

Stochastic prey arrivals and crab spider giving-up times: simulations of spider performance using two simple “rules of thumb”

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Summary. We compared the patch-choice performances of an ambush predator, the crab spider *Misumena vatia* (Thomisidae) hunting on common milkweed *Asclepias syriaca* (Asclepiadaceae) umbels, with two stochastic rule-of-thumb simulation models: one that employed a threshold giving-up time and one that assumed a fixed probability of moving. Adult female *Misumena* were placed on milkweed plants with three umbels, each with markedly different numbers of flower-seeking prey. Using a variety of visitation regimes derived from observed visitation patterns of insect prey, we found that decreases in among-umbel variance in visitation rates or increases in overall mean visitation rates reduced the “clarity of the optimum” (the difference in the yield obtained as foraging behavior changes), both locally and globally. Yield profiles from both models were extremely flat or jagged over a wide range of prey visitation regimes; thus, differences between optimal and “next-best” strategies differed only modestly over large parts of the “foraging landscape”. Although optimal yields from fixed probability simulations were one-third to one-half those obtained from threshold simulations, spiders appear to depart umbels in accordance with the fixed probability rule.

Key words: Foraging – Rules of thumb – Spider – Stochastic model – Yield profile

Optimal foraging theory began as a largely mathematical inquiry into the question: how should an idea animal forage? (Krebs et al. 1983). This early emphasis on “ideal” behavior has shifted as a result of recent evidence. Experiments indicate that although animals may approach optimal behavior, perfection is rarely achieved and suboptimal performances are common and striking (e.g. Morse and Fritz 1982). Consequently, instead of focusing only on some idealized optimum, many researchers are now concerned with how animals make decisions in a way that approximates an optimal solution (McNamara and Houston 1980;

McNamara 1982). Decision-making algorithms that foragers might plausibly use have been given the name “rules of thumb” (Janetos and Cole 1981; Krebs et al. 1983).

We became interested in rules of thumb after observing crab spiders (*Misumena vatia*: Thomisidae) ambush prey on common; milkweed (*Asclepias syriaca*) umbels. Crab spiders face the problem of choosing the optimal umbel on which to hunt. Because arrival of prey at umbels is highly variable in time, selection of this umbel is not easy. Imagine a spider that has recently arrived at an umbel and then waited in ambush for several hours without encountering a single prey. The spider must decide whether to move to another umbel or remain. Critical to this decision is the reason for the absence of visitors. Visitors may have been absent by chance alone, even though on average the umbel is frequently visited, or because clouds and cool weather temporarily deterred flight. Visitors might also be absent because the umbel is new and not yet attractive to pollinators, although within a day it will mature enough to become extremely attractive. Or, the umbel may represent an unredeemably poor site in which to wait in ambush for prey.

Perhaps it is thus not surprising that crab spiders often remain for prolonged periods on conspicuously inferior umbels – that is, ones that attract few or even no prey (Morse and Fritz 1982; Morse 1986a). We have reached the impression that the environment is so unpredictable for crab spiders that any single strategy is unlikely to stand out as markedly superior to all deviant behavior. This possibility has been neglected in most tests of optimal foraging theory although theoreticians have pointed out that the likelihood of an organism adopting an optimal policy depends on the payoff (Kacelnik 1984). In this paper we attempt to assess how clearly an optimum stands out above the yields associated with non-optimal behavior. We simulate the foraging of individual spiders, using visitation patterns for prey that were obtained from field observations of the milkweed system.

We begin by reviewing key features of crab spider natural history. Then we discuss the methods used and results obtained in characterizing sequences of prey arrival at milkweed umbels. Finally, we describe two simulation models of spider foraging, both of which lead to spiders eventually

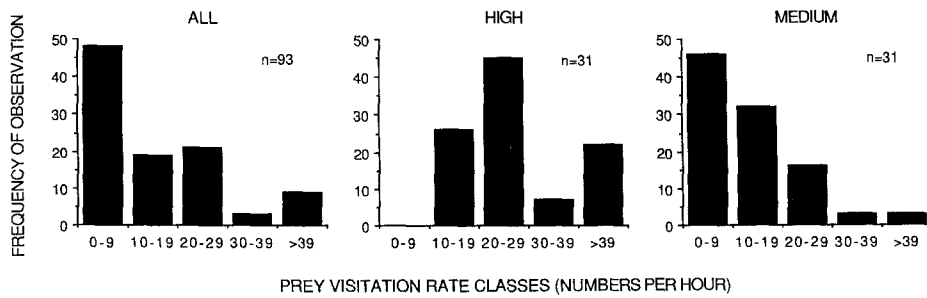


Fig. 1. Frequency distributions of visitation rates at medium, high, and all umbel qualities. “All” represents the data pooled from the three different qualities. Frequency distribution at low visitation rate is not depicted, because all 31 observations fell at 0–9 on the abscissa

selecting umbels with the highest visitation rates. These models use variances and means in visitation rates that were observed in the field. Both models give an optimum yield associated with a particular “rule of thumb” behavior. The optima, however, are not our major concern in this paper. Instead we quantify how “clear” or “sharp” these optima are. Given the stochastic environment in which the spiders forage, how much might the spiders lose by departing from the optimum behavior?

