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The Foraging Behavior of Lacewing Larvae on Vertical Rods

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Abstract

The foraging behavior of lacewing larvae (*Chrysopa carnea* Stephens, Chrysopidae, Neuroptera) on vertical lucite rods was observed under a variety of experimental conditions to investigate the decision processes responsible for the distribution of foraging effort. Food deprivation increased the duration of searching on all parts of the rod, whereas contact with prey at the rod tip induced only a local enhancement of searching activity. Searching at the rod tip did not decline with repeated trials on the same rod, but the duration of searching on the rest of the rod was reduced, evidently reflecting recognition and avoidance of previously-searched substrates. There were indications that the larvae compensated for changes in the surface area, radius of curvature, and length of the rod. Searching patterns at the tip and on the rest of the rod proved to be independently modifiable, suggesting a two-tiered hierarchy of foraging decisions. The total duration of the search depended primarily on the pattern of vertical movement and the number of reascents, rather than the searching effort per unit area. Evidence of a negative geotaxis was found only during the initial ascent of the rod, and no sequential pattern in the lengths of vertical excursions was observed. The decision process appeared to involve a combination of variable control factors interacting with a generally constant, random probability of change or reversal of direction. The resulting investment of foraging time corresponded surprisingly well with expectations derived from optimal foraging theory, thereby testifying to the power of approximate, semi-random decision processes.

The allocation of an animal's time and effort in foraging entails a series of essentially economic decisions, choices that turn on the amount available for investment and the expected return from each of the possible courses of behavior (Staddon 1980). As a consequence of this resemblance to microeconomic theory, the optimal decision strategy for an active forager, in terms of maximizing the net yield of nutritional "currency," can often be precisely specified, at least for particular, simplified systems (Krebs 1978; Krebs et al. 1981). Foraging is also similar to economics, however, in that the choice among available investment options is conditioned by information, the knowledge one possesses that is pertinent to predicting future states of nature. It is difficult, for example, to confine a search to a particular area unless the animal is in some sense aware of the configuration and boundaries of the region and of its own position within it. Other foraging decisions might require information concerning the history of searching in the given area, the proportion of the region that has already been covered, the thoroughness of the prior exploration, or the temporal patterning of food discoveries. To be fully confident of the advantage of leaving an area, an animal ought to be able to estimate the expected yield from similar patches of food and the cost of traveling to another region.

An insufficiency of information does not, however, necessarily doom a forager to arbitrary selection among unknowable alternatives. It is perfectly feasible to formulate decisions based on imperfect information, behavioral patterns that involve "rules of thumb" or approximate decision processes, which may be inferior to the mathematical optimum but generally superior to totally undirected choices (Breck 1978). Since omniscience is rare and ignorance pervasive in the real world, it should not be difficult to uncover empirical evidence of approximate decision processes. It may well be, in fact, that the central behavioral questions involved in foraging concern the analysis of what information a foraging animal actually possesses, what it does with this information, and what reliance it places on approximate, semi-random solutions to foraging problems.

A second complicating factor in real-world foraging is spatial complexity. Because few prey species are found on a uniform, featureless surface, movement between prey patches will often require more than a single strategic decision. In spatially complex habitats, the discovery of a food item represents the outcome of an hierarchical series of decisions among successively smaller conceptual categories. An insectivorous bird, for example, might be thought to

choose first among possible hunting areas, then among tree species within the area, then among individual trees, then among microhabitats on the tree. When searching in one set of circumstances has become unproductive, a predator should switch to alternative behavioral patterns, beginning at the lowest level of the hierarchy. Persistent lack of success would then lead to switching at progressively higher levels, until a sufficient density of prey was encountered.

