to Kansas) and south into Mexico (Stebbins 1966, Sherbrooke
1981). *Phrynosoma cornutum* measures 69 mm snout-vent length at attainment
of sexual maturity (Pianka and Parker 1975) and may reach 94 mm (males)
or 114 mm (females); the corresponding span in body weight is approxi-
mately 20-90 g (Munger, unpubl. data). *Phrynosoma modestum* measures
approximately 50 mm at attainment of sexual maturity (Pianka and Parker
1975) and may reach 60 mm (males) or 67 mm (females) with adult weights
ranging from approximately 6-17 g (Munger, unpubl. data).

Whitford and Bryant (1979) claimed that there was little overlap
in the diet of *Phrynosoma modestum* and *P. cornutum* at their study site.
Munger (1982b), however, found substantial dietary overlap at the site
of the present study, with both species relying heavily on *Pogonomyrmex
desertorum*. Therefore, I investigated the use of space by both species,
and examined both intra- and interspecific overlap in home range.
Lizard Location

In order to be able to repeatedly determine the location of horned lizards at the site, I tagged a total of 49 horned lizards with either a radioactive tag or a small radiotransmitter. Each individual was located approximately once every other day, typically at midday, for a total of 8-40 sightings. The location of each lizard was recorded to the nearest meter, relative to the nearest artificial landmark. Later, using an aerial photograph of the site, I translated all locations into absolute coordinates. Table 4 shows the dates during which individual lizards were tagged.

Radioactive Tags. *Phrynosoma modestum* individuals vary from roughly 5-15 g adult body weight; they would have difficulty carrying a 3-4 g transmitter. Radioactive tags are extremely light, and are therefore a reasonable alternative. "Seeds" of iridium-192 (Alpha Omega, Inc.) were obtained through the Department of Radiation Oncology at the University of Arizona Health Sciences Center. Ir-192 has a half-life of 74 days, which is long enough to allow recovery of the seeds throughout much of a field season, through short enough not to persist in the environment should a seed be lost. The seeds consist of iridium encapsulated in a platinum-iridium casing, measure 1 mm in diameter x 3 mm long, and were used after their activity had fallen to the range of 100-350 μCi. Initially seeds were injected subdermally on the dorsal side of the thigh. However, in order to reduce trauma, I subsequently attached seeds at the base of the tail, dorsally, with silicone rubber sealant.

Radioactively tagged lizards were located using a PR-4 Log-lin pulse rate meter and a high-energy gamma scintillation probe (Eberline Co.).
Fig. 10. Layout of study site.—Small squares represent the 24 pens (each 50 m on a side). Squares with solid lines represent pens that are inaccessible to adult horned lizards; dashed lines delimit pens that are accessible. Larger rectangles represent the borders of 14 sub-areas into which the random centers of range were assigned (see text); numbers in brackets refer to the number of centers of range occurring in each rectangle in 1980 and 1981 (in that order). A barbed wire fence (dotted line) surrounds the site.
The probe was attached to the end of a 2 m pole, and was passed back and forth near the ground surface as searching was conducted. With the tags used, lizards were typically detectable at 3-5 m. Because of this short range, extensive searching was sometimes necessary to locate a lizard. When the observations on a particular lizard were terminated, the tag was removed and the lizard released.

Radiotransmitters. Because of their larger size, P. cornutum individuals easily accommodated small radiotransmitters. An SM1 transmitter (AVM, Inc., Champaign, IL) with a loop antenna was attached to the back of the animal with silicone rubber sealant. The loop passed around the chest just posterior to the front legs and was attached to the ventral surface with silicone rubber sealant. This reduced the probability of the wire catching on sticks or rocks as the lizard passed over them. Every 2-4 weeks, the transmitter was removed and replaced with one that had a fresh battery. The lizards were located with a hand-held Yagi-style antenna and 12 channel receiver (Wildlife Materials, Inc., Carbondale, IL). The range of detection of this equipment was 50-150 m and proved much more convenient than radioactive tags. Observations of lizards with transmitters did not reveal any significant encumbrance caused by the transmitters (Munger, pers. obs.).

Visual Sightings. Because it was not feasible to radiotrack all lizards, I supplemented radiolocation data with the locations of lizard captures by myself and other workers at the site. All horned lizards captured were marked by toe clipping and their species and sex recorded. Four years of work at the site, involving a number of research activities, resulted in a total of approximately 1700 captures and recaptures,
including locations of radiotagged lizards. Forty-nine lizards were used in the home range area analysis (Table 4) and 295 in home range overlap analysis (Fig. 10).

Treatment of Radio-location Data

In order to determine if horned lizards occupy a circumscribed home range, it was necessary to compare the actual home range to a random expectation of home range area. In brief, to obtain this random expectation I determined the area of an ellipse which approximately enclosed the actual locations occupied by the lizard. Working with the set of vectors between actual lizard locations, I randomized the direction and order of those vectors, thereby constructing a set of random coordinates from which a new elliptical area could be calculated. Randomization was performed 100 times for each lizard to give a distribution of random areas with which the real area could be compared. Figure 11 depicts this process.

This analysis was performed on a DEC PDP-8 OS/8 minicomputer. Home range area (for both real and randomized sets of coordinates) was calculated in the following manner. The two coordinates farthest apart were considered to define the endpoints of the major axis of an ellipse of length $a$. The pair of points farthest apart in a direction perpendicular to the major axis determined the length of the minor axis ($b$). Area was calculated as: $\text{area} = \frac{1}{2} \pi ab$. Use of ellipses to describe home ranges has the disadvantages that it is sensitive to outlying points and does not provide any sort of frequency distribution of spatial use. The method is, however, sufficient for the present study as I am
Fig. 11. Process of calculating elliptical home ranges for actual as well as randomized data (data shown are idealized).
primarily concerned with determining if lizard movements are nonrandom and therefore require only a relative measure of home range.

Randomization was performed in the following manner. First, the set of vectors which connect the actual coordinates for a lizard was determined. Each vector was then decomposed into its X and Y components and each component was randomly assigned a sign (+ or -). A new sequence of vectors was constructed by randomly choosing (without replacement) from the set with randomly assigned signs. Finally, coordinates derived from the random set of vectors were used to calculate the area of an enclosing ellipse, as described above. Note that the order of this set of vectors is random, and the direction of each vector in that set is randomly chosen from four possibilities (0°, 90°, 180°, or 270° from the direction of the original vector), but the length of each vector is the same as the length of the original vector from which the random vector was derived. This latter restriction insures that the distances moved by "random lizards" are of realistic magnitude.

An additional test was performed to dispense with the possibility that a simple error in the computer program might create a consistent bias. For each lizard, one random set of coordinates was treated to a subsequent set of randomizations as though it were a real data set. Any bias due to the randomization process should appear in the distribution of areas resulting from double randomization of vectors as well as in that from single randomizations.
Home Range Overlap

The number of times the paths of two lizards cross provides a reasonable relative measure of the overlap of their home ranges. In this study, I counted the number of inter-lizard intersections of between-capture line segments (each segment connecting one capture with the next capture location of a particular lizard) in the actual data and compared that number with the number of intersections that would be expected if home ranges were placed at random (Fig. 12). Fewer intersections in the analysis of the actual data would indicate that horned lizard home ranges overlap less than expected by random and that the distribution of home ranges tends towards uniform. Analysis was limited to data from 1980 and 1981 (the years in which radiotracking was performed); the data from each year were examined separately.

Randomization was performed in the following manner:

1. For each lizard, each year, a center of range (COR; simply the center of a rectangle that bounds the capture points) was calculated. Not meant to be a measure of activity, the COR simply serves as a reference point. For each lizard, the distance and direction from each capture point to the COR were calculated.

2. The entire study site was divided into 14 subequal areas and the number of COR's in each area determined. The proportion of actual COR's in each of these 14 areas was used as the probability that a random COR would be placed in that area. This process was necessary to reduce the effects of heterogeneity in habitat and sampling effort (see below and Fig. 10).
Fig. 12. Process of determining degree of home range overlap for actual as well as randomized data (data shown are idealized).
(3) COR's were assigned randomly to one of the 14 sub-areas, in the proportions determined by (2) above, then randomly assigned coordinates within that sub-area.

(4) New coordinates were calculated for each capture point of a lizard relative to the randomly placed COR of that lizard, using the direction and distance from the original COR.

(5) In the same manner as described above, the number of inter-lizard intersections of between-capture segments was determined for this randomized set of locations.

(6) The randomization was performed a total of 100 times to produce a random distribution against which the number of intersections of the actual location data could be compared.

The test measures overlap independently of the characteristics of home range. By randomly placing the COR, then moving the "cloud of locations to that COR, the dispersion of location points of any one lizard remains constant, only the placement of the COR changes.

It should be noted that this test is a very conservative one. The amount of time I spent searching for lizards varied from area to area within the study site. In addition, it is probable that not all areas provide equally suitable habitat for horned lizards. These factors will lead to an apparent (in the case of heterogeneous sampling effort) or real (in the case of heterogeneous habitat) clumping of observed home ranges. Therefore, even if the observed home ranges are more dispersed within suitable habitat than would be expected by random placement, it would be difficult to show it with this test, in which randomization of COR's will disperse home ranges throughout the study area as though
sampling effort and favorable habitat are homogeneous. Partial compensa-
tion for this bias was provided by artificially dividing the study into
14 sub-areas and holding the frequencies of home ranges within each of
those sub-areas the same as it was for the real data (Fig. 10).