Natural history of the system

Misumena vatia is a sit-and-wait predator at flowers throughout northeastern North America. Adults frequent flowers of the common milkweed, a rich source of nectar for bees, butterflies, moths, and other insects (Morse 1981a, 1985; Morse and Fritz 1982). Milkweed produces its flowers in round, compact umbels that are often separated from each other by 2–5 cm. Umbels bloom sequentially up the stem and thus present hunting sites that differ markedly in the rewards offered to nectar-feeding insects. Nectar-feeding insects accordingly visit umbels in a frequency proportional to the number of nectar-producing flowers contained on the umbels (Morse and Fritz 1982; Morse 1986b). Spiders must select which of these discrete patches (umbels) to use as a hunting site, each of which differs several-fold in the number of prey that it attracts. Since flowers produce nectar for only three to four days (Fritz and Morse 1981), the best sites are continually changing.

We have demonstrated that the site chosen is of considerable importance to these spiders; individuals that usually select sites with maximum numbers of insect visitors become significantly larger and lay significantly larger clutches than do those that make the “correct” choice less frequently (Fritz and Morse 1985). Larger clutches, in turn, translate into larger numbers of young emerging from the egg sac of the spiders’ brood (Morse and Fritz 1987).

Methods for estimating prey visitation rates and spider departure rates

We studied adult female crab spiders on milkweed in an open field in Bremen, Lincoln Co., Maine, USA. This site is further described elsewhere (Morse 1981b). Spiders were tested on milkweed stems containing three umbels: one with 25 or more nectar-producing flowers (“high-quality”), one with 5–10 such flowers (“medium-quality”), and one with 0 nectar-producing flowers (“low-quality”). We used this as our experimental arena because during most of the flowering season as many as 50% of the flowering stems of

Table 1. Parameters of best-fit gamma distributions and chi-square tests of goodness-of-fit to field visitation data. Gamma probability densities are two-parameter functions of the form

$$\text{prob}(\text{random variable} = x) = (x/A)^{B-1} \exp^{-x/A} / A \int_0^{\infty} \exp^{-u} u^{B-1} du$$

A and B are constants such that the mean = AB , and the variance = $A^2 B$

Umbel type	A	B	Mean	variance	Chi-square with 4 degrees of freedom	
High	3.7	0.3	1.1	4.1	1.42	$P > 0.2$
Medium	1.0	0.5	0.5	0.5	0.23	$P > 0.5$
Low	0.1	0.2	0.03	0.002	0.11	$P > 0.5$
All ^a	0.8	0.8	0.64	0.5	1.98	$P > 0.1$

^a All represents high, medium, and low umbels lumped together

a clone contain umbels with this combination of flowers (Morse 1981b). Spiders were randomly assigned to one of these three umbels, one spider per stem. To control for feeding state, we used only individuals that had not eaten for more than a day. We thus subjected them to a hunting and feeding regimen that is routinely experienced by these spiders (Morse 1979, 1981a). All tests were run between 10:00 a.m. and 16:00 p.m. on clear or partly cloudy days, times during which insects visit milkweed flowers frequently (Morse and Fritz 1982).

The spiders were monitored for 2 h each, and any movements or responses to prey were recorded. During this period all insect visitors to the umbels of a stem were recorded, as well as the length of their visits and the number of flowers that they probed. The commonest visitors were bumblebees (*Bombus vagans* and *B. terricola*) and honeybees (*Apis mellifera*). We followed the spiders for two hours because in an earlier study (Morse and Fritz 1982) most individuals that shifted umbels during a six-hour period had moved by the end of 2 h. In all we collected 31 runs of two hours apiece from 24 different spiders.

