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# Testing predictions of foraging theory for a sit-and-wait forager, *Anolis gingivinus*

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Research in foraging theory has been dominated by studies of active foragers choosing among patches and among prey within a patch. Studies of central-place foraging have mainly focused on loading decisions of an animal provisioning a central place. The problem faced by a sit-and-wait forager that encounters prey at a distance has received little attention. In this study we tested foraging theory predictions for such foragers, *Anolis gingivinus* females in the West Indies island of Anguilla. We presented lizards with antlion larvae at various distances. Experiment 1 showed that an individual's probability of pursuing prey decreases with the prey's distance and is best described by a sigmoidal function (which may be as steep as a step function). This function's inflection point defines a cutoff distance. Experiment 3 tested how cutoff distance changes as a function of prey size. Cutoff distances were greater for larger prey, as predicted for an energy-maximizing forager. Experiments 2 and 4 tested how cutoff distance changes as a function of prey abundance. As predicted, cutoff distances were greater at a site where prey abundance was lower. Furthermore, cutoff distances decreased immediately following prey augmentation and returned to previous values within one day of ending augmentation. Thus, anoles' foraging behavior is a dynamic process, consistent with the qualitative predictions of foraging theory. We attribute the success of this study in supporting fundamental foraging theory predictions to the lizards exhibiting natural behavior under field conditions and to particular advantages of studying sit-and-wait foragers. *Key words:* Anguilla, *Anolis gingivinus*, cutoff distance, encounter at a distance, foraging theory, lizards, partial preferences, prey abundance, prey size, sit-and-wait foragers, threshold, zero-one rule. *[Behav Ecol 9:74–84 (1998)]*

Choosing a patch in which to forage and choosing prey within that patch are two general types of decisions faced by animals when they forage (MacArthur and Pianka, 1966; Stephens and Krebs, 1986). Questions in patch choice include which patch to forage in and when to leave the patch, and a question in prey choice is whether to pursue or ignore a particular prey item once it has been encountered. In recent years these questions have been addressed in an increasingly interdisciplinary fashion, emphasizing behavioral mechanisms and employing a variety of statistical and modeling techniques (Bell, 1991; Gallistel, 1990; Hilborn and Mangel, 1997; Houston and McNamara, 1988; Hughes, 1993; Mangel and Clark, 1988; Manly et al., 1993; Real, 1994).

Foraging theory was first developed for active foragers that search for patches and prey as they move through the environment (Emlen, 1966; MacArthur and Pianka, 1966). Consequently, most studies of optimal foraging theory have focused on such animals [note the prevalence of prey (diet) choice and patch choice studies in Table 9.1 of Stephens and Krebs, 1986, and Appendix 1 of Gray, 1987]. The introduction of central-place foraging models (Orians and Pearson, 1979; Schoener, 1979) expanded the field to include other types of foragers. However, both theoretical and empirical work has concentrated on the two kinds of central-place foragers discussed by Orians and Pearson (1979): single-prey loaders and multiple-prey loaders. Such models apply, for example, to a bird that is provisioning for its chicks at a nest. Several studies have analyzed the decisions faced by relatively sessile sit-and-wait (ambush) foragers, such as insect larvae that construct sand pits (e.g., Eisner et al., 1993; Lucas, 1985; Lucas and Grafen, 1985). The problem of a sit-and-wait (Pianka, 1966) forager that encounters prey at a distance (Schoener, 1979) has been largely ignored in the study of foraging behavior (Schoener, 1987; Stephens and Krebs, 1986).

A total of 28 empirical papers that test predictions of central-place foraging theory are listed by Krebs et al. (1983), Stephens and Krebs (1986), and Gray (1987). The majority of these deal with loading decisions of a provisioner to a central place, and a few focus on patch-choice or prey-choice decisions of an active forager searching away from its central place. The five theoretical papers (other than Orians and Pearson, 1979, and Schoener, 1979) on central-place foraging listed by Gray (1987) also deal with provisioning. None of the above 33 papers addresses the decision faced by a sit-and-wait forager.

Foraging theory has been most commonly tested with birds, mammals, insects, and fishes (reviewed by Krebs et al., 1983; Pulliam, 1974; Pyke, 1984; Schoener, 1987; Stephens and Krebs, 1986). Recent years have seen a growth in the number of lizard foraging studies, as lizards are gaining the status of model organism in ecological studies, and foraging is recognized as an important factor in lizard ecology (Huey et al., 1983; Vitt and Pianka, 1994).

Foraging theory predictions have been tested in only a few lizard studies by direct observation of foraging and have so far focused on testing predictions of patch-choice (Eifler, 1995; Munger, 1984) and prey-choice models (Christian et al., 1984; Diaz and Carrascal, 1993; Kaufman et al., 1994; Lichtenbelt, 1993; Paulissen, 1987; Troyer, 1984) of active foragers. Direct observations can be more easily made of herbivory (e.g., Christian et al., 1984; Eifler, 1995; Lichtenbelt, 1993; Troyer, 1984) than of insectivory (e.g., Diaz and Carrascal, 1993; Kaufman et al., 1994; Munger, 1984; Paulissen, 1987). The most common approach to studying diet of insectivorous lizards is through stomach analyses (e.g., Bergallo and Rocha, 1994; Bullock et al., 1993; Diaz and Carrascal, 1990, 1993; Durtsche, 1992, 1995; Gasnier et al., 1994; Howland et al., 1990; Paulissen, 1987; Rummel and Roughgarden, 1985; Scott et al., 1976; Sexton et al., 1972; Simon, 1976; Stamps and Ea-

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son, 1989; Vitt and Carvalho, 1995; Vitt and Colli, 1986; Vitt et al., 1995). Such studies provide an overwhelming amount of indirect evidence for selectivity in prey choice. However, some predictions of foraging behavior theory cannot be tested using stomach analyses.

The avoidance of reptiles as subjects for testing foraging theory may be partially attributed to the notion that reptiles eat little and would thus not be motivated by food. Mainland anoles (Guyer, 1988), however, and island species in particular (Andrews 1976; Roughgarden, 1995) are food limited, and should thus experience strong selection pressure to be efficient foragers. In addition, reptiles are considered to lack the cognitive abilities (such as learning) that would be necessary for optimal foraging (Rand, 1994). In a previous study, we have shown that this predicament is not true for *Anolis* lizards (Shafir and Roughgarden, 1994b). Anoles in the wild are motivated by food rewards and have the cognitive abilities required to associate food rewards with particular stimuli. Simple rules of thumb exist that would allow a lizard to forage optimally (Roughgarden, 1995). Simulations of lizards with different memory lengths show that a short memory suffices for a lizard to quickly change its behavior (Shafir and Roughgarden, 1994a) to converge on the optimal behavior (Shafir and Roughgarden, 1996). Thus, we expect anoles' foraging behavior to conform with the main predictions of foraging theory for an energy-maximizing (Schoener, 1971) sit-and-wait *Anolis* lizard.