Results

Home Ranges

The horned lizards studied here occupied areas much smaller than
would be expected if their movements were random (Table 4). Figure 13
shows that very few home range areas derived from a randomization of
location data are less than home range areas calculated from actual
location data; for 13 lizards, not a single random home range was smaller
than the actual home range. If these lizards moved randomly, the
distribution of proportions would be spread fairly evenly across the
possible proportions, as shown in the lower half of Fig. 13. The overall
increase in home range size caused by randomizing location data was 94%.
For P. cornutum females, this increase was 48%; for males, 115%. For
P. modestum females the increase was 103%; for males, 135%. Figure 14
compares the areas calculated from the actual location data to the average
area resulting from 100 randomizations of that data for P. cornutum and
P. modestum. For each lizard, the area calculated from the actual data
was paired with the average random area in a Wilcoxon matched-pairs
signed-rank test (one-tailed, Siegel 1956). The probabilities that the
differences between real and average random areas are due to chance are
as follows: \[ .015 < p < .05 \] (Wilcoxon test statistic, \( T = 19, \)
\( N = 13 \)) for P. cornutum females and \( p = .005 \) for males \( (T = 5, N = 10) \);
## TABLE 4
Home Range Characteristics of Horned Lizards
Tagged with Radioactive Tags or Radiotransmitters

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\[s = 12205.0 \quad 16448.8\]
TABLE 4—Continued

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<td>605 27 22</td>
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<td>5051</td>
<td>n.d.</td>
<td>18 July 80-31 July 80</td>
<td>7</td>
<td>62.6 13.0</td>
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<td>4053</td>
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<td>28 Aug. 80-11 Sept. 80</td>
<td>12</td>
<td>81.4 40.6</td>
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<td>0520</td>
<td>61</td>
<td>10 Aug. 80-28 Sept. 80</td>
<td>36</td>
<td>78.3 33.7</td>
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<td>53</td>
<td>15 Aug. 80-24 Sept. 80</td>
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<td>101.9 27.4</td>
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<td>4898 124 2</td>
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<tr>
<td>0245</td>
<td>43</td>
<td>25 June 81-16 July 81</td>
<td>10</td>
<td>69.5 37.8</td>
<td>2067</td>
<td>3568 73 9</td>
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<tr>
<td>3111</td>
<td>49</td>
<td>10 July 81-22 July 81</td>
<td>12</td>
<td>110.4 27.0</td>
<td>2343</td>
<td>3993 70 5</td>
<td>10</td>
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<tr>
<td>2025</td>
<td>64</td>
<td>24 May 81-6 June 81</td>
<td>13</td>
<td>94.9 13.6</td>
<td>1012</td>
<td>1739 72 7</td>
<td>5</td>
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\[
\bar{X} = 1355 \\
\bar{s} = 902.9
\]

*value given is average for the span observed. n.d.=no data.*
Fig. 13. Comparison of observed home ranges to home ranges derived from random data. If horned lizards moved randomly, the distribution for actual observations would resemble that in the lower half of the figure.
Fig. 14. Histograms depicting areas of observed home range areas and areas of home ranges derived from random data. (a) *Phrynosoma cornutum*.
Fig. 14.--Continued. (b) P. modestum.
for \textit{P. modestum}, p < .005 for both males (T = 5, N = 15) and females (T = 0, N = 11).

Averages, as presented above, obscure inter-individual variation, which is substantial in this case. The effect of randomizing coordinates varied from a 57% decrease to a 549% increase in the area of the calculated home range (Table 4). This indicates that, although as a group \textit{P. cornutum} and \textit{P. modestum} do actively restrict their home ranges, some individuals do not tend to remain in a limited area.

Home Range Overlap

For the 1981 data set, randomization of COR's led to an increase in the number of intersections of between-capture segments. This indicates that, although some overlap of home ranges occurred, the overlap was less than would be expected if the locations of the home range of individual horned lizards are independent of the locations of other horned lizards. The number of intersections for the real data set, 448, was lower than the number of intersections for 93 of the randomizations (Fig. 15, Table 5). Thus the probability of getting that few intersections by chance alone is roughly 0.07, a number very close to the conventional cutoff of 0.05.

For the 1980 data, there was essentially no difference between the observed overlap and that expected. Fifty randomizations had a higher number of intersections, 50 had a lower number.
Fig. 15. Comparison of observed home range overlap to overlap of home ranges derived from random data. -- The number of inter-individual intersections of line segments drawn between lizard captures is used as a relative measure of overlap (see Fig. 12 and text). Mean shown is of all 100 randomizations.
### TABLE 5
Home Range Overlap: A Comparison of Observed Overlap With Random Expectation

<table>
<thead>
<tr>
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<tr>
<td></td>
<td>Crossed Did Not</td>
<td>Crossed Did Not</td>
<td>Crossed Did Not</td>
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<td>All lizards</td>
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<td>609.0 106405.3</td>
<td>448 66187</td>
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<td>P.c. f vs. P.c. f</td>
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<td>23.6 2695.4</td>
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<td>81.1 8871.1</td>
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<td>P.c. m vs. P.c. m</td>
<td>10 1094</td>
<td>13.5 1090.5</td>
<td>44 5882</td>
<td>106.7 5819.3</td>
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<tr>
<td>P.c. f vs. P.m. f</td>
<td>121 25137</td>
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<td>19.6 2840.4</td>
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<tr>
<td>P.c. f vs. P.m. m</td>
<td>72 13214</td>
<td>59.5 13226.5</td>
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<td>93.4 10891.6</td>
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<tr>
<td>P.c. m vs. P.m. f</td>
<td>44 7914</td>
<td>63.6 7894.4</td>
<td>13 3111</td>
<td>29.5 3094.5</td>
</tr>
<tr>
<td>P.c. m vs. P.m. m</td>
<td>39 4147</td>
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<td>156.1 11842.9</td>
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<td>P.m. f vs. P.m. f</td>
<td>124 13099</td>
<td>104.0 13119.0</td>
<td>0 692</td>
<td>2.8 689.2</td>
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<tr>
<td>P.m. f vs. P.m. m</td>
<td>106 15369</td>
<td>99.4 15375.6</td>
<td>12 6893</td>
<td>54.9 6850.1</td>
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<tr>
<td>P.m. m vs. P.m. m</td>
<td>24 3532</td>
<td>18.9 3537.1</td>
<td>53 12373</td>
<td>149.0 12277.0</td>
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<tr>
<td>All P.c. vs. all</td>
<td>76 23992</td>
<td>104.7 23954.3</td>
<td>82 17523</td>
<td>211.5 17385.8</td>
</tr>
<tr>
<td>All P.m. vs. all</td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>P.m.</td>
<td>254 32000</td>
<td>222.3 32031.7</td>
<td>65 19958</td>
<td>206.8 19816.2</td>
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<td>Male vs. male</td>
<td>73 8773</td>
<td>64.0 8782.0</td>
<td>293 30058</td>
<td>411.9 29939.1</td>
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<tr>
<td>Female vs. female</td>
<td>272 47774</td>
<td>256.9 47789.1</td>
<td>24 6247</td>
<td>46.1 6224.9</td>
</tr>
</tbody>
</table>

Note.—The number of intersections given for randomly derived data is the mean for 100 randomizations.

See text and Fig. 12.
Discussion

Home Ranges

The individual *P. cornutum* and *P. modestum* in this study typically traversed areas much smaller than would be expected if their movements were random. Such behavior will tend to limit their foraging to a relatively restricted subpopulation of ant colonies. Unfortunately, these results do not provide an absolute test of condition (1) (evolution to prudence requires repeated exploitation of a limited subpopulation of prey) because our knowledge of the horned lizard-ant system is insufficient to dictate just how restricted the exploitation of ant colonies by horned lizards must be. However, the results presented here do indicate that condition (1) is much more likely met than if horned lizards moved at random.

Few previous data exist concerning the use of space by horned lizards. Lowe (1954) concluded that *Phrynosoma solare* are extremely sedentary, and may be found in the same area for several years. Baharav (1971) concurred, stating that *P. solare* often remained in relatively small home ranges. Pianka and Pianka (1970) concluded, based on their finding that a number of fecal pellets are often found in a small area, that *Moloch horridus* (an Australian agamid, ecologically very similar to *Phrynosoma*) is sedentary.

On the other hand, Tanner and Krogh (1973) concluded from their low recapture success that *P. platyrhinos* does not have a limited home range. Reliance on recaptures, however, may lead to false conclusions. Unlike some other iguanid lizards, horned lizards are not conspicuous
animals. They seldom sit on exposed perches and, instead of running when approached by an observer, they tend to remain immobile, relying on their cryptic coloration (Milne and Milne 1950, Pianka and Parker 1975, Sherbrooke 1981). Therefore, they are often extremely difficult to locate visually. By using radioactive tags and radiotransmitters, I was able to find lizards that otherwise would have escaped notice. Through repeated observations I was able to show that these lizards do not move randomly over the landscape.