Observed visitation patterns and spider behavior

The frequencies of visitation rates to low, medium, and high-quality umbels summarize the spatial variability in prey visitation that spiders were likely to encounter at our study site (Fig. 1). We fit each of the frequency distributions in Fig. 1 to a gamma function, a two-parameter function that can be used to approximate a wide variety of probability distributions (McNamara and Houston 1985). In all instances, our frequency distributions of visitation rates were well described by a gamma function (see Table 1). Thus, we can use gamma distributions to represent the umbel-to-

Table 2. Tests to determine whether spider giving-up times differed among umbel types

Umbel type	<i>N</i>	Sum of scores	Expected sum if no differences	Expected standard deviation if no differences	Mean score
High	46	2560.5	2392.0	150.5	55.7
Medium	29	1521.0	1508.0	136.2	52.5
Low	28	1274.5	1456.0	134.7	45.5

* Chi-Square Approximation to Kruskal-Wallis Test applied to Rank Sum Scores (average scores were used for ties):

χ^2 with 2 d.f. = 2.0, $P > 0.36$

Therefore, we accept the H_0 that giving-up times are the same on all umbel types

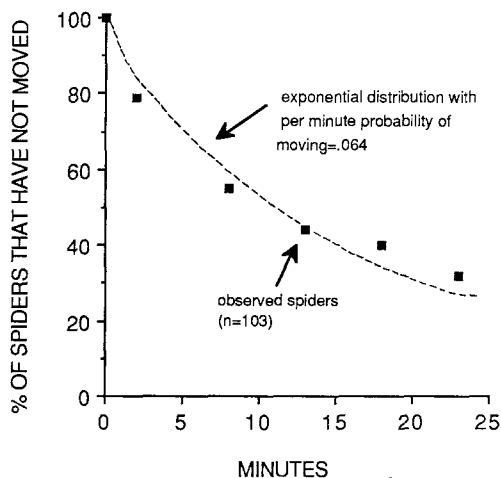


Fig. 2. The percentage of spiders that remain on an umbel for varying lengths of time. The *solid points* are actual field data for spiders hunting on umbels that were not visited by prey (the sample size is 103 spider observation bouts). The *dashed line* is the best-fit exponential distribution, which has as its only estimated parameter a per-minute probability of leaving = 0.064. This best-fit model explains 92% of the variance in the data, which is significant at the $P < 0.01$ level

umbel variability in visitation rate at our study site (see Fig. 1).

Since we watched spiders continuously for 120 min, we also obtained frequency distributions of giving-up times for spiders on each of the umbel types. To test whether these distributions differed among umbel types we performed a Kruskal-Wallis nonparametric analysis of variance on the rank sums. On the basis of this test we accepted the hypothesis that distributions of giving-up times did not differ among umbel types (see Table 2). Lumping together umbel types, we found that the frequency distribution of giving-up times fit an exponential distribution. In particular, the probability that a spider has not moved within t minutes is given by a function $f(t) = \exp - \lambda t$, where λ is the per minute probability that a spider does move (see Fig. 2). Such exponential distributions result when departures occur with some fixed probability, denoted λ in the preceding $f(t)$.

Simulation models

Overview. In both of our simulation models foraging proceeds according to a simple decision process. Variation among umbels with respect to visitation rates was represented by a gamma distribution. The effectiveness of each

decision rule was measured by the average yield (intake per unit time) it produced. This average was calculated from simulations of 20 spiders foraging according to a particular rule for 2 h; we chose two hours because most spiders that move during a day do so in considerably less time than this, and the period is of sufficient duration for spiders to move several times under field conditions (Morse and Fritz 1982). We used 20 simulations per decision rule because that is our best guess of the number of siblings that are likely to survive the high egg and juvenile mortality characteristic of spiders, and thereby present a genetic cohort to the scrutiny of natural selection. Although simulations of 10 and 40 spiders gave similar results in a few trial runs, we expect an order of magnitude increase in the number of simulations would have smoothed out the yield profiles we discuss later. The general approach we adopted assumes that spiders are unable to carry over information about the quality of their umbel from one day to the next.

Both models share the same core structure and basic set of input parameters (Fig. 3), but differ in the decision process that governs umbel choice. At the start of a run (and after each subsequent move) a spider occupies an umbel that is randomly assigned a visitation rate from a gamma distribution. Visitation rate has visitors/h as its units, whereas what we really want is a random sequence of arrivals at each umbel. Since we know that prey arrivals occur as a Poisson process (Morse and Fritz 1982), we can easily generate random arrivals using our mean visitation rate. We did this by converting mean visitation rates to mean waiting times (if λ = mean number of visits per hour, then $1/\lambda$ = mean hours between visits). The mean waiting times define an exponential probability density, from which we can randomly draw a sequence of interarrival times. While waiting on an umbel between prey visits, the spider consults its decision rule every minute. The decision rule either tells the spider to move or to continue waiting. If the spider captures a visitor, that capture is recorded and added to a running total. Whenever a spider consumes a prey item, it requires a certain amount of handling time, which is specified in each simulation. If the spider moves, a new visitation rate is drawn from the gamma distribution and in turn used to simulate random arrivals at the new umbel. Upon arriving at a new umbel the spider starts applying its decision rule all over again. Thus the spider's behavior at each umbel is assumed to be independent of its feeding history at previously visited umbels. For each decision process this simulation procedure was repeated using a range of behavioral (in particular, "cost of moving")