The power of semi-random, hierarchical decision structures to generate complex and adaptive foraging behavior has not been subject to experimental analysis. One group of organisms that appears especially suitable for such an investigation is the guild of aphidophagous predators, including coccinellids, syrphids, and lacewings. These insects feed on aphids and other sessile prey that typically congregate at the growing tips of plants. Since the distribution of aphids among stem tips is commonly quite patchy and irregular, the decision of the amount of effort to invest in any given area is crucial to the predator's success and continued survival. All of these insects are apparently contact predators, incapable of recognizing their prey at a distance (Fleschner 1950). The profitability of extended searching in a patch is, therefore, mostly a matter of inference from prior information, rather than of detection of new resource concentrations from a distance. Although much of the behavioral research on aphid predators has involved observation of their locomotion on horizontal surfaces in the laboratory (Fleschner 1950; Banks 1957; Dixon 1959; Kaddou 1960; Bänisch 1964; Chandler 1969; Bond 1980), they are virtually arboreal in their natural habitats, foraging mainly in crevices and clefts in the foliage, along leaf veins and edges, and at the tips of growing shoots (Bänisch 1964). Since they customarily forage in spatially complex environments, they are excellent candidates for investigation of hierarchical decision structures. A few, mostly qualitative studies have been made of their searching behavior on complex substrates (Fleschner 1950; Banks 1957; Dixon 1959; Bänisch 1964), but little is known of the behavioral mechanism involved. To examine the effects of spatial complexity on foraging and to investigate the information requirements of the underlying decision process, a series of experiments were performed on second-instar larvae of the green lacewing, *Chrysopa carnea* Stephens.

General Methods

Subjects

Lacewing eggs were obtained from a laboratory culture maintained by the University of California Agricultural Experiment Station in Albany, California. All animals used in this study were second- to tenth-generation descendents of adults captured in the field. The larvae were reared individually in 15-ml shell vials in a controlled environment: 21.0 ± 0.5 °C, about 50% relative humidity, and a 16 L:8 D (long day) light cycle. Freshly killed pea aphids, *Acyrtosiphon pisum* (Harris), were supplied in excess once daily. Experiments were conducted on the day following the first moult, approximately 7 to 8 days after hatching.

Apparatus

Searching behavior was observed on cylindrical lucite rods of standard dimensions: 10 cm long and 8 mm in diameter. The rods were graduated in 1-cm intervals and interchangeably mounted at the center of a circular arena 11 cm in diameter, to which the animals were confined with a heated nichrome wire. The apparatus was placed adjacent to a vertical mirror to facilitate continuous observation and was illuminated from above at about 4000 lux.

During pilot trials, the larvae spent a large proportion of their searching time following the circumference of the upper edge of the cylinders. To distinguish responses to the rod tip itself from the apparent attractiveness of sharp edges, the upper rim of each cylinder was smoothly ground away, leaving an approximately hemispherical surface. This alteration had the added advantage of bringing the surface area of the tip interval into rough equivalence with that of each of the lower, "stem" intervals on the rod. Any difference in searching activity per interval between the stem and the tip should, therefore, reflect a response to the topography of the rod, rather than a consequence of edges or differences in surface area.

In the process of locomotion, particularly on vertical surfaces, chrysopid larvae secrete copious quantities of viscous material from the adhesive gland at the tip of the abdomen (Spiegler 1962). Because of the possibility that traces of this substance left on the apparatus might influence the subsequent behavior of the animals, the rods were scrubbed thoroughly in hot Alconox solution and the surface of the arena was covered with a clean sheet of absorbent paper (Bench Kote) prior to each trial. Tests with ninhydrin spray

(Spiegler 1962) before and after cleaning demonstrated that this procedure was generally effective in eliminating residues of the adhesive substance.