Home range has been defined, in a modification of Burt (1943) by Jewell (1966), as "... the area over which an animal normally travels in pursuit of its routine activities." Previous studies of home range in lizards (e.g., Milstead 1957, Tinkle et al. 1962, Jorgensen and Tanner 1963, Bostic 1965, Ferner 1974, Simon 1975, Krekorian 1976, Fitch and von Achen 1977, Ruby 1978) and other vertebrates (e.g., Adams and Davis 1967, Speth 1969, Zach and Falls 1978, Mares et al. 1980, Getty 1981) have assumed that if, for example, the observer can draw a set of line segments around the exterior-most capture points (thereby constructing a convex polygon; Southwood 1966) or can describe the points as a probability density function (Dice and Clark 1953, Jorgensen and Tanner 1963), then the organism has a home range. However, even a randomly moving water molecule does not have an equal probability of moving to any possible point in the universe; it will appear to remain in a relatively restricted area. If we made a number of sightings on such a molecule, we would be able to construct a convex polygon from the outermost of those points, or a probability density function that describes the distribution of those points.
The description of a home range for a randomly moving water molecule (or horned lizard) has little biological meaning. Home ranges that result from a nonrandom utilization of space should be distinguished from those resulting from a randomly moving organism. In order to determine if an organism actually employs a strategy of movement that restricts it to a limited area, it is necessary to have a random "yardstick" against which the actual home range can be compared. This type of comparison allows the observer to establish beyond a reasonable doubt, as I have done in this study, whether or not the organism studied has a circumscribed home range that results from it actually attempting to remain in an area.

Cooper (1978) states the problem well when he asks, "If an animal wanders during the study interval, does it lack a home range or is its home range the total area covered?" He presents a tests of the presence of nonrandom home range that compares the rate of change in area occupied with a constant, that constant gauged to the variability of the system. This approach is, to a degree, arbitrary; how different must the two values be before the organism is judged to not have a home range? Perhaps through randomizations, such as those performed in the present study, the rate of change in the area occupied by a randomly moving animal can be determined and compared with actual rates of change.

Mares et al. (1980) present a method for determining the number of sightings of an animal necessary to accurately determine the area of a home range. The method uses a sampling effort curve in which the percent change in home range area due to the addition of another capture is plotted against capture number. At low capture numbers, addition of
another capture substantially increases the calculated home range. As more captures are added to the analysis, the percent-change approaches zero. Two criteria are applied in determining whether a given number of captures is sufficient for describing home range size: (1) the percent-change for that number and higher numbers must be statistically indistinguishable from zero; and (2) the slope of the percent-change vs. capture line must be zero.

Figure 6 presents the sampling effort curves for the actual location data and for randomizations of that data. Both curves approach zero percent-change with increasing number of captures. The curves are, in fact, statistically indistinguishable (Kolmogorov Smirnov test: \( p > 0.1; \) Siegel 1956).

Considering the curve for real data first, zero is included in the 95%-confidence interval of percent-change for capture #25 and higher. For this same interval, the slope of percent-change vs. capture number curve is indistinguishable from zero \( (r = 0.001, p \gg 0.05) \). This indicates that 25 captures are sufficient to accurately define the home range of \( P. \ cornutum \) and \( P. \ modestum \), using the methods of this study.

The random curve yields similar results. Zero is included in the 95%-confidence interval of percent-change at captures #34 and higher; the slope of the curve for this interval is indistinguishable from zero \( (r = .469, p > 0.05) \). Thirty-four captures is sufficient to accurately describe the home range of a lizard that moves randomly. It therefore appears that the sampling-effort curve technique of Mares et al. (1980) does not quantitatively distinguish between home ranges due to random
Fig. 16. Sampling-effort curve for home ranges.--The effect (measured in %-change in area) of adding a capture to home range area calculations, determined for each capture. Curve for real data depicts the means for all lizards studied. Random data curve depicts the grand means for all lizards studied, and includes 10 randomizations for each lizard. Numbers immediately below the graph indicate the numbers of lizards with the corresponding number of captures.
movements and home ranges resulting from a strategy in which movements are restricted to a particular area.

It is, of course, reasonable to assume that an organism which has a burrow or nest will remain in the area of that burrow or nest. Other organisms, such as non-breeding birds and ungulates, which have no established burrow or nest, have less reason to remain in an area. In particular, there appears to be no scarcity of suitable shelter for horned lizards (Tanner and Krogh 1973). For these animals, it is likely that the importance of knowledge of resource locations or escape sites are the reasons an individual maintains fidelity to an area.

Home Range Overlap

In order for a long-term foraging strategy to evolve in horned lizards, not only must horned lizards have home ranges, but those home ranges must be relatively exclusive (condition #2). I tested the prediction that overlaps among the home ranges of individuals are less than would be expected if those home ranges were placed at random with respect to one another. In only one of the years tested was there a significant (p = 0.07) difference between observed home range overlap and overlap of randomly placed home ranges. However, as mentioned earlier, this test is a conservative one--because the process of randomization disperses home ranges into areas that are unsuitable habitat or areas that were sampled relatively little, it is difficult to achieve the result that randomization will lead to an increase in home range overlap. Due to the conservative nature of this test, I regard the significant trend in the 1981 data as sufficient grounds to reject
the notion that horned lizard home ranges are located randomly with respect to one another and that the overlap of home ranges is as great as would be expected if the home ranges were placed at random.

It is obvious, however, that home ranges are not absolutely exclusive: There were a substantial number of inter-lizard intersections in both years. As with condition (1), a definitive judgement on condition (2) cannot be made until the dynamics of the horned lizard-ant system are known well to determine to what degree home ranges must be exclusive in order for a prudent strategy to evolve.

Exclusiveness in home range can result from two processes, either from defense of the home range (territoriality) or from a low density of lizards coupled with there being an advantage in avoiding overlap. I will discuss these processes in turn.

Based largely on the conclusion of Lynn (1965) that *Phrynosoma* shows relatively little sophistication in intra-individual display, the reviews of Carpenter (1967) and Stamps (1977) labeled *Phrynosoma* as an exception among the normally territorial iguanid lizards. Stamps (1977) felt that the long distance between individuals and the lack of use of a perch would make home range defense disadvantageous. However, the possibility of horned lizards exhibiting defense of a home range should not be dismissed merely because their display is simple.

Brown (1964) theorized that two requisites must be met for territorial behavior to evolve. First, there must be intraspecific competition for a limiting resource (e.g., space or food). Second, that resource must be economically defensible; that is, the benefits gained from defense must outweigh the costs of defense. For horned lizards,
it is unknown whether any resources are limiting. As this study is concerned with the evolution of foraging strategy, let us assume for the sake of argument that food is limiting. For territoriality to have evolved in horned lizards, the benefits gained from defending a subset of ant colonies against the depredations of other horned lizards must be larger than the costs associated with that defense. Because horned lizards occupy large home ranges but move slowly and use few vantage points, it seems inconceivable that horned lizards could defend their home ranges enough to make them absolutely exclusive. Absolute exclusiveness is not required, however; any level of defense would be favored by natural selection if it results in a net gain. Therefore, the head bobbing displays exhibited during encounters (Lynn 1963; Whitford and Whitford 1973; Tollestrup 1981) may be the tools of a low level of home range defense. Encounters may not be sought out, but may be utilized when they occur to enforce a significant, but not absolute degree of exclusiveness.

Several factors may lead horned lizard individuals to voluntarily avoid the home ranges of other individuals. For instance, ant colonies in areas occupied by horned lizards are more likely to have been recently harvested and therefore less likely to be available to subsequent harvesting than colonies in unoccupied areas. Horned lizards that avoid the home ranges of others avoid areas of reduced resource availability. Ability to employ a strategy of mutual avoidance would require that horned lizard densities are not limited by resource availability but are low due to other factors, such as predation.
It would be difficult to distinguish between a low level of home range defense and exclusiveness that resulted simply from low density coupled with an advantage of avoiding home range overlap. How can an observer determine whether horned lizards use encounters to convince other lizards to stay away or to indicate to themselves that they should go no further?

Conclusion

The results of the present study indicate that horned lizards tend to possess circumscribed, exclusive home ranges. Although this strategy of spatial utilization would potentially permit horned lizards to evolve a long term foraging strategy, that conclusion is, in a sense, purely academic, in view of the conclusion of Munger (1982d). That study examined condition (3), that colonies of Pogonomyrmex desertorum are a resource that responds favorably to variation in harvesting intensity. Colonies were subjected to several levels of artificial harvesting in an attempt to determine if reduction of harvesting intensity could result in an increase in long term yield. In none of the five experiments performed was such a result obtained, leading to the conclusion that horned lizards do not so benefit from an attempt to harvest colonies of P. desertorum prudently.

Even assuming that such a conclusion is valid, the characteristics of horned lizard home ranges described here obviously affect horned lizards in several important ways other than by simply allowing prudence to evolve. For example, fidelity to an area allows the lizard to learn the location of shelter sites, hiding places, and ant colonies, as well
as to keep track of the reproductive status of potential mates, and therefore makes for more efficient use of environmental resources.