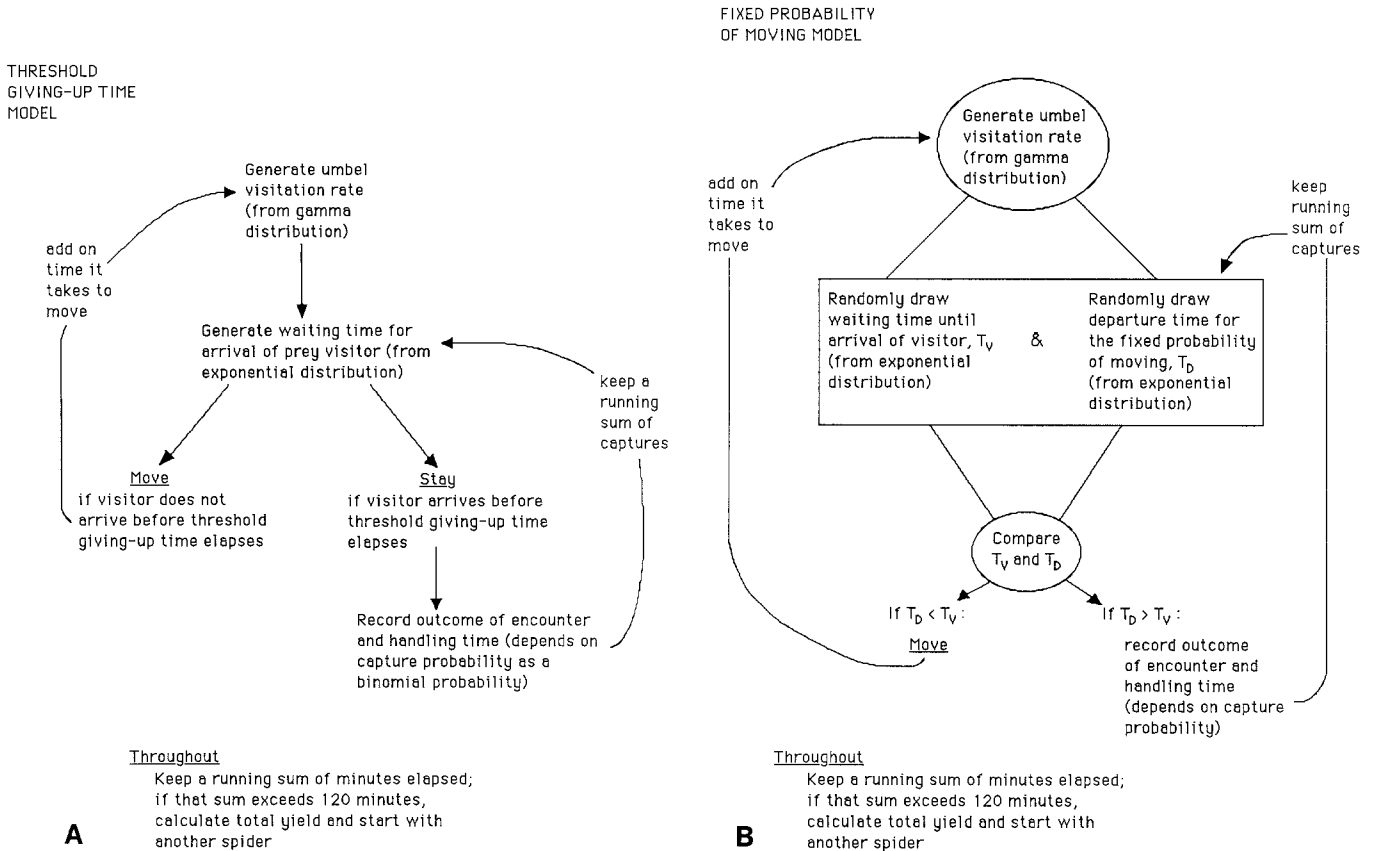


Fig. 3. Flowchart for threshold-giving-up time simulation (A) and fixed probability of moving simulation (B)

and environmental (different gamma distributions) parameters.