The encounter-at-a-distance class of models (Roughgarden, 1995; Schoener, 1979) applies to a wide variety of animals; for example, some insectivorous birds (Bibby and Green, 1980), raptors (Village, 1990), insects (Holling, 1966), and lizards (Pianka, 1966) that search for prey from a central-place perch and are faced with the decision of whether to pursue or ignore prey items that they detect. This study is unique in its explicit aim of testing the main qualitative predictions of an encounter-at-a-distance type of foraging model.

### Foraging theory predictions

The most common modeling approach in foraging theory has been rate maximization (Stephens and Krebs, 1986), though other methods are now available that may be appropriate for modeling certain foraging decisions (Hilborn and Mangel, 1997; Houston and McNamara, 1988; Mangel and Clark, 1988). Rate-maximizing foraging theory predicts a cutoff distance up to which a lizard should pursue prey and beyond which the lizard should ignore prey (Roughgarden, 1995; Schoener, 1979). Due to intrinsic variance in this threshold, the prediction is of a sigmoidal probability decision function, with the inflection point demarcating the cutoff distance for pursuing prey (Krebs and McCleery, 1984; Krebs et al., 1983; Stephens, 1985; Stephens and Krebs, 1986). If there were no variance in the threshold, the probability function would be a step function. Alternatively, contrary to foraging theory predictions, the probability function for pursuing prey at different distances may not have an inflection point. Prey may be pursued with some constant probability that is independent of distance, up to some limit. Or prey may be pursued with a monotonically decreasing probability that is a function of the prey's distance. Examples of these strategies are illustrated in Figure 1.

The first experiment shows that an individual's probability of pursuing prey decreases with the prey's distance and is best described by a sigmoidal function (which may be as steep as a step function), demarcating a cutoff distance. Experiment 2 tests the prediction of foraging theory that for maximizing net rate of energy intake the cutoff distances of lizards living in an environment where prey abundance is high should be shorter than those of lizards living in an environment where prey abundance is low. Experiment 3 tests the prediction that the cutoff distance should be greater for larger prey than for smaller prey. Experiment 4 tests the prediction that an individual's cutoff distance should decrease following an increase in prey abundance and increase following a decrease in prey abundance. In particular, it tests whether the change in cutoff distance occurs on a temporal scale of hours rather than over a longer time scale.

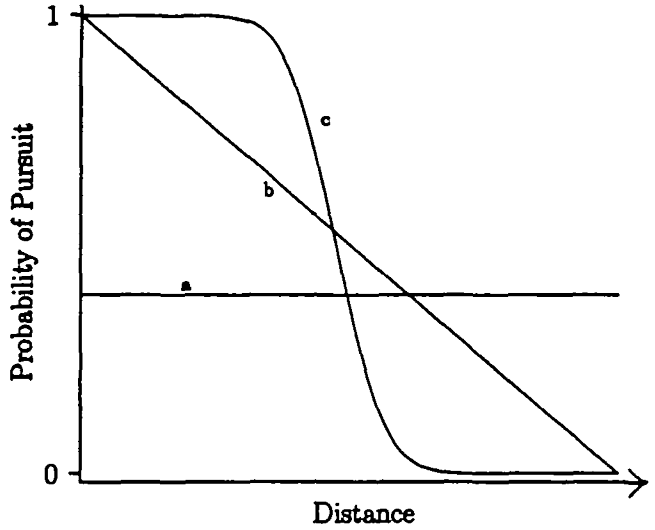

**Figure 1**
Schematic representation of three types of functions that could describe a lizard's probability of pursuing prey at different distances: constant probability (a), monotonically decreasing probability (b), and a sigmoidal function (c).

## METHODS

### Animals and study sites

The experiments were conducted on the island of Anguilla, in the northeastern Caribbean, from May through July 1994. This period coincided with the dry season, during which the population is dominated by adults, and juveniles are rare. All the experiments were conducted with adult females of *Anolis gingivinus*, the only anole on this island. Females are motivated to accumulate fat deposits which can then be used during egg laying (Andrews and Rand, 1974; Lichtenbelt, 1993; Stamps, 1977). Anoles in Anguilla suffer an extremely low predation pressure (McLaughlin and Roughgarden, 1989), making this island especially attractive for testing a model of energy-maximizing in the absence of predation.

Experiment 1 was conducted at three sites. Savannah Bay (SB) is a xeric site consisting of a palm trees grove located along the eastern coast of the island. Katouche Rim (KR), on the western coast, is at an elevation of about 50 m; it is the more xeric part of a dry forest that extends to the bay below. Katouche Canyon (KC) is at sea level and is the more mesic part of that forest.

All subsequent experiments were done at KC and KR. The SB site was abandoned by the end of May because it became very hot and dry and lizard activity was much reduced. We conducted experiments in the morning, while lizards were at the peak of their foraging activity, before the mid-day temperature high (0830–1300 h at KC; 0800–1200 h at KR).

All the experiments were conducted around the lizards' natural perches; lizards were never handled during the duration of the study. These lizards are territorial, so by flagging the main perches that an individual used, we could identify individuals by the tree on which they were located. We became familiar with the habits, perch sites, and particular marks of individuals and could confidently identify them. When necessary, the tip of the tail of a lizard was marked with a few spots of dilute water-based paint administered with a spray gun, which facilitated identification. At the end of the study, lizards were measured and weighed with an Acculab (Newtown, Pennsylvania) Pocket Pro C/50 electronic portable diamond balance.

### Measuring arthropod abundance

We used sticky plates to measure arthropod abundance at KC and at KR. Every 5–6 days we dispersed 10 white paper plates on the ground in each site. The central area of each plate (17 cm diameter) was covered with a thin layer of Tree Tanglefoot (The Tanglefoot Company, Grand Rapids, Michigan). Plates were placed in the afternoon and collected 24 h later. We counted all the arthropods on each plate and measured their body lengths to the nearest millimeter with calipers. The number of arthropods in each size class caught on 10 plates (2270 $cm^2$) was converted to number per square meter.