**Summary**

Two aspects of the use of space were studied for two species of horned lizard: (1) Do they utilize limited home ranges or do they wander randomly? (2) Is use of home ranges exclusive? Both questions are important in considering long-term foraging strategies of horned lizards. Repeated contacts with a discrete subpopulation of prey (as would occur with a limited home range) and relatively exclusive use of that subpopulation (as would occur with non-overlapping home ranges) are requisites for the evolution of a long-term, prudent strategy.

Forty-nine individuals were tagged with radiotransmitters or radioactive tags. Their movements were compared with a computer generated random model. It was found that horned lizards typically occupy areas much smaller than they would if they moved randomly, that is, they have a limited home range. "Home ranges" calculated from location points of randomly moving lizards share several characteristics with the limited home ranges of lizards not moving randomly. Randomly derived location points can be surrounded by a convex polygon, or characterized by a probability density function, and lead to a percent change in area vs. capture number curve very similar to that shown by lizards not moving randomly. Therefore, none of these techniques distinguishes between home ranges that result from non-random utilization of space and those that result from a randomly moving organism.
Observed home range overlap of horned lizards was compared with the overlap that would be expected if home ranges were located at random with respect to one another. In one of the years tested, reduced overlap was detected. Because of the conservative nature of the test used, it was concluded that home range overlap among individual horned lizards is reduced below that expected from random placement. Reduced home range overlap can result from territorial defense or from mutual avoidance.
CHAPTER 4

OPTIMAL FORAGING?: PATCH USE BY HORNED LIZARDS

Introduction

All food items are not alike, nor are they distributed homogeneously. A forager could be insensitive to this heterogeneity, taking food items irrespective of their quality and foraging in areas without regard to the concentration of food. Alternatively, if a forager could base decisions of which food items ("prey" if the forager is a predator) to consume on the net energetic return of those food items or could alter its spatial use so as to concentrate its foraging effort in areas where food items are most concentrated, it could potentially increase its rate of net energy intake while foraging. If the rate of energy intake is important in determining the overall Darwinian fitness of an individual, then natural selection should favor those individuals that base their foraging decisions on the quality and distribution of prey. These ideas form the basis of a rapidly growing body of theory, reviewed by Pyke et al. (1977), which is collectively known as optimal foraging theory.

If food items (hereafter called prey) are concentrated in relatively discrete areas, these areas are called patches. Pyke et al. (1977) present three types of decisions that can be made by a forager faced with patchily distributed resources:

1. Which patches should be foraged in?
2. What route should be followed within a patch?
(3) When should a patch be abandoned in favor of searching for other patches?
Subsequent discussion focuses on the third question.

Unless the renewal of prey following harvesting is instantaneous, foraging will deplete the number of prey within a patch, gradually reducing the rate at which prey can be harvested (Charnov et al. 1976). At some point, the patch will become so depleted the predator should move elsewhere. Krebs et al. (1974) and Charnov (1976) developed models which predict to what degree a predator should deplete a patch before leaving. Recently, McNair (1982) attempted a synthesis of these models. Several predictions regarding the decision of when to leave a patch have been derived by these authors.

One set of predictions concerns the threshold giving-up time (GUT; defined as the time since the last capture of a prey item that a forager will wait before abandoning a patch). First, the GUT should be shorter for patches within a relatively good habitat than for patches within relatively poor habitat. That is, a forager should persist within a patch longer if its expected return outside of that patch is lower (Krebs et al. 1974). Second, Krebs et al. (1974) predicted that GUT's should be equal among patches within a habitat. The basis of this prediction has been criticized by McNair (1982) who derived an alternative: GUT's should be longer in better patches.

A second set of predictions will be tested in this study. First, a forager should leave a patch when the instantaneous rate of capture within that patch (the marginal capture rate) has fallen to the overall average rate of harvest for the habitat as a whole (the overall habitat
rate). Calculation of the overall habitat rate includes not only the harvest from patches but also the travel time between patches. Thus the forager should leave a patch if it could do as well, on the average, elsewhere; further exploitation of the patch would decrease its rate of return below the average. This treatment is termed the marginal value theorem (Charnov 1976).

Second, if an organism is foraging optimally and if one patch type can be judged to be of uniformly better quality than another, then the total time spent in a patch (residence time) should be longer and the total harvest from a patch should be higher in the better of two patch types. These latter predictions are from McNair (1982) although they were not presented there in an empirically testable form.

In the present study I test these predictions for horned lizards foraging on desert ants. Ants are a common and predictable prey of horned lizards in a number of arid areas (Munger, pers. obs.), and are consumed in large quantities (Pianka and Parker 1975, and refs. therein; Whitford and Bryant 1979; Rissing 1981; Shaffer and Whitford 1981).

The availability of ants is strongly heterogeneous. High densities occur at the entrances to underground colonies, where individual worker ants begin and end foraging forays, and on pathways used by ants traveling between a colony entrance and a concentrated resource (Baharav 1971, Davidson 1977, Rissing 1981, Shaffer and Whitford 1981). Horned lizards use both of these patch types (colony entrances and columns of foraging ants) as well as ants found while traveling between these patches and while engaged in other activities such as basking (Baharav 1971; Whitford and Bryant 1979; Shaffer and Whitford 1981; Munger, pers.
obs.). Individual ants are captured with a quick flick of the tongue and are swallowed whole; handling time is minimal.

Patches of ants at colony entrances decrease in quality as a result of predation by horned lizards. This is not only a consequence of the loss of workers from a finite pool, but also may be due to workers ceasing surface activity in response to the loss of colony members (Gentry 1974, Whitford and Bryant 1979, Rissing 1981, Munger 1982, 1983d). Because of the small size of individual workers, a large number of ants must be eaten to satisfy a horned lizard. Thus cumulative harvest vs. time functions for a horned lizard eating ants will more closely approximate continuous functions (assumed by the marginal value theorem) than they would for large prey items. In addition, colonies of the ant most common at the study site, *Pogonomyrmex desertorum*, are relatively small. The number of ants that can be harvested from a single colony in a foraging bout appears to be insufficient to cause satiation, at least for the larger horned lizards at the study site. Therefore several colonies are often visited in one day.

The patchiness of ants as a resource, the ease with which horned lizards can be observed, and the small but particulate nature of ants all make this an excellent system for the study of optimal patch use.

**Materials and Methods**

**Study Site**

This work was carried out 6.5 km E, 2 km N of Portal, Cochise Co., Arizona, in an area of relatively homogeneous Chihuahuan desertscrub, at an elevation of 1,330 m. The study site is on a gently sloping
bajada, about halfway between the base of the Chiricahua Mountains and the center of the San Simon Valley. The substrate is generally a sandy loam with occasional rocky areas, especially near washes. The principal perennial vegetation consists of *Flourensia cernua*, *Gutierrezia* sp., *Ephedra trifurca*, and *Prosopis juliflora*. The spaces between these perennials are generally bare, except during both the winter and summer rainy seasons when a rich community of annual plants may develop. See Munger (1982, 1983b) for a more complete description of the study site.

The Organisms

*Phrynosoma cornutum*, the Texas horned lizard, and *P. modestum*, the round-tailed horned lizard, have similar ranges, which extend from SE Arizona into Texas, and S into Mexico (*P. cornutum* extends N to Kansas) (Stebbins 1966; Sherbrooke 1981). *Phrynosoma cornutum* measures 69 mm snout-vent length at attainment of sexual maturity (Pianka and Parker 1975) and may reach 114 mm (females), or 94 mm (males) with a corresponding span in body weight of 25-90 g (Munger, unpubl. data). *Phrynosoma modestum* measures 50 mm at sexual maturity (Pianka and Parker 1975) and may reach 67 mm (females), or 60 mm (males) with adult weights ranging from approximately 6-17 g (Munger, unpubl. data). Both lizards are relatively flat-bodied and slow-moving. They rely on cryptic coloration to avoid detection, and on horns and scaliness to deter attack (Pianka and Parker 1975; Sherbrooke 1981). Horned lizards are active April through September; the remaining months are spent underground (Munger, unpubl. data).
Two ant species comprise most of the diet of these lizards on the study site (Table 1). *Pogonomyrmex desertorum* occurs in colonies of 200-400 individuals (Whitford and Bryant 1979). The workers emerge from the colony entrance and forage individually for seeds and insect matter (Davidson 1977). They appear to be similar to *P. californicus*, a preferred prey species of *Phrynosoma platyrhinos*, in colony size, worker foraging behavior, and liability to horned lizard predation (Rissing 1981). Two species of *Myrmecocystus* (depilis and mimicus; these cannot easily be distinguished in the field and were lumped in subsequent considerations) forage extensively on plant exudates as well as on insect matter. Colonies contain approximately 1,900 individuals (Shaffer and Whitford 1981).

**Observations**

A total of 26 horned lizards (seven *P. cornutum* females, five *P. cornutum* males, seven *P. modestum* males, seven *P. modestum* females) were observed, each for a full day, to obtain an accurate description of their foraging behavior. Most of the lizards had been tagged with radiotransmitters or radioactive tags (Munger 1983a) for several days previous to the observations; this facilitated location of the lizard on the day of observation. Untagged lizards were typically found during the late afternoon of the day prior to scheduled observations, followed until they sought shelter for the night, then observed for the following day. An attempt was made to begin all observations before the lizards became active in the morning. Observations continued until the lizard sought shelter from the hot midday sun, were recommenced as it became
cooler or cloudy in the afternoon, and were discontinued when the lizard became inactive at night.