Assumptions. We do not know what it costs a spider to move among umbels. We expect the calorie costs to be minimal, but the time lost from foraging to be potentially significant. In our models a “cost to moving” was a parameter that we entered into our simulations as a time cost. Since cost ultimately is converted to a reduction in yield/time, a time cost suffices to reduce this ratio.

Because we lacked data on the energy value of individual prey items, we tabulated all prey as equivalent; thus our units of yield were prey captured per unit of time. This aggregation of all visitors into one prey type is a reasonable simplification for the milkweed system because the relative frequency of the prey types arriving at flowers does not change with mean visitation rate (Morse 1986b).

We omitted risk from our model because in the course of ten years studying *Misumena* foraging on milkweeds, we never saw a spider lost or eaten while searching for umbels. We also assumed that spiders could not evaluate umbel quality independent of visitation rates, and that a spider’s probability of capturing a visitor does not vary with umbel quality. Both of these assumptions have been borne out by field observations (Morse 1986a).

Decision rules. For our simulations, we selected the two simplest rules of thumb that we could imagine:

1) **Threshold Giving-Up Time** (abbreviated TGUT): A spider always leaves an umbel when some fixed amount of time has elapsed without any prey visiting the umbel.

If the environment were deterministic, this giving-up time could be calculated according to the marginal value theorem (Charnov 1976). It would simply be the time at which the average rate of prey harvest in an umbel equals the rate expected if a move were made.

2) **Fixed Probability of Moving** (Abbreviated FPOM): The probability that a spider will leave an umbel is some constant ‘p’. Although this might appear to be a self-evident “rule”, one can imagine the ‘p’ being adjusted to different environmental circumstances. Different probabilities of moving will produce different yields. We simulated this simple behavior because field observations supported it; as noted above, spider giving-up times fit an exponential probability distribution (Fig. 2), which suggests that departure is indeed a result of a random departure process with a fixed probability.

Analyzing model output. Since we do not know the net caloric gain associated with each prey item, or the cost of travel, we cannot predict an optimal behavior. We can, however, explore how well hypothetical optima stand above surrounding suboptimal yields, and the extent to which yield topographies are influenced by the variance of visitation rates.

In Figs. 4 and 5 we present the yield topographies of two different series of simulations. First we will discuss Fig. 4 to develop an intuitive idea of what one might mean by a “clear optimum” and then we develop two quantitative measures of the “clarity of an optimum”. In Fig. 4a, as one moves away from a giving-up time of three minutes, yield falls off sharply and no other peak in the range of