### General experimental design

To determine how far a lizard would pursue prey, we presented a lizard with antlion larvae (Neuroptera; Myrmeleontidae; Myrmeleontinae) placed inside a feeder located at different distances from the perched lizard. We only tested a lizard when she was in a survey posture (Rand, 1967; Scott et al., 1976), which is associated with foraging (Stamps, 1977). The feeder consisted of a rectangular slate of wood (18×6.5 cm) with a trapezoidal feeding compartment at one end. Three wooden rods (10 mm diameter) were attached to the slate to form the short base (2.5 cm long) and the two sides of a trapezoid, and translucent plastic tubing (6 mm diameter) formed the long base (4.5 cm long). Distance between the two bases was 5.5 cm. We placed an antlion into this compartment and covered it with a plastic cylindrical cap (25 mm diameter, 10 mm high) with a dry leaf glued to the top of the cap; the leaf covered the entire compartment. The feeder was placed at a predetermined distance on the ground in front of a lizard, with the translucent long base of the trapezoidal compartment most close to the lizard and perpendicular to her line of vision.

From a distance of 2–3 m away from the feeder, we slowly pulled on a monofilament line attached to the leaf on top of the cap. The leaf and cap would slide off the feeder, uncovering the antlion. In 70% of the presentations the antlion began to move immediately when it was exposed (the antlion began moving within 93 s in 90% of the presentations, $N$ = 484). Once it began moving, the antlion moved continuously until the end of the presentation (if the antlion died during a presentation, it was immediately replaced). The antlion hopped around the compartment but was unable to escape from it. When it was directly behind the long base of the compartment, the antlion may have been partially hidden from the lizard's view, but since that side of the compartment was translucent, the antlion's movements could still be noticed. Due to the trapezoidal shape of the compartment, the antlion was fully visible to the lizard when it was in any other part of the compartment.

Once the antlion was uncovered, if the lizard went to the feeder and ate the larva, the trial was recorded as a "pursuit." If the lizard did not go to the feeder and eat the larva within seven minutes since the larva began to move, the feeder was removed, and the trial was recorded as an "ignore." If the lizard left its perch and began moving towards the feeder before the end of 7 min, she was allowed an extra 2 min to reach the feeder. This protocol of a presentation was followed in all the experiments.

### Experiment 1: shape of the decision function

Experiment 1 determined the shape of a lizard's probability of pursuit function. In particular, it tested whether this function has an inflection point identified by a cutoff distance, as predicted by foraging theory. Each of 25 lizards was presented with a 5-mm-long antlion larva at three distances during a single morning (median interpresentation time was 34 min, the 10th and 90th percentiles were 14 and 87 min, respectively, $N$ = 51). Three lizards were tested twice, on different days. A series of three presentations to one lizard constituted one set (5 of a total of 28 sets included only 2 presentations). Fifteen sets were done in the mesic site (KB), and 13 sets were done in the xeric sites (5 in KR, and 8 in SB).

For some lizards the presentations were at distances of 10, 50, and 100 cm, and for others the distances were 25, 75, and 125 cm. For each lizard, the order of presentations was determined at random, but constrained by a latin-square design for the whole experiment, so that all order of presentation combinations would be about equally represented.

### Determining cutoff distances in experiments 2, 3, and 4

In experiments 2, 3, and 4, the order of presentations followed a distinct protocol. The protocol was motivated by the finding from experiment 1 that a cutoff distance exists which is the point of inflection of the probability of pursuit function (see Results). The first presentation was always at 25 cm. If the lizard pursued the antlion, the next presentation was at 125 cm. Thereafter, if the lizard pursued the antlion, the following presentation was at a distance 50 cm greater than the previous one (so at 175 cm, then at 225 cm, and so on). Once the antlion was ignored, the following (and last) presentation was at a distance 25 cm less than the previous one (so at 150 cm, or at 200 cm, and so on). If the lizard ignored the presentation at 125 cm, the next presentation was at 75 cm. The following (and last) one was at either 50 cm or at 100 cm, depending on whether the antlion at 75 cm was ignored or pursued, respectively. The nearest distance at which an antlion was ignored was determined to be the cutoff distance.

If the lizard ignored the antlion in the first presentation, at 25 cm, the next presentation was at 10 cm. If the antlion at 10 cm was pursued, then the cutoff distance was determined to be 25 cm. If the lizard ignored the antlion at 10 cm, we held the feeder next to where she was perched to test if she was satiated; no lizard ever ignored the antlion at such close distance. In such a case, the cutoff distance was determined to be 10 cm.

This protocol allowed narrowing-in on the cutoff distance within a 25 cm resolution. The mean number of presentations per lizard that were required to determine a cutoff distance was 4.0 ($N$ = 100). The median interpresentation time was 34 min (the 10th and 90th percentiles were 18 and 80 min, respectively, $N$ = 290). Of the 100 cutoff distances that were determined in experiments 2, 3, and 4, eight cutoff distances could not be determined during a single morning, and presentations were extended over 2 consecutive days. Because antlions were ignored in some presentations and antlions eaten on the last presentation with a particular lizard could no longer affect the cutoff distance, the mean number of antlions that a lizard consumed before the cutoff distance was determined was only 1.8. Thus, the effect of the experiment itself on the state of a lizard was small.

### Experiment 2: effect of prey abundance

To test whether lizards' cutoff distances are affected by the availability of prey in the environment, we compared the cutoff distances of 10 lizards in KB with those of 10 lizards in KR for 5-mm-long antlions (only one of these lizards had been previously tested in experiment 1). Arthropod abundance in KB was greater than in KR (see Results). We also compared the cutoff distances of 18 lizards (the same 10 individuals in each site and 8 new ones in each site) for 3-mm-long antlions. We tested lizards in both sites concurrently, alternating between sites every 1–3 days.

### Experiment 3: effect of prey size

To test whether lizards have different cutoff distances for prey of different sizes, we compared the cutoff distances of 18 individuals in KB to 3-mm-long antlions and to 7-mm-long antlions. The presentations of 7-mm prey were done contemporaneously with experiment 2; these were compared to the cutoff distances of the same individuals to 3-mm prey, which were determined during experiment 2. When we measured cutoff distances of the same individual to more than one prey size in experiments 2 and 3, we allowed a mean of 9 days between measurements.

### Experiment 4: effect of prey augmentation

Experiment 4 had two objectives. The first was similar to that of experiment 2: to test the effect of prey abundance on cutoff distance. In this experiment, however, prey abundance was manipulated experimentally at the same site, rather than studying lizards at two sites that differed in prey abundance. The second objective was to determine how quickly the cutoff distance changed in response to changes in prey abundance.