Observation Protocol

To initiate searching, the larva was picked up with a camel's hair brush and released on the rod about 2-4 cm above the base. It usually proceeded to climb the rod all the way to the tip, either directly or after first descending to the base and returning. If the larva left the rod without first reaching the tip, it was picked up from the arena and the trial was restarted. To assure a uniform behavioral sample, only that portion of the search commencing with the first entrance into the tip interval was considered in the subsequent analysis. The sequence of movements between adjacent intervals and the duration of searching and pausing within each interval were recorded on computer tape with a digital event recorder. Recording was terminated when the larva abandoned the rod and wandered out into the arena,

Analytical Measures

From the perspective of foraging theory, the measure of primary interest is the duration of active searching. It was defined in this study as the elapsed time between the initial entrance into the tip interval and the animal's departure from the rod, excluding periods in which the larva was motionless. To investigate the underlying behavioral mechanism, the search duration was considered to be partitioned into two components: the number of "visits," or entries into suc-

cessive centimeter intervals in the course of a trial, and the "dwell time," the duration of active searching within a single visit (Fig. 1).

Evidence from pilot studies suggested that the dwell time in the terminal interval differed strikingly from that on the remainder of the rod. The dwell time component was, therefore, computed separately for the two regions. For each centimeter interval, the number of visits, the cumulative duration of active searching, and the amount of time spent motionless ("pause time") were calculated from the recorded sequence of events. To obtain an average measure for the "stem," totals for these three primary variables were pooled across the nine lower intervals of the rod. The mean dwell time in each region was then estimated from the ratio of the total search duration in that region to the number of visits. Analysis of the spatial distribution of searching effort thus entailed the evaluation of effects on two variables, mean dwell time and pause time, in two locations, the tip and stem intervals.

Because of the rarity of directional reversals during ascent, the number of visits proved to be almost entirely a function of the number of reascents. Analysis of the visits component of the search duration was, therefore, mainly concerned with the sequential pattern of vertical movements. Analyses of behavioral sequences can be very complex, especially if the generating process contains systematic, nonrandom elements, as, for example, a tendency for the length of descending runs to increase in the course of a trial. If, however, the generation of reascents is considered (to

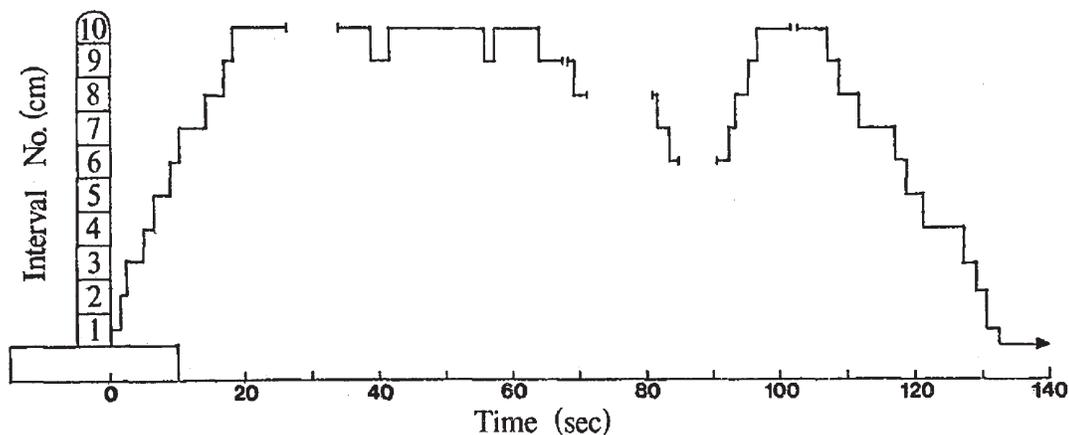


Figure 1. Time course of a typical rod search. Each tread in the step function, represents a visit to that interval. The width of the tread corresponds to the dwell time for that visit. Gaps indicate pauses, which are measured independently from the dwell time.

a first approximation) as a Poisson renewal process, two measures — the number of reascents and the total duration of descending runs — together suffice to account for the pattern of vertical movement. The ratio of their means across a sample of searching trials provides the best estimate of the primary generating parameter: the rate or probability of reascent. Some justification for this simplifying assumption will be provided in a post hoc analysis.