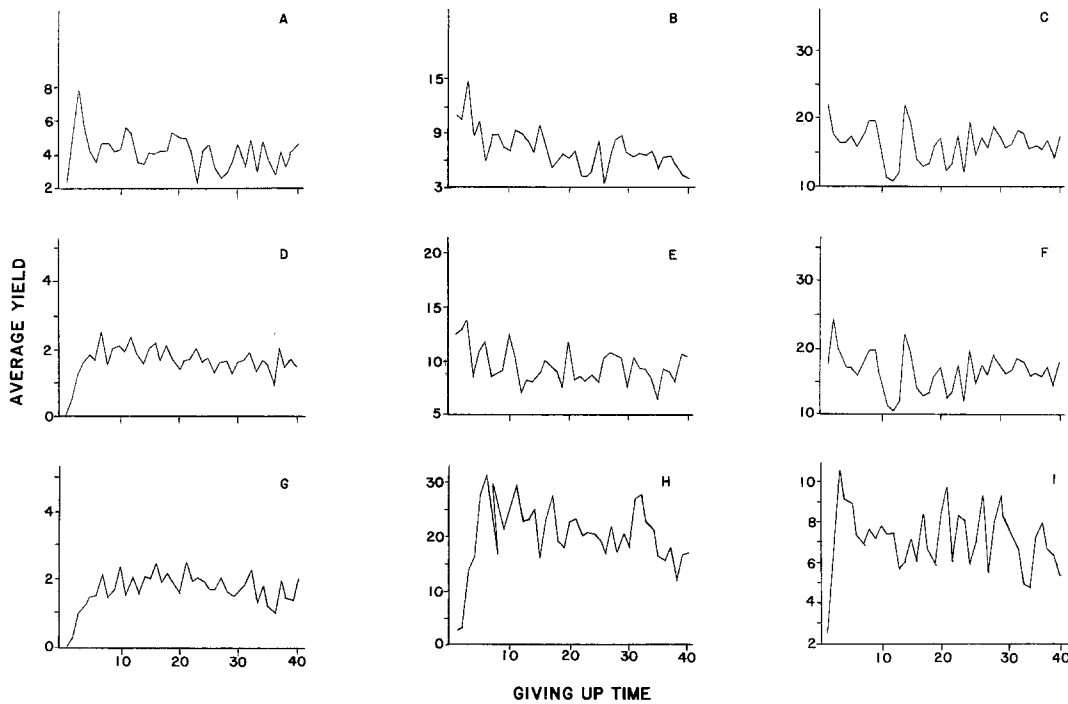


Fig. 4. Yield profiles obtained from 100 independent simulations in each of nine (A-I) different environments. Yield is measured as net number of prey captured in 200 h, with giving up time corresponding to the number of minutes that must elapse without prey before a spider will move. The cost of moving is 1 prey unit for A-C, 5 prey units for D-F, and 10 prey units for G-I. The mean and variance in prey visitation rates per umbel per hour were as follows: 0.5 and 0.25 for A, 1.0 and 1 for B, 3.7 and 3.7 for C, 0.2 and 0.04 for D, 2 and 2 for E, 3.7 and 3.7 for F, 0.2 and 0.04 for G, 0.4 and 0.08 for H, 1.5 and 0.75 for I

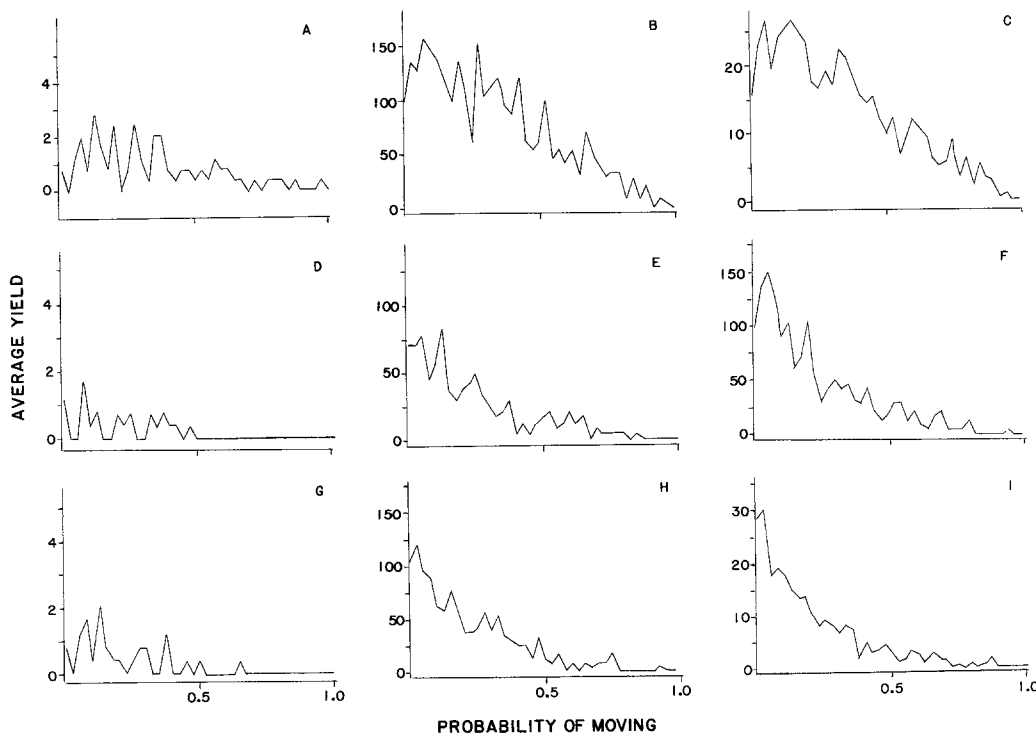


Fig. 5. Yield profiles obtained from 100 independent simulations in each of nine (A-I) different environments. Yield is measured as net number of prey captured in 2000 h, but in this case the horizontal axis represents different fixed probabilities of moving per minute. Note that the observed per-minute probability of moving is 0.064 for crab spiders (see Fig. 2). The cost of moving is 1 prey unit for A-C, 5 prey units for D-F and 10 prey units for G-I. The mean and variance in prey visitation rates per umbel per hour were as follows: 0.05 and 0.025 for A, 0.4 and 0.08 for B, 1 and 1 for C, 0.02 and 0.004 for D, 0.2 and 0.04 for E, 0.4 and 0.16 for F, 0.05 and 0.075 for G, 0.5 and 0.25 for H, and 1.5 and 0.75 for I

giving-up times produces a yield near the three-minute optimum – we would call this peak a very clear optimum. In stark contrast, no optimum is clear in Fig. 4d; there are several relatively indistinguishable peaks (e.g., 6 min, 12 min and 37 min). One might interpret Fig. 4d as evidence that an organism has considerable leeway with respect to giving-up time.