The experiment was conducted with 16 of the 18 lizards at KR for which cutoff distances to 3-mm antlions had been previously determined in experiment 2. We augmented prey to a particular lizard by placing next to the lizard's tree a 4-cm-high rectangular wooden frame (80×50cm) with 1 mm screening on the bottom, that contained eight antlions. Three of the antlions were 4 mm long, three were 5 mm long, and two were 6 mm long. Forty sea-grape (*Coccoloba uvifera*) leaves, which were scattered over the antlions, covered most of the screening. Antlions became visible to the lizard as they emerged from beneath a leaf and were quickly eaten. Because prey was augmented to up to four lizards at a time, not all the lizards could be watched during the entire augmentation period. After adding antlions to a frame, we waited until the lizard noticed them and had eaten at least one before moving to another lizard. A researcher continuously circulated between the lizards to ensure that no other lizard (e.g., the male resident of the same tree or a neighbor) had come to the frame. If another lizard had approached the frame, it was scared away.

For each lizard, we augmented prey abundance early in the morning of the first day of the experiment with that individual, and we tested the lizard's cutoff distance to a 3-mm antlion later in the same morning. This cutoff distance is referred to as "during" augmentation. The first presentation to a lizard was a mean 79 min after the frame with antlions had been placed. After the cutoff distance had been determined, we removed the frames and checked for antlions. Cutoff distance could not be determined for three individuals. Two of these lizards ate the eight antlions and then disappeared into the canopy of their respective trees for the rest of the morning. The third lizard ate seven antlions, ignored the antlion in the first presentation (at 25 cm), and then disappeared for the rest of the morning. These three lizards were probably satiated by the augmented antlions and are not included in the analysis.

**Table 1**

**Mean (SE) number of arthropods per square meter caught on sticky plates over 24 h at KC and KR ($n$ = 10 sampling days)**

| Size class (mm) | KC | KR | $z$ | $p$ |
|---|---|---|---|---|
| 1–2 | 1546.6 (123.3) | 177.1 (27.9) | −3.745 | <.001 |
| 2–3 | 78.0 (11.1) | 40.5 (8.6) | −2.198 | <.05 |
| 3–4 | 162.1 (15.9) | 23.3 (4.2) | −3.745 | <.001 |
| 4–5 | 44.9 (11.3) | 12.3 (2.5) | −3.043 | <.005 |
| 5–6 | 6.2 (1.4) | 9.3 (1.9) | 1.057 | ns |
| 6–7 | 9.3 (1.7) | 5.7 (1.9) | −1.320 | ns |
| 7–8 | 11.5 (3.7) | 2.6 (0.9) | −1.625 | ns |
| 8–9 | 7.0 (2.1) | 1.8 (0.9) | −1.996 | <.05 |
| >9 | 4.0 (1.3) | 4.0 (1.0) | 0.203 | ns |

Mann-Whitney *U* test statistics given.

Of the remaining 13 lizards, 9 had eaten all of the 8 antlions, 2 had eaten 7 antlions, and 2 had eaten 6 antlions. Most of the antlions were eaten before the beginning of the first presentation; 36 of the 40 augmented antlions that we saw being eaten by a lizard were eaten before the first presentation to that lizard.

The cutoff distance during prey augmentation was compared to that individual's previous cutoff distance to a 3-mm antlion (from experiment 2; between 23 and 38 days earlier for each individual) to test for the effect of prey augmentation. The earlier cutoff distance is referred to as "before" augmentation. On the following day, we did not augment prey and we tested the lizard's cutoff distance again. Comparing this cutoff distance, "after" augmentation, to the cutoff distance during augmentation provided an estimate of the rate of decay of the influence of prey augmentation.

## RESULTS

### Arthropod abundance and lizards' weights

Arthropods were consistently more abundant in KC than in KR throughout the duration of the study (Table 1). Arthropods 1–2 mm long were the most abundant, and ants accounted for 86% and 63% of these at KC and KR, respectively. Ants are an important component of anoline diets (Bullock et al., 1993; Roughgarden, 1995; Stamps et al., 1981; Vitt and Carvalho, 1995).

The difference in the abundance of arthropods between the two sites was also reflected in the condition of the lizards at the two sites. Both adult males and adult females were heavier relative to their snout-vent length at KC than at KR. When a linear regression is passed through the combined data of weight as a function of snout-vent length for males at both sites, 83% ($N$ = 12) of males' weights at KR lie below the regression line, and 77% ($N$ = 13) of males' weights at KC lie above the regression line ($p$ < .001, combined probability of two-tailed binomial distributions). For females, 81% ($N$ = 21) at KR lie below the regression line for females at both sites, and 79% ($N$ = 24) at KC lie above the regression line ($p$ < 0.0001).

### Experiment 1: shape of the decision function

Of the 51 distance-pair combinations, in which a lizard was offered an antlion at two distances, there were no "ignore–

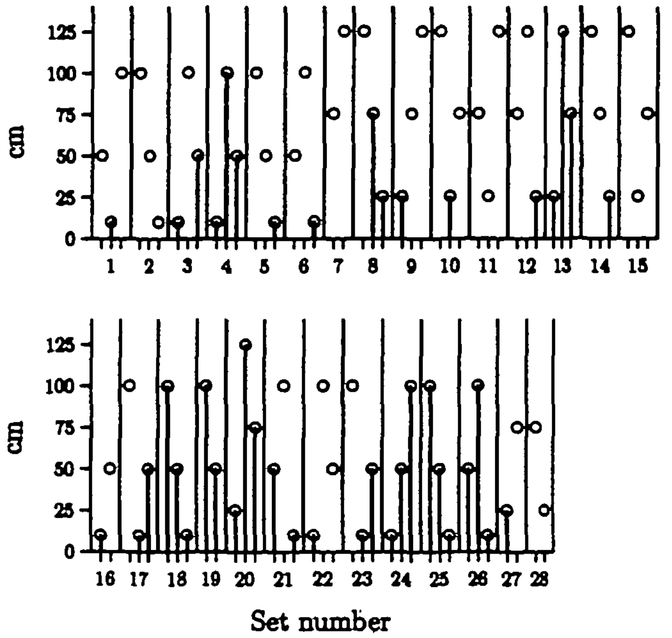

**Figure 2**
The behavior of individual lizards in experiment 1, showing that no lizard ever ignored prey near and chased prey far. Each set is a sequence of two or three presentations of a 5-mm-long antlion larva to a particular individual. Circles represent the distance of the presentation; a line is drawn to the circle if the lizard pursued the antlion. Presentations were administered at a random order and appear in the order in which they were conducted. Sets 1–15 were done at KC (mesic site), and sets 16–28 were done at SB and KR (xeric sites).

chase" cases of a lizard ignoring the antlion at the closer distance and pursuing it at the farther distance (Figure 2).