Experiment 1: Deprivation and Prey Contact

The two most consequential pieces of information for a foraging predator are the expected number of prey per patch and the recent history of prey discovery. The optimality literature has focused much of its attention on these two variables, hypothesizing that the expectation sets a standard against which the recent experience in the patch is judged, thereby determining the appropriate moment for departure (Charnov 1976a; Krebs 1978). It has been argued that the most readily accessible long-term gauge of the richness of the habitat may be the animal's level of hunger motivation (Charnov 1976b; Wilson 1976), and manipulation of hunger appears to provide a satisfactory mimicry of the expectation variable, at least in lacewings (Bond 1980).

Experience within the particular patch is more difficult to control satisfactorily, since the critical factors are less readily isolated. The experimental literature has held primarily to a time threshold model, under the assumption that the elapsed time since the last previous encounter with prey provides a feasible measure of the recent rate of prey discovery, and that whatever experiential variable the animal is actually tracking is probably correlated with it (Krebs et al. 1974). This assumption is not always tenable, however. In the case of lacewings, there is some evidence that the decision to abandon a patch is reached without regard to a specific time threshold (Bond 1981); chrysopid larvae appear to operate as if the distribution of prey among patches were not distinguishable from a Poisson function.

Vacant stem tips must be vastly more common in the real world than would be expected from the distribution of the number of prey individuals on occupied tips, however. It therefore seems reasonable to assume that an indifference to the number of prey encountered in a patch, or the patch-specific encounter rate, should not hold for vacant patches. One would

expect even a very primitive predator to draw a distinction between potential patches, i.e. appropriate substrates for prey aggregation, and patches that have shown evidence of prey actually having been present. The first experiment was therefore concerned with the modifications of searching behavior that were induced by changes in the level of deprivation and by the discovery of a single aphid at the rod tip.

Methods

Thirty-four larvae were satiated by confining them for 30 min with an excess of freshly-killed pea aphids. They were then randomly assigned to two equal-sized treatment groups and deprived of food for either 2 or 8 h. Earlier studies (Bond 1978) provided evidence of the efficacy of the satiation procedure and demonstrated that larvae exposed to these two levels of deprivation displayed significantly different levels of hunger.

Each animal was required to search the same rod twice in succession. The first search by each larva was unrewarded, but a freshly-killed, first-instar pea aphid was placed at the rod tip before the predator was released for the second trial. If the larva subsequently abandoned the rod without having encountered the aphid, it was picked up from the arena, and the trial was restarted. Upon discovery of the aphid, the larva characteristically grasped it between its mandibles and transported it to the side of the tip interval, where it commenced feeding in a head-downward position. As a consequence of this behavior, the meal was invariably terminated when the predator released the remains of its prey, allowing the body to fall away from the rod and out of the predator's reach (Bond 1978). The duration of feeding was recorded, along with the sequence and timing of the subsequent search.

Results

A three-way analysis of variance (Deprivation \times Experience \times Location), with repeated measures within deprivation treatments, was performed on the dwell time and pause time measures from the 68 searching trials. The total search duration, duration of descents, and number of reascents were treated similarly, except that the analysis design did not include a Location factor. To reduce the effects of a strong positive skew in the distributions of all five measures, they were transformed before analysis with natural logarithms. Means of each variable for each treatment combination are displayed in Table 1.

Table I. Mean Search Measures from Deprivation Experiment

Deprivation	Experience	Location	Total search time (s)	Dwell time (s)	Pause time (s)	Duration of descents (s)	No. of reascents
2h	Before Feeding		61.63				
		Tip		13.32	1.85		
		Stem		2.18	9.35	32.71	0.824
	After Feeding		67.31				
Tip			14.55	21.71			
		Stem	2.20	0.16	28.70	1.176	
8h	Before Feeding		109.03				
		Tip		14.82	19.66		
		Stem		3.05	13.61	51.76	2.118
	After Feeding		108.69				
Tip			26.77	38.51			
		Stem	3.24	5.44	45.22	1.765	