By contrasting Fig. 4a, d (and several other yield topographies), we selected two aspects that reflect the clarity of an optimum point on a yield curve:

1) how high it reaches above neighboring points, or how sharply yield falls off as one moves away from the optimum;

2) the extent to which the optimum is unrivalled by other peaks in the yield curve.

To quantify these two notions of “clarity of an optimum”, we used the following indices:

a) local clarity or LC = Mean % reduction in yield relative to the maximum yield for the four strategies closest to the optimal strategy (in terms of minutes for TGUT simulation and in terms of probability for the FPOM simulation). Thus if the optimal strategy was a 6-min giving-up time, we would calculate the % reduction in yield for 4, 5, 7 and 8-min giving-up times.

b) global clarity or GC = Mean % reduction in yields for the four yields most similar to the maximal yield, regardless of how similar their underlying behavioral rule is to the optimal rule. In other words, we looked for the four next-highest yields and calculated the mean % reduction in yield they represented compared to the optimal performance.

According to these indices, Fig. 4a has both a higher LC and GC than does Fig. 4d (in general the two indices were correlated in our simulation output). LC is a measure of the gradient in yield in the neighborhood of the optimum point, whereas GC measures the extent to which there are competing optimum points distant from the single highest optimum.

Ultimately it would be useful to develop more general and rigorous measures of yield topography than our ad hoc GC and LC indices. As a first step, however, GC and LC will suffice for quantifying differences among yield topographies. To organisms making decisions about whether or not to move, GC and LC reflect the penalties suffered by suboptimal behavior. If penalties are minor, the selective pressure for a particular optimal behavior would not be sharp.

Results of simulations

For a wide variety of visitation regimes, yield profiles from both TGUT and FPOM models were either remarkably jagged or quite flat – so that distinct optimal points are rarely evident (see Figs. 4 and 5). The “jaggedness” of the yield profiles is certainly a reflection of the low number of simulations per decision rule, as well as the inherent stochasticity of the process. But as we argued earlier, we think that a limited number of simulations is appropriate because natural selection would have only a limited number of trials to “evaluate” for each particular genotype that entered the spider population. Our results clearly also depend on the particular means and variances in visitation rates that we used as input variables for the model. Rather than exhaustively simulating foraging success for a wide

Table 3. Multiple linear regressions relating “clarity of optimum” indices as the dependent variable to: mean in visitation rates (“mean” below), variance in visitation rates (“variance” below), variance to mean ratio for visitation rates (“clumping” below), and the cost to a spider of moving among umbels (“cost” below). Because “clumping” is a ratio of mean and variance, the regression analysis should be interpreted with caution; it is intended merely to highlight relationships. The clarity of optimum indices, which are percentages, were $\arcsin \sqrt{P}$ transformed. Asterisks are used to draw attention to significant predictor variables

A Regressions for TGUT simulations where 37 cases enter into the analysis (a case is one set of simulations)

	Predictor	Coefficient	Standard error	Significance
Global Clarity Index $r^2=0.79$	mean*	-0.11	0.03	0.0004
	variance*	0.04	0.01	0.0007
	clumping*	0.21	0.08	0.0117
	cost*	-0.01	0.005	0.0288
Local Clarity Index $r^2=0.47$	mean*	-0.15	0.04	0.0004
	variance	-0.02	0.02	0.3319
	clumping*	0.35	0.1	0.0034
	cost	0.004	0.008	0.5643

B Regressions for FPOM simulations where 28 cases enter into the analysis

	Predictor variables	Coefficient	Standard error	Significance
Global Clarity Index $r^2=0.40$	mean*	-0.10	0.10	0.3249
	variance	-0.08	0.12	0.5569
	clumping	0.12	0.14	0.3763
	cost	0.02	0.007	0.0038
Local Clarity Index $r^2=0.50$	mean*	-0.40	0.13	0.0058
	variance	0.27	0.16	0.0984
	clumping	0.10	0.17	0.5714
	cost	0.009	0.009	0.2933

variety of visitation schemes, we focused on the actual range of means and variances obtained from field observations (i.e. Table 1). Thus our results are particular to the crab spider system for which we gathered visitation data.