The data were compared against two null models (Figure 1). One null model is that each individual has a constant probability of pursuing prey, which is independent of the distance of the prey. For each individual, we calculated the probability of observing any combination other than ignore–chase based on that individual's probability of pursuing prey. For example, the first lizard in Figure 2 pursued an antlion in only one of three presentations. If she had pursued the antlion in the presentation at 50 cm and had ignored the presentations at 10 cm and at 100 cm, or had she pursued the antlion at 100 cm and had ignored it at 10 cm and at 50 cm, we would observe an ignore–chase.

Of the three possible combinations of one chase and two ignores, only chasing the nearest presentation and ignoring the middle and far presentations would result in no cases of ignore–chase. Therefore, that individual's probability of no cases of ignore–chase was one-third. Similarly, there is only one combination out of three possible ones, of no cases of ignore–chase when pursuing two out of three presentations, so that probability is also one-third. The probability is one-half in the case of pursuing one out of two presentations. The data from lizards that pursued or that ignored prey at all distances was not informative for testing the hypothesis. The product of the independent probabilities of no cases of ignore–chase for each individual is $(\frac{1}{3})^{15} \times (\frac{1}{2})^{2} = 1.6 \times 10^{-7}$. Thus, the constant probability null model was strongly rejected.

The second null model tested was a linearly decreasing probability of pursuit with distance. For each pair of presentations (near and medium; medium and far) of each individual, we calculated the probability of no cases of ignore–chase assuming that the probability of pursuit of that individual for prey at those distances were those of the population's mean. The mean probabilities for the mesic (KC) and the xeric (KR and SB) sites were computed separately. The proportion of chases at each distance, at each site, was based on 6–10 presentations (the number of presentations at 25, 75, and 125 cm in the xeric sites was too small to allow estimating a proportion of pursuit at those distances). Mean probability of pursuit declined linearly with distance at both mesic ($y = 0.823 - 0.0066x$, $r^2 = .868$, $p = .007$, $N = 6$ distances) and xeric ($y = 1.06 - 0.0056x$; $r^2 = .997$, $p = .032$, $N = 3$) sites.

From the linear regressions, we calculated the probability of pursuing an antlion at each distance at both sites. For each case of each distance-pair combination, the probability of "ignore–pursue" is the product of the independent probability of ignoring near times the independent probability of pursuing far. The probability of getting any behavior pair other than ignore–pursue, then, is one minus that product. This probability raised to the *n*th power, where *n* is the number of cases in a particular distance-pair combination, yields the probability of not getting any cases of ignore–pursue in that distance-pair combination by chance. The product of the probabilities of not getting any cases of ignore–pursue in each of the distance-pair combinations yields the probability of not getting any cases of ignore–pursue by chance in the whole experiment.

For example, from the linear regression for KC, the probability of pursue at 10 cm is 0.757; thus the probability of ignore is $1 - 0.757 = 0.243$. The probability of pursue at 50 cm is 0.493. The probability of ignore at 10 cm and pursue at 50 cm is the product of the two independent probabilities, $0.243 \times 0.493 = 0.120$. The probability of not getting the combination ignore–pursue is $1 - 0.120 = 0.880$. Because the distance-pair combination 10–50 was presented to six lizards in KC (Figure 2), the probability of not getting any cases of ignore–pursue is $0.880^6 = 0.464$. This is the probability of not observing any cases of ignore–chase at KC at the 10–50 distance-pair combination by chance.

In a similar fashion, we calculated the probabilities for the 25–75, 50–100, and 75–125 distance-pair combinations at KC, and the corresponding probabilities for KR and SB. The product of these probabilities equals 0.031. This is the probability of obtaining no cases of ignore–pursue in the 51 distance-pair presentations by chance. The linearly decreasing probability of pursuit model was thus also rejected.

The data are consistent with a nonlinearly decreasing probability function, with an inflection point identifying a cutoff distance. While this function may be as steep as a step function, it is possible that the decline in probability of pursuit is less steep but that we failed to observe any violations of the step-function hypothesis within the resolution of our experiment. We employed a Monte Carlo method to calculate confidence intervals for the standard deviation around the mean cutoff distance that is consistent with our results, assuming a normal distribution for the cutoff distance (and assuming a constant variance within the distance range tested). We simulated an experiment in which prey were presented to a lizard at 75 and at 125 cm. For each pair of presentations, a mean cutoff distance was chosen at random from a uniform distribution between 0 and 200 cm (increasing this range did not affect the results). Then a cutoff distance for the 75-cm presentation was chosen at random from a normal distribution with the randomly chosen mean and with a particular standard deviation being tested. If the cutoff distance was >75 cm, then the simulated lizard pursued the prey, otherwise the lizard ignored it. Another cutoff distance was chosen at random from the same distribution (same mean and standard deviation) for the 125-cm presentation, and it determined

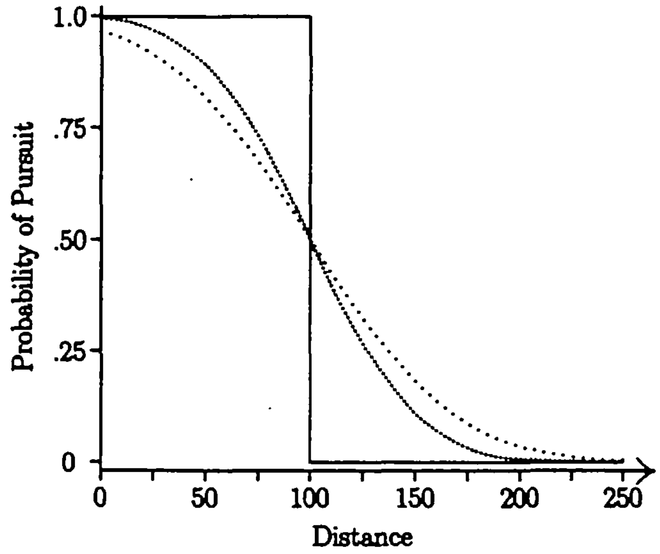

**Figure 3**
The lizards' behavior in experiment 1 was consistent with a step function determining the probability of pursuing prey. Confidence intervals were obtained by a Monte Carlo method; the 80% (dense dots) and 95% (less dense dots) confidence curves are shown. The cutoff distance varied between individuals and sites; in this example the function is drawn for a cutoff of 100 cm.

whether the lizard pursued or ignored that prey. An experiment ended when 15 cases of pursuing the near (75 cm) presentation and ignoring the far (125 cm) presentation had occurred. This is the number of such cases that we obtained in experiment 1 (Figure 2). Then, the number of cases of ignoring near and pursuing far in that experiment was recorded. We were not concerned with the number of cases in which prey was either pursued or ignored in both presentations. We repeated each experiment with a particular standard deviation 1000 times.