Effects of deprivation. Animals at the lower deprivation level appeared to turn back more readily during the initial ascent, and it was also generally more difficult to elicit feeding in these larvae. Their search of the tip was often so cursory that they missed contact with the aphid altogether. When they did encounter the prey, they often brushed it aside, as if they did not recognize it as food. Once they could be induced to pierce the aphid's cuticle, however, even low-deprivation animals usually proceeded to feed for several minutes. The mean duration of feeding was significantly different between deprivation treatments: 378 ± 99 s for 8-h animals and 159 ± 58 s for 2-h animals ($t(32) = 3.98$, $P < 0.001$).

The primary effect of deprivation on the search measures consisted of an increase in the pause time ($F(1,32) = 7.39$, $P < 0.025$) and in the dwell time ($F(1,32) = 5.30$, $P < 0.05$), both on the tip and on the stem. There were suggestions of a similar effect on the visits component of the search, with deprivation producing an increase in both the number of ascents and the duration of descending runs. This effect was not statistically significant, however ($F(1,16) \leq 3.09$, $P \geq 0.09$). Because the relative difference between treatments was similar for these two measures, the estimate of the probability of reascent was virtually identical for animals at the two deprivation levels (2 h = 0.0326; 8 h = 0.400) ($z = 0.87$, $P = 0.38$; binomial test;

Cox & Lewis 1966). The total search duration was roughly 50% higher for 8-h than for 2-h animals, though the difference was only marginally significant ($F(1,16) = 3.71$, $P = 0.07$).

Effects of prey contact. As had been previously observed, the tip interval was treated very differently from the remainder of the rod, both before and after prey contact. Both the mean dwell time ($F(1,32) = 384$, $P < 0.001$) and the pause time ($F(1,32) = 10.4$, $P < 0.01$) were significantly higher at the tip than on the stem. The main effect of location on pause time, however, was clearly only a reflection of the strong interaction of the prey contact and location factors, and the significant effects of prey contact were exhibited entirely in such interactions. Contact was seen to increase the duration of pausing at the tip, while decreasing it substantially along the stem ($F(1,32) = 4.12$, $P = 0.05$). There was a conspicuous increase in dwell time at the tip following feeding, particularly in the high-deprivation animals ($F(1,32) = 4.55$, $P < 0.05$), which was wholly a reflection of an increase in dwell time in the first tip visit following feeding ($t(50) = 4.20$, $P < 0.002$). The mean dwell time for later visits did not differ significantly from that observed before feeding ($t(111) = 0.76$, $P > 0.3$). Movement on the stem was relatively unaffected by contact, and the treatment had no apparent influence on the pattern of vertical movement or the total search time.

Discussion

The primary consequence of food deprivation was an increase in the duration of searching, apparently mediated mainly by an increase in the dwell time on all parts of the rod. The pattern of vertical movement was less conspicuously affected by the treatment, but the tendency in the data is clearly toward an increase in the number of reascents with increasing deprivation. In a study of searching by coccinellid larvae, Dixon (1959) found a significant negative correlation between the number of reversals of direction and the duration of deprivation. He employed levels of deprivation greatly in excess of those used here, however, potentially severe enough to induce debility and inanition. It seems possible that his observations could be ascribed less to a strategic modification of searching behavior than to a reduction in the larva's capacity to reascend the rod. The increase in pause time with deprivation was also observed in chrysopids by Bänisch (1964), who attributed the effect to weakness and exhaustion resulting from starvation. While exhaustion could be important in cases in which the deprivation was prolonged, however, the high velocities exhibited by 8-h animals during extensive searching in an open arena (Bond 1980) seem incompatible with a simple inanition hypothesis. Conceivably, extensive pausing at less extreme levels of deprivation could represent an effort to conserve energy in preparation for the approaching larval moult. Moulting is an energetically demanding process, one that entails a considerable increase in the risk of mortality. At high deprivation levels, when prey are relatively scarce, it may be to the larva's advantage to husband its accumulated energy stores to offset the stresses of moulting, rather than to risk dissipating them in a futile search for additional prey.