Lizards were watched, by naked eye or with 7x35 binoculars, from distances of 2-20 m, this distance depending on the landscape and the movements and temperament of the lizard. A portable blind, consisting of a 0.8 m wide, 1.2 m high piece of 9.5 mm plywood with a 75x200 viewing hole, was typically used to hide the observer from the lizard's view; the blind was not used on several occasions when the lizard seemed more wary of the blind than of the observer. Prey items usually could be identified through binoculars. In those cases where the prey item was not easily identifiable, an educated guess as to its identity was made, based on the apparent size of the item and the relative proportions of various prey species in the diet of the observed lizard on that day. A number of individuals of each prey species were weighed after oven drying to allow estimation of the actual mass of prey eaten.

Observations were recorded on a portable cassette tape recorder (Radio Shack model CT-48). During most of the day, brief voice descriptions of prey items taken, behaviors and movements were recorded along with the time to the nearest minute. During foraging bouts at colonies, the tape recorder was left running and each event of prey consumption recorded. This provided a second by second record of the times at which prey items (ants) were harvested at a patch (ant colony entrance), and allowed the construction of cumulative harvest vs. time curves.

In order to determine the marginal capture rate, a function of the form
was fitted to the data (where \( y \) is the cumulative number of ants harvested at the patch, \( x \) is the time spent at that patch, and \( a \) and \( b \) are fitted parameters) using a non-linear regression program (BMDP3R; Dixon and Brown 1979). The derivative of this function with respect to \( x \) is of the form
\[
abe^{-ax}
\]
and is equivalent to the instantaneous rate of harvest at time \( x \). Substitution of the time when the lizard abandoned the colony for \( x \) in equation (2) yields the instantaneous rate of capture at the moment the lizard left the colony (hereafter termed the rate at departure; see example, Fig. 17).

An estimate for the overall habitat rate was calculated by dividing the total mass of prey taken for the day of observations by the time spent foraging. Time spent foraging at colonies, moving between colonies, or sitting near a pathway from which ants were harvested was considered to be "foraging time." Time spent basking in the sun, sitting in the shade, interacting with other lizards, and performing other activities during which potential prey were ignored was not considered to be foraging time. Note that although the calculation of overall habitat rate included ants and other prey harvested in areas away from as well as at colony entrances, I calculated rates at departure for only those patches that occurred at colony entrances.
Fig. 17. Method used to determine the marginal capture rate at the moment a horned lizard terminated its foraging bout at an ant colony. Lizard 1010, a *P. cornutum* female, is depicted. A negative exponential function (see text) is fitted to the cumulative harvest vs. time data (for clarity, every tenth point is shown in this figure). The slope of the line tangent to the function at any moment is equivalent to the instantaneous rate of capture (marginal capture rate) at that moment, and is calculated by taking the derivative of the function with respect to time. The rate at departure is calculated by evaluating the derivative at the moment the lizard left the colony, yielding a rate in ants per time. This value was multiplied by the dry weight per ant to yield the values in Tables 7 and 9, and Fig. 19.
Slope = $a b e^{-a x} = 0.0027$

= instantaneous rate of capture at $T_{\text{leave}}$

$y = 118.6 (1 - e^{(-0.00084)x})$

Lizard left colony

TIME AT COLONY (sec)

CUMULATIVE NUMBER OF ANTS TAKEN AT COLONY
Results and Discussion

General Foraging Behavior

The horned lizards observed took a variety of prey items, but concentrated on *P. desertorum* and *Myrmecocystus* spp. (Table 6). *Phrynosoma cornutum* individuals harvested the majority of their prey at or near colony entrances. This contrasts with the result of Whitford and Bryant (1979) who observed that *P. cornutum* took a few prey at colony entrances. *Phrynosoma modestum* tended to harvest ants in areas not near colony entrances, an observation which agrees with those of Shaffer and Whitford (1981). There was a wide variance in the number of colonies visited each day by individual horned lizards (Fig. 18). *Phrynosoma cornutum* females made the most use of patches at colony entrances, *P. modestum* individuals the least.

Rate at Departure vs. Overall Habitat Rate

The marginal value theorem predicts that a forager should leave a patch when the marginal capture rate at that patch has fallen to the average rate of capture for the habitat as a whole. A plot of the rate at departure for each colony against the overall habitat rate experienced by the foraging lizard should therefore yield a regression with a slope of one. Such a relationship appears to hold for horned lizards: The slope is significantly greater than zero (p = .007) and a slope of one lies within the 95% confidence intervals of the slope (.298 to 1.775; see Fig. 19, Table 8). Lizards that are experiencing higher overall habitat rates leave colonies when the marginal capture rate at that
TABLE 6
Total Prey Items Taken by Individual Horned Lizards During Observations

<table>
<thead>
<tr>
<th>Lizard #</th>
<th>Harvested at Colony</th>
<th>Harvested Away From Colony</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. cornutum females</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0033 (1-6)</td>
<td>156</td>
<td>28(29)</td>
</tr>
<tr>
<td>0033 (7-10)</td>
<td>121</td>
<td>8(7)</td>
</tr>
<tr>
<td>0504</td>
<td>23</td>
<td>3</td>
</tr>
<tr>
<td>0003</td>
<td>171</td>
<td>1</td>
</tr>
<tr>
<td>1010</td>
<td>113</td>
<td>5</td>
</tr>
<tr>
<td>0023</td>
<td>201</td>
<td>14</td>
</tr>
<tr>
<td>0015</td>
<td>275</td>
<td>16</td>
</tr>
<tr>
<td>Totals</td>
<td>889</td>
<td>14</td>
</tr>
</tbody>
</table>

P. cornutum males
<table>
<thead>
<tr>
<th></th>
<th>Harvested at Colony</th>
<th>Harvested Away From Colony</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004</td>
<td>79</td>
<td>26(4)</td>
</tr>
<tr>
<td>2015</td>
<td>8(1)</td>
<td>27(3)</td>
</tr>
<tr>
<td>4004 (nothing eaten)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0530</td>
<td>36</td>
<td>39</td>
</tr>
<tr>
<td>1051</td>
<td>1(10)</td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td>115</td>
<td>39</td>
</tr>
</tbody>
</table>
TABLE 6--Continued

<table>
<thead>
<tr>
<th>Lizard #</th>
<th>Harvested at Colony</th>
<th>Harvested Away From Colony</th>
</tr>
</thead>
<tbody>
<tr>
<td>5051</td>
<td>24(1)</td>
<td></td>
</tr>
<tr>
<td>4055</td>
<td>9(1)</td>
<td>46(22)</td>
</tr>
<tr>
<td>0310</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>0403</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1033</td>
<td>13</td>
<td>12</td>
</tr>
<tr>
<td>3011</td>
<td>7(1)</td>
<td>1</td>
</tr>
<tr>
<td>0520</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td>21</td>
<td>50</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Harvested at Colony</th>
<th>Harvested Away From Colony</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. modestum males</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2035</td>
<td>13</td>
<td>46(8)</td>
</tr>
<tr>
<td>4034</td>
<td>(nothing eaten)</td>
<td></td>
</tr>
<tr>
<td>2031</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>1014</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>4030</td>
<td></td>
<td>7</td>
</tr>
<tr>
<td>2003</td>
<td>26</td>
<td>1</td>
</tr>
<tr>
<td>2040</td>
<td>11</td>
<td>1</td>
</tr>
<tr>
<td>Totals</td>
<td>44</td>
<td>13</td>
</tr>
</tbody>
</table>
TABLE 6--Continued

Note.--Entries are the number of individuals of a particular species eaten by a lizard during the day it was observed. Numbers in parentheses represent ants not positively identified, but counted in that category on the basis of the apparent size of the prey item and the frequencies of identified prey items in the diet.