When the standard deviation was 40.5 cm, 80% of the simulated experiments ended with one or more cases of the lizard ignoring the near presentation and pursuing the far presentation. When the standard deviation was 55 cm, the probability was 95% of obtaining at least one such case. So 40.5 cm and 55 cm represent the 80% and the 95% confidence intervals, respectively, for the standard deviation. Such sigmoidal cumulative distribution functions are shown in Figure 3.

### Experiments 2 and 3: effect of prey abundance and size

At KC, where prey abundance was higher than at KR, cutoff distances were shorter than in KR (Figure 4). Cutoff distances were shorter for both the 3-mm-long antlions (Mann-Whitney *U* test, $Z = -2.38$, $p = .018$, two-tailed, $N = 18,18$) and for the 5-mm-long antlions ($Z = -3.16$, $p = .002$, two-tailed, $N = 10,10$).

We weighed antlion larvae whose body length (excluding the head) ranged between 2.5 and 7.5 mm. The dry weight of antlion larvae increases by approximately the cube of their body length; dry weight (mg) = $0.012 \times \text{length}^{3.3}$ ($r^2 = .98$, $p < .001$, $N = 16$ mean weights of five larvae whose body lengths were within 0.5 mm of each other). Therefore, the difference in mass between a 5-mm-long and a 7-mm-long larva is much greater than the difference between a 3-mm-long and a 5-mm-long one.

The cutoff distances of KC lizards to 7-mm-long antlions were greater than the cutoff distances of the same individuals to 3-mm-long antlions (Wilcoxon signed-ranks test, $Z = -2.1$, $p = .036$, two-tailed, $N = 18$; Figure 4). The cutoff distances to 7-mm prey were also greater than those for 5-mm prey, but this difference was based on a smaller sample size than in the 7 mm versus 3 mm comparison and was not statistically significant ($Z = -1.42$, $p = .156$, two-tailed, $N = 10$; Figure 4). We approximated the statistical power of this test to be 0.32 using the JMP software package (SAS Institute, Cary, North Carolina) for a *t* test; in most comparisons the *t* test and the Wilcoxon signed-ranks test yielded similar probability values (see Thomas and Juanes, 1996). There was no significant difference between the cutoff distances to 3-mm-long and 5-mm-long prey at either KC ($Z = -1.34$, $p = .181$, two-tailed, $N = 10$, power $= 0.23$; Figure 4) or at KR ($Z = -0.63$, $p = .526$, two-tailed, $N = 10$, power $= 0.08$; Figure 4).

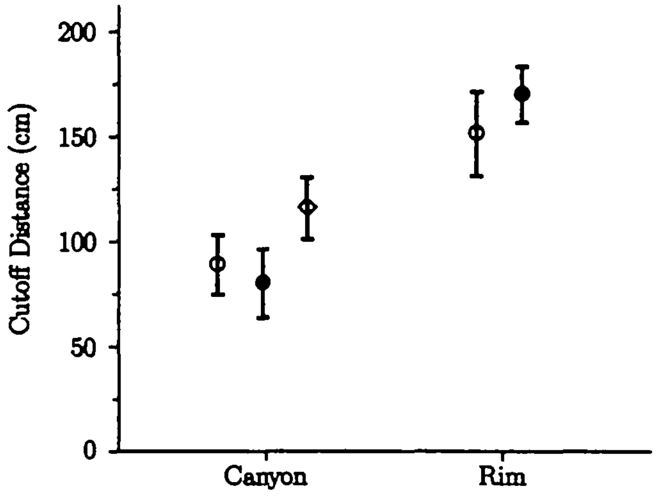

**Figure 4**
Mean (± SE) cutoff distances at Katouche Canyon and Rim to 3-mm-long (open circles), 5-mm-long (filled circles), and 7-mm-long (diamonds) antlions.

### Experiment 4: effect of prey augmentation

The mean cutoff distance during augmentation was about one-half the cutoff distance of the same individuals before augmentation (Wilcoxon signed-ranks test, $Z = -2.63$, $p = .009$, two-tailed, $N = 13$, Figure 5). One day after augmentation, the cutoff distances were about twice as far as during augmentation ($Z = -2.76$, $p = .006$, two-tailed, $N = 13$; Figure 5) and were not different from those before augmentation ($Z = -0.24$, $p = 0.82$, two-tailed, $N = 13$, Figure 5).

## DISCUSSION

Individual-based models are becoming a popular alternative in ecological studies (DeAngelis and Gross, 1992). Such models make predictions about population- and community-level phenomena based on detailed description of the behavior of individuals. Of course, the success of such attempts is strongly linked to how well the behavior of individuals is captured by the model. In this study we tested fundamental predictions of foraging theory for an *Anolis* lizard.

### Comparing basic prey-choice and encounter-at-a-distance models

The foundation of foraging theory was developed with the basic prey-choice and patch-choice models (Charnov, 1973; Emlen, 1966; MacArthur and Pianka, 1966; Maynard Smith,

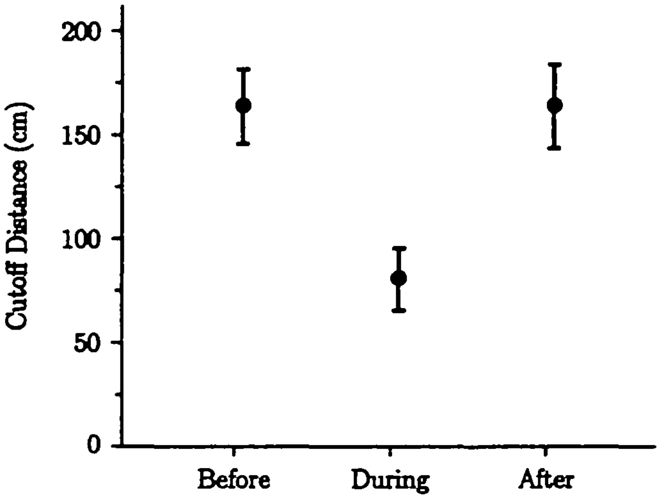

**Figure 5**
Mean (+ SE) cutoff distances of 13 lizards at KR for 3-mm-long antlions, before, during, and one day after prey augmentation.

1974; Pulliam, 1974; Schoener 1969; 1971; 1974; Timin, 1973; Werner and Hall, 1974; see discussion in Schoener, 1987). Central-place foraging models (Andersson, 1978; Aronson and Givnish, 1983; Kacelnik and Houston, 1984; Naganuma and Roughgarden, 1990; Orians and Pearson, 1979; Roughgarden, 1995; Schoener, 1979) are extensions of the basic models (Stephens and Krebs, 1986). The different types of foraging models share many characteristics, so it is sometimes tempting to consider them different versions of the same model. The encounter-at-a-distance and the single-prey loader models may seem theoretical alternatives, but as Stephens and Krebs (1986) point out, these models deal with two different questions: encounter-at-a-distance deals with a decision made from a central place, while the single-prey loader model deals with the animal's decision of how to exploit a patch when it is already there (away from a central place).