Chrysopid larvae clearly modify their searching behavior in response to prey contact, but the effects appear to be confined to a transient redistribution of effort in the terminal interval. The mechanism is probably analogous to the intensive searching behavior elicited by prey contact in an open field (Bond 1980). The total duration of the search was identical before and after feeding. Whatever the mechanism the larvae employ to determine their foraging investment on the rod as a whole, therefore, it is apparently unresponsive to the discovery of prey.

Experiment 2: Repeated Trials

A second category of information that is pertinent to foraging success is the history of prior foraging efforts at a particular site. Predatory efficiency is generally enhanced when animals can systematically avoid areas they have previously searched and depleted. A degree of avoidance can often be achieved by fairly simple mechanisms, even in the absence of memory for specific locations. Bänisch (1964), for example, has contended that unrewarded searching on model plants induces a central inhibitory state that effectively prevents additional ascents until the animal has been allowed to search on a horizontal surface for a sufficient period of time. This suggestion appears to be open to test.

To explore Bänisch's hypothesis, a second experiment was performed, in which chrysopid larvae were required to search the same rod, without contact with prey, five times in rapid succession. This design had the auxiliary advantage of supplying a control for the treatment sequence in the deprivation experiment. Because the prey-contact treatment was always second in the series, it was logically possible that the effects attributed to prey discovery were actually consequences of repeated searching trials on the same substrate. Repeated, unrewarded trials should provide an appropriate test for this possibility.

Methods

Fifteen larvae were satiated and deprived for 2 h, as described previously. They were then subjected to five successive unrewarded searching trials on the same, standard 10-cm rod. The rod and arena surface were exchanged for clean materials prior to the first trial for each subject, but were not altered between trials within subjects.

Results

After the second successive search of the same rod, the larvae showed an increasing reluctance to make the initial ascent for a new searching trial. At times, several restarts were required to induce the animal to climb to the tip. Analysis of variance, using repeated measures and a logarithmic transformation of the dependent variables, was performed on each of the five search measures, as described in the deprivation experiment; the mean values are displayed in Table II.

The major significant effect of repetition was the virtual elimination of pausing in the later trials

Table II. Mean Search Measures from Repeated Trials Experiment

Trial No.	Location	Total search time (s)	Dwell time (s)	Pause time (s)	Duration of descents (s)	No. of reascents
1	Tip	62.98	11.14	3.50	33.12	1.294
	Stem		2.14	5.10		
2	Tip	55.92	10.04	0.21	27.86	1.294
	Stem		2.24	0.77		
3	Tip	31.72	9.03	0.86	17.70	0.467
	Stem		1.57	0.00		
4	Tip	37.13	8.55	0.08	17.87	1.000
	Stem		1.42	0.37		
5	Tip	40.98	9.60	0.00	20.08	0.667
	Stem		1.54	0.00		

($F(4,56) = 4.81, P < 0.01$). Dwell time on the stem declined by over 30% between the first two trials and the last three. Tip dwell time was only slightly reduced with repetition, however, and there was no significant main effect ($F(4,56) = 1.92, P > 0.1$): The number of reascents was reduced significantly by repetition ($F(4,56) = 2.54, P = 0.05$), along with the duration of descending runs ($F(4,56) = 4.01, P < 0.01$). Because the decline in the duration of descents was proportionately somewhat less than the decrease in the number of reascents, the estimate of the probability of reascent declined slightly with repetition, from 0.0481 per s for the first two trials to 0.0383 per s for the last three. The decrease was not significant, however ($z = 0.86, P = 0.39$, binomial test; Cox & Lewis 1966).