Codes:

<table>
<thead>
<tr>
<th>Code</th>
<th>Species Description</th>
<th>Approximate dry weight in mg.</th>
</tr>
</thead>
<tbody>
<tr>
<td>P.d.</td>
<td><em>Pogonomyrmex desertorum</em></td>
<td>2</td>
</tr>
<tr>
<td>P.m.</td>
<td><em>P. maricopa</em></td>
<td>2.5</td>
</tr>
<tr>
<td>M.spp.</td>
<td><em>Myrmecocystus depilis</em> or <em>M. mimicus</em></td>
<td>1</td>
</tr>
<tr>
<td>N.c.</td>
<td><em>Novomessor cockerelli</em></td>
<td>3.5</td>
</tr>
<tr>
<td>Ph.spp.</td>
<td><em>Pheidole sitarches</em>, <em>Ph. xerophila</em>, <em>Ph. desertorum</em></td>
<td>0.006</td>
</tr>
<tr>
<td>I.p.</td>
<td><em>Iridomyrmex pruinosis</em></td>
<td>0.006</td>
</tr>
<tr>
<td>C.i.</td>
<td><em>Conomyrma insana</em></td>
<td>0.01</td>
</tr>
<tr>
<td>b.b.</td>
<td>&quot;blister beetle,&quot; probably <em>Megetra cancellata</em></td>
<td>216</td>
</tr>
<tr>
<td>c.</td>
<td>coleopteran</td>
<td></td>
</tr>
<tr>
<td>s.l.</td>
<td>sphinx moth larva, probably <em>Hyles lineata</em></td>
<td></td>
</tr>
</tbody>
</table>
Fig. 18. Histogram showing the number of ant colonies visited by each horned lizard on the day it was observed.
### TABLE 7

Characteristics of Foraging Bouts by Horned Lizards at Ant Colonies

<table>
<thead>
<tr>
<th>Lizard ID</th>
<th>Species</th>
<th>Sex</th>
<th>Colony #</th>
<th>Ant sp.</th>
<th>Time at Colony (sec)</th>
<th># Eaten at Colony</th>
<th>Harvest Rate (mg/1000 sec)</th>
<th>Rate at Departure</th>
<th>Overall Habitat Rate</th>
<th>Alternate Reason for Leaving</th>
</tr>
</thead>
<tbody>
<tr>
<td>2033</td>
<td>P.m.</td>
<td>m</td>
<td>1</td>
<td>P.d.</td>
<td>1408</td>
<td>26</td>
<td>6.28</td>
<td>4.12</td>
<td>22.6</td>
<td>b</td>
</tr>
<tr>
<td>2040</td>
<td>P.m.</td>
<td>m</td>
<td>1</td>
<td>P.d.</td>
<td>1650</td>
<td>12</td>
<td>37.06</td>
<td>22.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2035</td>
<td>P.m.</td>
<td>m</td>
<td>1</td>
<td>M.sp.</td>
<td>1150</td>
<td>17</td>
<td>4.94</td>
<td>4.46</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0310</td>
<td>P.m.</td>
<td>f</td>
<td>1</td>
<td>P.d.</td>
<td>3180</td>
<td>8</td>
<td>10.2x10^-13</td>
<td>4.24</td>
<td>16.46</td>
<td>a</td>
</tr>
<tr>
<td>0520</td>
<td>P.m.</td>
<td>f</td>
<td>1</td>
<td>M.sp.</td>
<td>7200</td>
<td>53</td>
<td>7.70</td>
<td>2.60</td>
<td>6.72</td>
<td>b</td>
</tr>
<tr>
<td>1033</td>
<td>P.m.</td>
<td>f</td>
<td>1</td>
<td>P.d.</td>
<td>912</td>
<td>13</td>
<td>1.46</td>
<td>16.46</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0530</td>
<td>P.c.</td>
<td>m</td>
<td>1</td>
<td>P.d.</td>
<td>384</td>
<td>33</td>
<td>19.16</td>
<td>86.54</td>
<td>26.26</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>M.sp.</td>
<td>236</td>
<td>6</td>
<td>15.12</td>
<td>26.26</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>3</td>
<td>M.sp.</td>
<td>1654</td>
<td>33</td>
<td>1.86</td>
<td>26.26</td>
<td>a,d</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>4</td>
<td>P.d.</td>
<td>960</td>
<td>8</td>
<td>15.92</td>
<td>26.26</td>
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<tr>
<td>2004</td>
<td>P.c.</td>
<td>m</td>
<td>1</td>
<td>P.d.</td>
<td>641</td>
<td>70</td>
<td>111.78</td>
<td>167.28</td>
<td>50.0</td>
<td>a</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>2</td>
<td>P.d.</td>
<td>150</td>
<td>9</td>
<td>3.02</td>
<td>44.0</td>
<td>50.0</td>
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<tr>
<td>0003</td>
<td>P.c.</td>
<td>f</td>
<td>1</td>
<td>P.m.</td>
<td>1542</td>
<td>171</td>
<td>323.46</td>
<td>79.2</td>
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<td>b</td>
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<tr>
<td>0504</td>
<td>P.c.</td>
<td>f</td>
<td>1</td>
<td>P.d.</td>
<td>976</td>
<td>23</td>
<td>0.109</td>
<td>117.44‡</td>
<td>57.2</td>
<td>b</td>
</tr>
<tr>
<td>1010</td>
<td>P.c.</td>
<td>f</td>
<td>1</td>
<td>P.d.</td>
<td>4177-4380</td>
<td>113</td>
<td>5.48</td>
<td>5.10</td>
<td>24.0</td>
<td>c</td>
</tr>
<tr>
<td>0033*</td>
<td>P.c.</td>
<td>f</td>
<td>1</td>
<td>P.d.</td>
<td>381</td>
<td>25</td>
<td>94.86</td>
<td>87.8</td>
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<td>2</td>
<td>P.d.</td>
<td>760</td>
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<td>15.64</td>
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<tr>
<td>Lizard ID</td>
<td>Species</td>
<td>Ant Colony</td>
<td>Time at Colony (sec)</td>
<td>Harvest Rate (mg/1000 sec)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>-----------</td>
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<tr>
<td>0033* P.c.</td>
<td>f</td>
<td>3 P.d.</td>
<td>274</td>
<td>245.28</td>
<td>87.8</td>
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<td>4 P.d.</td>
<td>837-917</td>
<td>42.80</td>
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<td></td>
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<td>5 P.d.</td>
<td>313</td>
<td>17.5</td>
<td>58.0</td>
<td>87.8</td>
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<tr>
<td></td>
<td></td>
<td>6 P.d.</td>
<td>154</td>
<td>20.22</td>
<td>111.0</td>
<td>87.8</td>
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<tr>
<td></td>
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<td>7 P.d.</td>
<td>367</td>
<td>83.30</td>
<td>26.8</td>
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<tr>
<td></td>
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<td>8 P.d.</td>
<td>1319</td>
<td>8.60</td>
<td>26.8</td>
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<td></td>
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<tr>
<td></td>
<td></td>
<td>9 P.d.</td>
<td>402</td>
<td>30.88</td>
<td>26.8</td>
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<tr>
<td></td>
<td></td>
<td>10 P.d.</td>
<td>1069</td>
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<td>6.66</td>
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<tr>
<td>0023 P.c.</td>
<td>f</td>
<td>1 M.sp</td>
<td>528</td>
<td>0.90</td>
<td>12.50</td>
<td>79.0</td>
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<td>68.30</td>
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<td></td>
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<td>3 P.d.</td>
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<td>98.88</td>
<td>17.24</td>
<td>79.0</td>
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<tr>
<td></td>
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<td>4 P.d.</td>
<td>1992</td>
<td>19.84</td>
<td>.028</td>
<td>79.0</td>
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<td>79.0</td>
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<tr>
<td>0015 P.c.</td>
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<td>1 P.d.</td>
<td>1195</td>
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<tr>
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<td>1968-2040</td>
<td>51.60</td>
<td>6.80</td>
<td>82.8</td>
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</tr>
</tbody>
</table>
TABLE 7--Continued

Notes.--
Lizard species: P.m. = *Phrynosoma* modestum; P.c. = *P. cornutum.*
Alternate reasons for leaving colony: a = moved to shade immediately after termination of foraging bout; b = nothing eaten after foraging bout, satiation possible; c = possible displacement by another horned lizard; d = lizard fled grasshopper (*Taenipoda equus*).
*Lizard 0033 was observed on two separate days: colonies 1-6 on July 31, 1980; colonies 7-10 on September 24, 1979.*
†In those cases where the computer-fit function deviated substantially from the data points near the end of a foraging bout, rate at departure was also estimated by eye, or by computer analysis on the final 10-20 points.
‡Because the computer fit to this data set as extremely poor, the fit-by-eye value was used in all analyses.
colony is higher; lizards experiencing lower overall habitat rates leave when the marginal capture rate is lower.

Somewhat troubling, however, is the large variance among the rates at departure of individual lizards that foraged at more than one colony. Although it appears to be contrary to the prediction of the marginal value theorem (rate at departure for each colony should be the same as the overall habitat rate), this pattern could be due to other factors. For example, such variation would occur if horned lizards use a time frame shorter than a full day when determining the overall habitat rate (as discussed by Cowie 1977). This would result in the constant adjustment of the marginal capture rate at which a lizard should leave a colony. This problem can be resolved somewhat by considering that the overall habitat rate used in these analyses is an average for the day of observation. It is therefore reasonable to compare the overall habitat rate for each lizard to the average for all rates at departure for the same lizard on the same day. Plotting the mean rate at departure against the overall habitat rate does yield a cleaner relationship—the amount of variance explained ($R^2$) nearly doubles (Table 8, Fig. 20).