An obvious question is whether features of the visitation regime influence our “clarity of optima” indices in any consistent manner. The pertinent features of the visitation regimes are: the mean, the variance, and the variance/mean ratios in the visitation rates associated with each umbel. In addition we varied the cost to a spider (in terms of calories or fraction of prey units) of moving from one umbel to another, assuming that the spider is sure to find another umbel. To examine quantitatively how the topography of yield profiles varied with simulation parameters we performed the following multiple linear regression:

Clarity of optimum index = a_1 (mean of visitation rates) + a_2 (variance of visitation rates) + a_3 (variance/mean of visitation rates) + a_4 (cost of moving) + constant (The regression was actually performed using the $\arcsin \sqrt{P}$ transformation of the indices.) The results of these regressions are summarized in Table 3. The one consistent relationships seems to be that an increase in mean visitation rates tends to decrease the clarity of optima (significantly so in 3 of 4 cases). Thus, as the mean reward rate at flowers increases, predators will suffer smaller and smaller penalties for de-

viating from the so-called optimum behavior. Otherwise, relationships between simulation parameters and clarity of optima indices are weak or dependent on which index, and which simulation (TGUT versus FPOM) is examined.

On average, the optimum yields obtained from FPOM simulations were one-third to one-half those obtained from TGUT simulations. For instance, using the visitation regimes we observed in the field, crab spiders could perform two times better by selecting an optimum fixed giving-up time than by selecting an optimum probability of departure. This result is not surprising. It is surprising that real spiders seem to depart umbels according to a fixed probability rule, rather than according to some giving-up time threshold; the consequences of this behavior in terms of expected yield are substantial.

Discussion

Foraging theory has recently focused on identifying the optimum behavior associated with a variety of foraging problems. Even when models have included stochastic environments or variable rewards, the emphasis of the theory has remained the identification of a particular optimum point. Yet naturalists have raised doubts about optimal foraging theory because the organisms they observe in the field often engage in a variety of behaviors that do not seem to correspond to any conceivable optimal solution (Heinrich 1983). For example, our crab spiders spend the majority of their time in flower patches of higher than average prey visitation rates, but also spend hours, or even days, hunting in flower umbels where few or no prey visit. Occasional non-optimal behavior has become the focus of much debate in evolutionary biology and modern foraging theory. Sometimes non-optimal behavior is explained away post-facto by modifications of the original optimization model (see Gould and Lewontin 1979 for a critique of this practice). In other instances, examining limitations in the information available to animals can explain certain types of non-optimal behavior (Kacelnik et al. 1981).

Animals may also fail to optimize their expected yield because they are more concerned with minimizing the variance of their reward (Barnard and Brown 1985; Caraco and Gillespie 1986), than with expectations. Indeed, Caraco and Gillespie (1986) have recently analyzed a model of ambush spider foraging that predicts different strategies of movement depending on the variance of prey encounter rates. We did not apply this model to crab spiders because the model gives the predator only two alternatives: move every day or sit still (a dichotomy that does not conform to crab spider behavior).

We suggest here another explanation for why organisms often behave suboptimally – it simply may not matter much to the yields that are obtained. Using actual field data on visitation rates our stochastic simulations of two different types of decision processes (fixed giving-up time, and fixed probability of giving-up) indicate that optimum behaviors often do not stand clearly above alternative behaviors. For many visitation regimes, wide departures from the simulated optimal behavior produced almost no perceptible change in the yield to the spider. Of course a point optimum still exists; but the topography of yields is such that it might be difficult for natural selection to single out one stereotyped optimal behavior. For this reason we think much is to be gained by paying attention to entire yield

landscapes, not just optimal points. Field biologists would do well to quantify the yields foragers obtain when following a variety of different behaviors; theoreticians could contribute by developing a rigorous way of characterizing yield topographies (as opposed to our ad hoc “clarity of optima” indices). Finally we must address the question of whether our impression of “unclear optima” is simply an artifact of our models. We think not because the only guess that entered our models was the cost of moving, and the appearance of “unclear optima” was independent of this cost. For any cost of moving, there was a wide range of visitation rates and variances in visitation rates that produced yield topographies without any clear optima.

The most striking finding of our field observations is the suggestion that spiders seem to leave umbels at random, rather than following a fixed giving-up time. The evidence for this is the good fit of exponential probability distributions to the departure times of spiders. This does not mean, however, that the probability of moving is a constant – it could be adjusted by stomach fullness. A random departure process with a probability of leaving that varies with stomach fullness will lead spiders to spend most of their time on umbels with relatively higher than average visitation rates. We are currently experimentally testing the idea that spiders simply leave umbels at random, but at a rate determined by how well fed they are.

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