In the basic prey-choice models, the profitability of a prey item depends on the costs and gains (say, energetic) associated with handling it. Thus, large mealworms may be classified as one prey type, and small ones as another prey type (e.g., Krebs et al., 1977). In an encounter-at-a-distance model, the profitability of a prey item depends, in addition, on its distance from the predator. Thus, a large mealworm 50 cm away is a different prey "type" than the same mealworm 100 cm away, and it is different from a small mealworm 50 cm away.

## The zero-one rule

The energetic cost of pursuing prey should be considered in any prey-choice model (Bell, 1991; Pyke, 1984). In the basic prey-choice models, however, this cost is considered negligible because these models are concerned with the animal's decision of whether to take or ignore an item that it has already encountered. It is therefore useful to distinguish between models suited for animals that are active foragers (the basic models) and those suited for sit-and-wait foragers. One of the most commonly tested predictions of the basic prey-choice models, for example, is that when the abundance of a profitable prey item is sufficiently high, some prey items of lower profitability should be ignored (the zero-one rule, Schoener, 1987; Stephens and Krebs, 1986; Stephens, 1990). This prediction is often tested using stomach contents analysis. Prey items found in the stomach can be classified according to their profitabilities based on their energy content and handling costs. The distance an animal pursued the prey items found in its stomach, of course, cannot be determined. Thus, the basic prey-choice models (but not the encounter-at-a-distance models) predict that an animal should not include items of low profitability (as determined by their energy content and handling costs) in its diet; stomach contents analysis is a valid test of this prediction only in active foragers that do not detect and evaluate food from a distance, thus meeting the assumptions of the basic prey-choice models (Pyke, 1984). For a sit-and-wait forager, the analogous zero-one prediction is that a particular prey type be pursued up to a cutoff distance and ignored beyond that distance (Roughgarden, 1995; Schoener, 1979). Testing this prediction, therefore, requires knowing the distance at which a particular prey item is pursued or ignored.

We distinguish between predictions about the shape of the probability function for pursuing (in case of a sit-and-wait forager) or accepting (in case of an active forager) prey and the shape of the function that illustrates an animal's choice behavior over time. We refer to the former as the decision algorithm and to the latter as the observed behavior. The zero-one prediction relates to the decision algorithm. Due to the stochastic nature of the decision-making process (Heisenberg, 1994; Smith et al., 1994), we expect the decision algorithm to be defined by a steep sigmoidal function rather than by a step function (Krebs and McCleery, 1984; Krebs et al., 1983; Stephens, 1985; Stephens and Krebs, 1986). When the zero-one rule is tested, part of the variance in the observed behavior may be due to this variance in the decision algorithm. Additional variance in the observed behavior may be contributed by the experimental conditions and by within- and between-subject variability (Gibbon and Church, 1981; Stephens, 1985). Partial preferences may be observed over time even if animals were employing a zero-one decision algorithm due to a variety of factors (Krebs et al., 1977; Krebs and McCleery, 1984; Mangel, 1989; Mangel and Clark, 1988; McNair, 1982; McNamara and Houston, 1987; Pulliam, 1975; Stephens, 1985). Therefore, the finding of partial preferences in many studies (e.g., Davies, 1977a,b; Elner and Hughes, 1978; Erichsen et al., 1980; Goss-Custard, 1977; Krebs et al., 1977; Lea, 1979; Mittelbach, 1981; Werner and Hall, 1974; additional references in Pyke, 1984) should not be interpreted as violation of the zero-one rule in the animals' decision algorithms.

Our test of the step-function prediction for the cutoff distance avoided or minimized many of the sources of variance that may lead to perceived violation of the zero-one rule. We did not average the cutoff distances from different individuals, thus avoiding variance associated with interindividual differences. We tested each individual during a single morning, thus minimizing possible intraindividual variance due to changes in nutritional requirements (Pulliam, 1975). Over a long time interval, as the values of state variables change, an animal's foraging strategy may change, violating the zero-one rule (Mangel, 1989; Mangel and Clark, 1988).

We used only one prey type, and the larvae were identical in size to within 1 mm. This avoided discrimination errors and potential differences in how the researchers and the animals studied classified prey (Krebs et al., 1977; Rechten et al., 1983) and made sampling unnecessary (Dow and Lea, 1987; Heinrich, 1979; Houston et al., 1982). Prey types differed only in their distance, which can be accurately measured by the researchers as well as by a lizard (Fleishman, 1992; Ott and Schaeffel, 1995). This contrasts with tests of the basic model in which an animal has to chose between two different prey items, which are likely to vary on several dimensions. Multidimensional evaluations may lead to different preference patterns than when options vary in only one dimension (Shafir, 1994).

Due to the natural conditions of the experiment, potential partial preferences associated with the time required for animals to learn the conditions of the experiment were avoided (see Snyderman, 1983). Furthermore, conducting the experiments in the field rather than transporting the animals to the laboratory eliminated many potential stresses on the lizards that would interfere with their natural foraging behavior (discussed in Jenssen et al., 1995; Shafir and Roughgarden, 1994b).

Any individual lizard encountered prey at random distances and time intervals, and prey were presented sequentially. Simultaneous or nonrandom encounters may violate the zero-one prediction (Engen and Stenseth, 1984; Lucas, 1983; McNair, 1979; Pyke, 1984; Schoener, 1987; Stephens and Krebs, 1986; Waddington, 1982). Finally, time intervals between presentations were sufficiently long to avoid a "digestive pause" effect, which could lead to rejection of a profitable item (Rechten et al., 1983).

The lizards' choice behavior in experiment 1 supported the existence of a cutoff distance in the lizards' decision algorithms. The constant and the monotonically decreasing probability functions (Figure 1) were rejected. Figure 3 shows the 80% and 95% confidence intervals for the deviation from a strict step probability of pursuit function consistent with the spatial resolution of our experiment.

### Effect of prey abundance and prey augmentation

Foraging theory predicts that to maximize rate of energy intake, as the abundance of prey increases, a sit-and-wait forager should decrease its cutoff distance for all prey items (Charnov, 1976; Roughgarden, 1995). In other words, as the abundance of high profitability (e.g., large and near) prey increases, prey of lowest profitability should begin to be ignored. Because profitability decreases with distance, there is a cutoff distance for each prey type beyond which its profitability is too low to be pursued, and this distance decreases as the abundance of high profitability prey increases.