It also appears that factors unrelated to the maximization of energy intake are important in causing a horned lizard to leave a colony at a specific time. Lizards were observed to leave colonies and go immediately into the shade, indicating that thermoregulatory considerations may have led to termination of that foraging bout. They occasionally left a colony but did not continue to forage afterwards, indicating that they may have become satiated. They also left colonies when approached by another horned lizard, indicating the possibility of
TABLE 8
Regression Analyses of the Relationship Between Rate at Departure and Overall Habitat Rate

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Note.--Analysis was performed using BMDP1R (Dixon and Brown 1979). Confidence limits were calculated using the method of Sokal and Rohlf (1969). "Culled data" refers to data from which terminations due to extraneous factors were removed (see text). "Alternate fits included": see Table 2. For analyses of all data points, each departure from a colony was considered to be a separate and independent observation (Fig. 3). For analyses using mean rates, a mean rate at departure was calculated for each lizard that foraged at more than one colony during the day it was observed (Fig. 4).
Fig. 19. Comparison of rate at departure with overall habitat rate.--The instantaneous capture rate at the moment a colony is abandoned (rate at departure) is predicted to equal the average capture rate for the habitat as a whole (overall habitat rate). A slope of 1.0 in a regression of rate of departure with overall habitat rate is consistent with this prediction. Open symbols represent foraging bouts that appear to have been terminated for reasons unrelated to maximization of energy intake; solid symbols represent foraging bouts for which no alternate reason for termination was observed (see Table 7, text). Data in this figure are derived from computer fits; alternate computer fits or fits-by-eye (Table 7) are not presented. Results of regression analysis appear in Table 8.
Fig. 20. Comparison of mean rate at departure with overall habitat rate: all data.--For each lizard, the rates at departure were averaged to give a mean rate at departure for that lizard on the day it was observed. Small symbols represent lizards that foraged at only one colony; large symbols represent means for lizards that foraged at more than one colony.
Fig. 21. Comparison of mean rate at departure with overall habitat rate: culled data. --Analysis includes only those colonies for which no alternate reason for termination of a foraging bout was observed (Table 7). Symbols as in Fig. 20.
displacement, and when approached by a male grasshopper (*Taenipoda equus*). These grasshoppers have on several occasions been observed to cause horned lizards to flee what is presumably misdirected mating behavior on the part of the grasshopper.

Inclusion of premature terminations in the data set for Figs. 19 and 20 could potentially cause an increase in the slope. However, although the exclusion of premature terminations led to a decrease in the slope (from 1.04 to .76), the decrease in slope was not significant, and the relationship dropped to a marginally significant level (Figs. 19, 21; Table 8).

Two important factors should have caused the slope to be less than one: (1) Both the marginal capture rate and the overall habitat rate used in this analysis are gross rates, that is, they do not take into account the costs associated with foraging, searching, or traveling between colonies. However, Charnov's (1976) original treatment was based on net rates (assimilated intake minus costs). If the costs of traveling between patches are higher than those of remaining within a patch, the forager should wait until its gross marginal capture rate has fallen somewhat below the gross overall habitat rate. For another lizard, the common iguana, the cost of walking is roughly four times the cost of resting (Moberly 1968). Horned lizards tend to walk a good deal more while moving between patches than while foraging in a patch. However, they are not simply "resting" while foraging in a patch; they make a number of movements which would lead to a higher metabolic expenditure. The difference between costs associated with foraging at a patch and the costs of other foraging activities (moving between
patches, etc.) are therefore probably somewhat less than fourfold. However, because I cannot assign precise costs to the complex behaviors of foraging and moving, this question will remain open for the time being. Cowie (1977) was able to make relatively precise adjustments for energy expenditure which gave him a much better fit for his laboratory data on foraging in great tits. (2) Stochastic models (e.g., Oaten 1977) predict that foragers should stay in patches longer than would be expected by a deterministic model such as the marginal value theorem. If there is uncertainty involved, a forager should be more persistent. Because of the rather wide confidence intervals for the slope in Figs. 19, 20, and 21, it is not possible to determine whether energetic costs or uncertainty have an appreciable effect.

Residence Time and Total Yield: The Full Span Test

In his theoretical treatment, McNair (1982) concluded that if it can be determined that one patch type is of better quality than another, then an optimally foraging individual must have a higher expected residence time (residence time = total time spent in the patch) and a higher expected total yield (total yield = number of prey harvested within the patch) when foraging in the better of the two patch types. Here I make the simple transition to an empirically testable prediction: If horned lizards forage optimally, they should forage longer and harvest more ants at "better" ant colonies. Six of the lizards observed in this study foraged at more than one colony during the day each was observed (Table 7), allowing tests of these predictions using intra-individual comparisons.
McNair's analysis was primarily concerned with optimal GUT's (recall that a GUT is the time a forager waits since harvesting its last prey item before abandoning a patch). In his treatment, he made two reasonably assumptions about patch characteristics: (1) Employing a higher GUT will, on the average, result in a larger total yield and a higher residence time in any given patch type, and (2) as residence time in a patch increases, additional increases in residence time will lead to smaller and smaller increases in total yield (in other words, a function describing the increase in total yield from a patch with increased residence time must have a negative second derivative, as it does in Fig. 17).

These assumptions formed the basis for the development of three criteria which must be met for one patch type to qualify as being of uniformly better quality than another. If a forager employs the same GUT at two different patch types, the better patch type will be the one in which (for all possible GUT's employed) (1) the expected residence time is higher, (2) the expected total yield is higher, and (3) the instantaneous capture rate is higher. I maintain that a correct translation of these criteria into an empirically usable form is as follows: One patch is of better quality than another patch if, for all possible residence times, the instantaneous capture rate at a given residence time is higher than at the other patch.

In the present study, this criterion was used to predict how the behavior of a horned lizard foraging at one ant colony should compare with the behavior of the same lizard foraging at a different colony. One colony was regarded as better than another if the instantaneous
capture rate at the former colony was greater than that at the latter at all times up to and including $T_{\text{lowest}}$ (which is defined as the lower of the residence times at the two colonies compared). Instantaneous capture rates were derived in the same manner as for the test of the marginal value theorem (Fig. 17). In practice, I employed the equivalent criteria that one colony was better than another if, at $T_{\text{lowest}}$, the former colony had the higher instantaneous capture rate, and if the cumulative harvest curve for the former colony was higher at all residence times over the span from the beginning of the foraging bout ($T_0$) to $T_{\text{lowest}}$ (Fig. 22). This provides a reasonable means for testing McNair's prediction: An optimally foraging horned lizard should have stayed longer than $T_{\text{lowest}}$ at the better of the two colonies. Because this test evaluates the colonies essentially over the full span of the foraging bouts, it is dubbed the "full span test."

Results of the Full Span Test

An optimally foraging lizard should stay longer and harvest a higher total yield at the better of two colonies. This prediction was not met when the data were subjected to the full span test, whether the marginal capture rates were derived strictly from computer fits, or included alternate fits (Tables 9 and 10). In approximately half of the comparisons, the lizard left the better colony after the shorter time, and in half after the longer time.

A subsequent analysis was performed in which colonies with termination due to other factors (see Table 7) were discarded from the analysis in cases where the possibility of premature termination caused
Fig. 22. Criteria used to determine if one patch is "better" than another: full span test and threshold rate residence time test. Under the full span test, one patch is better than another if the first derivative of its cumulative harvest vs. time function is higher than that at the second patch. In practice, one patch, represented by colony (a), was deemed better than a different colony, (b), if (1) its first derivative was higher at $T_{\text{lowest}}$ and (2) the cumulative harvest function was always higher for (a) than for (b), that is, (a) started at a higher rate and the curves neither crossed nor were concurrent. Under the threshold rate test, colony (a) was deemed better than colony (b) if (a)'s first derivative is higher than (b)'s at $T_{\text{lowest}}$. 
Full span test:
Predict that if \( f_a'(T) > f_b'(T) \) evaluated between 0 and \( T_{lowest} \), then \( T_{stop(a)} > T_{stop(b)} \).

Residence time prediction for threshold rate test:
Predict that if \( f_a'(T) > f_b'(T) \) evaluated at \( T_{lowest} \), then \( T_{stop(a)} > T_{stop(b)} \).
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Notes.—Each pair of horizontal lines represents the relevant quantities for the two colonies being compared. Figs. 22 and 23 describe the method of applying specific criteria to two colonies to determine which is "better" and therefore to predict which colony should have the longer residence time and the higher total harvest. Lizard and colony numbers as in Table 7.

**Derivatives in parentheses are from an alternate fitting of the cumulative harvest curve, either by eye or by a computer fit of the final 10-20 points. Alternate fits were performed in cases where there was a significant departure of the standard computer fit (fit to the complete span curve) and the data in the
terminal portion of the curve. A "yes" or "no" in parentheses indicates whether or not the appropriate prediction was met when the alternate fit was used.

†No prediction was possible using the full span criterion for this pair of colonies because the cumulative harvest functions of the colonies cross, indicating that the instantaneous harvest rate at one colony was not higher than that at the other colony at all points throughout the span from $T_0$ to $T_{\text{lowest}}$.

‡In several cases, the total harvest at a colony was lower than the fitted parameter ($b$). Because this led to mathematical problems, $N_{\text{lowest}}$ was chosen to be the largest integer less than ($b$).

§These responses to "prediction met" queries represent judgements that are ambiguous because the termination of a foraging bout at a colony may have been caused by factors other than an attempt to maximize energy intake (see Table 2 and text). These comparisons are not included in the "culled" tests of Table 4.

¶Judgement is not made regarding the prediction because of an ambiguity. One colony (#'s 1 and 4) is P. desertorum, the other colony is Myrmecocystus spp. (#'s 1 and 3). Individual Myrmecocystus spp. weigh approximately one-half what P. desertorum weigh. Because it is not known whether horned lizards use a mass per time or a number per time rate in making foraging decisions, judgements were only made if both rates were higher at one colony than at the other.
### TABLE 10
Summary and Analysis of Tests of Residence Time and Total Yield Predictions

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**Notes.**—

a. "Full span" refers to tests performed using the full span criterion. "Threshold rate" refers to tests performed using the threshold rate criterion. See text for further details.

b. Under "computer fit," all tests were performed using values derived from computer fits of the full data sets. Under "with alternates," certain tests used values derived from fits-by-eye or computer fits of the final 10-20 captures. See Tables 2 and 4 and text.

c. Y refers to the number of intra-individual predictions that were found to be true, N to the number that were false.

d. Z calculated for Signs test (Siegel 1956); P refers to the probability that the difference between Y and N predictions was due to chance.
ambiguity in judging the predicted trends of residence times. Pairings were not discarded in several inter-colony comparisons where a lizard appears to have terminated its foraging at one colony early, but still remained at that colony longer than at the other colony it exploited. If only those inter-colony comparisons which were not discarded are considered, there is no effect on the outcome: Horned lizards did not behave in the predicted optimal manner.

Threshold Rate Tests

For the full span test, residence time and total yield are considered together. I developed two other predictions in which total yield and residence time are decoupled. Analysis is focused on two "thresholds": $T_{\text{lowest}}$ when considering residence time and $N_{\text{lowest}}$ (the lower of the two total yields) when considering total yield. Then a simple question is posed. At which of the two colonies compared should the lizard have continued to forage longer than $T_{\text{lowest}}$ or to forage for more ants than $N_{\text{lowest}}$? Obviously, the lizard should have continued to forage at the colony that promised the higher future return. And because the marginal capture rate at any point provides a reasonable prediction of the rate for a subsequent period, the marginal capture rate at $T_{\text{lowest}}$ or $N_{\text{lowest}}$ should form the basis of the lizard's decision. These "threshold rate tests" compare the marginal capture rates of the two colonies at the threshold of $T_{\text{lowest}}$ for residence time predictions and at the threshold of $N_{\text{lowest}}$ for total yield predictions. The colony with the higher marginal capture rate at $T_{\text{lowest}}$ was predicted to have
Fig. 23. Criterion used to determine if one patch is better than another: threshold rate total yield test. Colony (a) was deemed better than colony (b) if (a)'s first derivative (i.e., instantaneous rate of capture) is higher than (b)'s at $N_{\text{lowest}}$ (the lower of the two total yields).
Total yield prediction for threshold rate test:
Predict that if $f'_a(T) > f'_b(T)$ evaluated at $T$ corresponding to $N_{lowest}$, then $N_{stop(a)} > N_{stop(b)}$.
been harvested for a longer time; the colony with the higher rate at \( N_{\text{lowest}} \) was predicted to have been harvested for a higher total yield.

I am not claiming that if a forager behaved as predicted then it was employing a mathematically optimal strategy. However, it should be obvious that a lizard will have a higher overall rate of energy intake if it stays longer to harvest more at the colony with the higher threshold rate than at the colony with the lower threshold rate. A forager that fulfills threshold rate predictions can be seen as acting adaptively, where adaptive is somewhere between random behavior and the mathematical perfection of optimal (Sih 1980).

Results of Residence Time Tests. The better the colony, the longer a horned lizard should forage at it. This prediction was not met, whether the marginal capture rates were derived strictly from computer fits, or included alternate fits (Tables 9, 11). In approximately half of the comparisons, the lizard left the better colony after the shorter time, and in half after the longer time.

As with the full span tests, a subsequent analysis was performed in which colonies with termination due to other factors (see Table 7) were discarded from the analysis in cases where the possibility of premature termination caused ambiguity in analysis. If only those inter-colony comparisons which were not discarded are considered, there is an interesting swing in the results: Lizards were more likely to leave colonies as predicted. In the comparisons of computer fitted curves the trend became statistically significant (\( p = .036; \) Table 11). Using alternate fits, the result was marginally significant (\( p = .075 \)).
Results of Total Yield Test. The better the colony, the more ants a horned lizard should harvest from it. This prediction was strongly upheld using either method of estimation of marginal capture rates (Tables 9, 11). After culling those comparisons which were ambiguous due to premature termination at one or both colonies, the results were essentially unchanged. Taken together, these results and those of the residence time tests indicate that horned lizards appear to base decisions on when to leave a colony on at least one aspect of the quality of the colony being exploited, the threshold rate.

General Discussion and Conclusions

Two predictions of optimal foraging theory have been tested for horned lizards foraging at colonies of desert ants. I found that: (1) As predicted by the marginal value theorem, horned lizards tend to leave a patch (an ant colony) when the marginal capture rate at that patch has fallen to the average rate of capture for the habitat. (2) Counter to a prediction based on McNair (1982), horned lizards do not tend to remain for a longer time and to eat more ants at the better of two colonies, when the judgement of which colony is better is based on a comparison of instantaneous capture rates over the full duration of the two foraging bouts (full span test).

In addition, I tested a second set of predictions of how a forager should behave to increase, but not especially maximize, its overall rate of energy intake. Instead of comparing instantaneous capture rates over the full span of the bouts, they were compared only at a threshold (the lower of the two residence times or the lower of the
two total yields. Horned lizards had a strong tendency to stay to eat
more ants at the colony with the higher threshold rate. However,
horned lizards had a significantly higher residence time at the colony
with the higher threshold rate only if data sets were culled to remove
terminations at colonies due to factors other than an attempt to
maximize energy intake.

Do horned lizards forage optimally? If "foraging optimally" means
maximizing energy intake while foraging, the answer is probably no. The
failure of horned lizards to meet the predictions of the full span test
indicates that they could do better. A number of studies have shown that
foragers exhibit behaviors that are consistent with predictions of models
of orimal patch use (e.g., Hassell 1971; Smith and Dawkins 1971; Smith and
Sweatman 1974; Murdoch et al. 1975; Zach and Falls 1976; Cook and Hubbard
1977; Cowie 1977; O'Connor and Brown 1977; Hubbard and Cook 1978; Pyke
1978b; Waage 1979; Lewis 1980; Sih 1980; Zimmerman 1981). However, most
of the predictions tested were qualitative (Cowie was an exception),
indicating that the behaviors may simply be adaptive without being
optimal. Even the support of a quantitative prediction in the present
study (slope of rate at departure vs. overall habitat rate equal to one)
is not convincing of proof of true optimality; a whole host of slopes
other than one are within the 95% confidence intervals of the data.

The discrepancy between support of the marginal value theorem
and rejection of the prediction of the full span test may simply result
from the fact that a failure to reject a prediction does not prove the
truth of the theory that led to that prediction. This, in turn, could
result from (1) failure to reject the prediction when it was, in fact,
false or (2) the possibility that foraging strategies other than that embodied in the marginal value theorem may lead to the predicted outcome. The results of this study do not allow me to determine which possibility is more likely.

There are a number of factors that may cause horned lizards to forage in a suboptimal manner. First, horned lizards are undoubtedly not perfect. They may have difficulty in assessing their overall habitat rate, their marginal capture rate, or the quality of the prey items taken. Second, factors outside the realm of foraging might lead to behaviors that are less than perfect at maximizing energy intake rate. In his work on notonectids, Sih (1980) showed that the possibility of being killed by one's own predators will cause foragers to employ strategies that lower their foraging rates. In the present study, a number of factors unrelated to a strategy of energy maximization were identified as potential reasons that horned lizards may have left colonies. These included thermal constraints, satiation, and interactions with other organisms. Removal of these premature terminations from the data set caused a switch in the results of the threshold rate test of residence time predictions. If other premature terminations could be identified, a similar switch could possibly occur for the full span test.

Do horned lizards forage adaptively? The answer is undoubtedly yes. As shown by my tests of the marginal value theorem and by the results of the threshold rate tests, horned lizards exhibit behaviors that would increase their rate of energy intake above what would be expected for a random forager. Why should horned lizards forage more
efficiently than a random forager? Although horned lizards do not have the high metabolic costs that endotherms have, they must still meet demands. In particular, females must consume enough energy to enable them to lay a large mass of eggs. Both sexes must store enough energy to prevent their starvation during their winters underground. In addition, horned lizards suffer from their own predators when exposed (Munger, unpubl. data; see reviews of relevant literature by Pianka and Parker 1975, and Rissing 1981). By increasing the efficiency of their foraging they reduce the amount of time they must spend foraging; they would therefore receive the same return for a lower risk.

**Summary**

The theoretical works of Charnov (1976) and McNair (1982) provide predictions concerning the optimal timing of departure from resource patches: (1) Foragers should depart patches when their rate of harvesting in that patch has fallen to the average rate of harvesting for the habitat as a whole, (2) foragers should stay longer and stay to harvest more food items in the "better" of two patches. I tested these predictions in the field by observing horned lizards foraging for ants in "patches" at or near ant colony entrances. I conclude that (1) the behavior of horned lizards is generally consistent with the first prediction; and (2) the second prediction is not met if foraging bouts are compared over their full duration, but is met if the test criteria are relaxed (an optimal solution is no longer guaranteed) so that colonies are only compared at a threshold, the lower of the residence times or the lower of the total yields. This latter result is...
strengthened if I disregarded foraging bouts that were apparently terminated for reasons unrelated to energy maximization. I conclude that horned lizards forage adaptively but not optimally.
REFERENCES