The analogous prediction in the basic prey-choice models is that the animal should begin rejecting the lowest profitability items encountered as the abundance of high profitability items increases (Stephens and Krebs, 1986). Because prey types are treated as discrete in the basic models, the prediction is that an increasing number of prey types will be dropped from the diet as the abundance of high ranking (in terms of profitability) prey types increases. In the encounter-at-a-distance models, a prey's profitability depends on its type (intrinsic properties) and on its distance, which is a continuous variable. The prediction, therefore, is for a continuous decrease of the cutoff distance for all prey items as the abundance of prey (that are close enough to be pursued) increases.

Experiments 2 and 4 confirmed the prediction that cutoff distance is a function of prey abundance and that when prey are rare, cutoff distances are greater than when prey are more abundant. The cutoff distance of lizards foraging in an area of low arthropod abundance (KR) was about twice that of lizards foraging in an area of high arthropod abundance (KC). When prey was augmented to lizards at KR, their cutoff distances decreased dramatically, and following cessation of augmentation their cutoff distances increased to their previous values.

The prediction of increased selectivity in prey choice with increased prey abundance has generally been supported in lizards (Durtsche, 1992; Kaufman et al., 1994) and in many other animals (reviewed by Krebs et al., 1983; Pyke, 1984; Stephens and Krebs, 1986; see also Demott, 1993). For a sit-and-wait forager, the prediction that prey should be pursued farther as prey abundance decreases seems to have been tested only in preying mantids (Holling, 1966; analyzed by Charnov, 1976), and the prediction was supported. In that study, the mantids were assumed to use the amount of food in their gut as a measure of their rate of food intake and as a proximate estimate of the prey abundance in the environment. This mechanism of assessing prey abundance may be very common in animals (Bell, 1991).

The quick adjustment of cutoff distances of the lizards in the augmentation experiment is consistent with stomach content being a proximate mechanism used by the lizards to determine their foraging behavior. The stomach fills as food is consumed, and it empties quickly in lizards. At preferred (high) ambient temperatures, such as those in this study, *Lacerta vivipara* completely emptied a full stomach within 12 h (Avery, 1973). Reports of exponential gastric evacuation rates are common (Avery, 1973), though Windell and Sarokon (1976) report linear gastric evacuation rates for *Anolis carolinensis* kept in the laboratory, with about 70% of the stomach emptied within 24 h. However, rates in the field are expected to be higher due to increased activity levels, and due to a natural diet that is lower in fat than that used in these laboratory studies (Avery, 1973; Windell and Sarokon, 1976). A "system memory" with an exponential decay rate that approaches zero within several hours would weight recent prey encounters most heavily relative to more distant ones and would be able to track environmental changes in prey abundance quickly (McNamara and Houston, 1985; Shafir and Roughgarden, 1994a).

The large differences in cutoff distances between the lizards at KC and those at KR, however, suggest that a longer memory component is also involved. If lizards were only basing their decisions on the amount of prey in their stomachs that they captured that day, we would see large shifts in cutoff distances within a morning (Shafir and Roughgarden, 1996). Experiment 1, however, showed that a lizard's cutoff distance within a morning is stable. The longer memory component may be some measure of the lizard's condition, such as the amount of fat reserves in its body. Lizards at KC were heavier for their length than those at KR, a reflection of the consistently higher abundance of arthropods at KC.

Thus, to be consistent with the quick adjustment in cutoff distance observed in experiment 4, with the stable behavior observed in experiment 1, and with the differences between sites observed in experiment 2, lizards must have balanced short- and long-term memory components. Although a short memory allows quick adjustments in behavior, it does not suffice for estimating the abundance of arthropods in the environment accurately and results in suboptimal behavior (Shafir and Roughgarden, 1994a, 1996). By employing a long memory, a lizard may achieve almost optimal behavior in a constant environment but may be slow in responding to environmental changes. The optimal mechanism would be one that balances short- and long-term memory components.

### Effect of prey size

Experiment 3 showed that the cutoff distance for larger prey is greater than that for smaller prey. This supports the assumption that *A. gingivinus* in Anguilla is an energy maximizer rather than a time minimizer. The strike distance of *Psammodromus algirus* is also greater for larger prey (Diaz and Carrascal, 1993). Larger prey take longer to consume (Diaz and Carrascal, 1993; Shafir and Roughgarden, personal observation) and would therefore be less attractive than smaller prey to a time minimizer. The fact that a large antlion is more attractive to a lizard than a small antlion suggests that the energy content of prey is of primary importance. Nutrient content considerations (e.g., Pulliam, 1975) are believed to be more important for herbivores than for insectivores (Illius and Gordon, 1993; Krebs and McCleery, 1984; Lichtenbelt, 1993).

However, the relatively small difference in cutoff distances between 3-mm and 7-mm antlions (Figure 4), despite their large difference in mass, suggests that other factors may be involved in assessing the profitability of prey in addition to its size and distance. For example, large prey may be better able to escape. The expected profitability of a prey item that has a high probability of escape is reduced and may decrease the cutoff distance for that prey (Roughgarden, 1995). We do not know how lizards assessed the probability of escape of small and large antlion larvae.

The structure of the anoline eye is similar to that of raptors, and these lizards have superb vision (Fleishman, 1992). It is highly improbable that lizards pursued larger prey farther because they could detect them farther. At KR, some individuals pursued 3-mm antlions as far as 300 cm, well beyond the cutoff distances in experiment 3 to even larger prey. Furthermore, we observed the "visual grasp" reflex (Fleishman, 1992), which occurs when an anole detects moving prey, in all prey presentations, including those in which the lizard ignored the prey.

## CONCLUSION

Our experiments show that the foraging behavior of the anoles we studied agreed qualitatively with the predictions of foraging theory. The mechanism by which the lizards arrived at their foraging decisions was not investigated; several methods that might be attainable by a lizard exist (Roughgarden, 1995). It is generally accepted that animals are often able to reach near optimal solutions to important behavioral problems (Mangel and Clark, 1988). Regardless of the precise mechanism, it seems that foraging theory captures the essential elements of the foraging behavior of individual lizards. These results increase our confidence in applying an individual-based modeling approach based on foraging theory to the study of the population biology of *Anolis* lizards.

The success of this study illustrates that *Anolis* lizards are a good subject for testing predictions of foraging theory. This may be partly due to their sit-and-wait mode of foraging. Lizards and other sit-and-wait foragers that encounter prey at a distance are likely to become model organisms in an area of study in which they have been traditionally ignored.

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