The relatively constant probability of reascent combined with the reduction in stem dwell time to produce a greatly altered pattern of vertical movement in the later trials, with much longer descending runs. In the first two trials, 24 of the incomplete descents (63%) were between 1 and 2 cm in length; in the last three trials, only 15 descents (34%) terminated in this interval. In contrast, 15 (34%) of the incomplete descents in the last three trials terminated in the lowest three intervals, while only 7 (18%) of those in the first two trials extended that far. Owing mainly to the change in the pattern of vertical movement, the total

search duration declined significantly with repetition ($F(4,56) = 11.76, P < 0.01$).

Discussion

With repeated searching, larvae were distinctly less likely to climb a rod they had abandoned; they were more likely to leave it upon their return to the base; and the duration of their search on the rod as a whole was reduced. These results are generally consistent with Bänisch's (1964) hypothesis of inhibition; though the source of the inhibitory effect remains elusive. Multiple trials required considerably more handling of the larva and disruption of its behavior, for example, and this could easily have been as important as the repeated rod exposures in producing a reluctance to ascend. It is also not clear whether the inhibition was substrate-specific, as is often true of habituation processes, or whether, as Bänisch assumed, the effect was the manifestation of some general avoidance condition. In the former case, the effect would not have been observed if the rods had been exchanged for novel substrates between successive trials: in the latter, even novel rods would have been treated similarly by the animal, if it were deprived of the opportunity for horizontal search. The next experiment presents some evidence that bears on this issue.

The effects of prey contact observed in the deprivation experiment were clearly not a simple conse-

quence of repeated trials on the same rod. The increase in pause duration and the concentration of pauses at the tip of the rod that followed prey contact were not evident when the trials were repeated without feeding. Repeated trials, in fact, eliminated pausing altogether. Repetition also did not increase the dwell time at the tip: the animals searched the tip upon each arrival almost as thoroughly as if they had never been there before.

Experiment 3: Rod Geometry

A third type of information relevant to searching success is a knowledge of the configuration of the substrate. Substrate configuration influences the distribution of prey, providing a direct indication of likely concentrations of food. If the predator is aware of the limits of the patch and of its position within it, foraging efforts can be invested in accordance with such fine-grained differences in the probability of prey encounter. That lacewings respond differentially to at least some features of substrate topography is evidenced by the non-uniformity of distribution of their searching activity on the rod. Despite the fact that each centimeter interval had approximately the same surface area, the mean dwell time was roughly six times as high at the tip as on the stem, whatever treatment regimen was applied. Bänisch (1964) observed a similar non-uniformity in the searching patterns of several aphidophagous predators and suggested that it may reflect a specific adaptation to searching for insect prey that tend to feed preferentially on the new growth at shoot tips.

The simplest mechanism that could produce this effect is a relative inhibition of lateral movement on the stem, presumably as a consequence of the curvature. Lacewings, like many other insects, will readily follow convex edges, such as the rim of a petri dish or the edge of a leaf blade, while exhibiting considerable reluctance to move across them. In Fleschner's (1950) study of the searching behavior of aphid predators on cones, in which the radius of curvature of the substrate decreases as the animal ascends to the tip, the illustrations clearly suggest that the frequency of vertically oriented movements is much higher toward the apex.

If curvature is responsible for channeling the larva into vertical movement, doubling the radius of the rod ought to reduce the strength of the orienting stimulus. An increased frequency of lateral movement would

then become evident as an increase in the mean dwell time on the stem and a decrease in the probability of reascent. On the other hand, a similar increase in the total surface area of the rod produced by doubling its length, while maintaining a constant radius, should have little influence. To test this hypothesis, an experiment was designed to manipulate the length and radius of curvature of the searching substrate.

Methods

For analysis of the influence of rod geometry on searching, two additional substrates, each with twice the surface area of the standard rod, were prepared: "long" rods, which were 20 cm × 8 mm, and "thick" rods, which were 10 cm × 16 mm. As in the previous experiments, the rods were graduated in 1-cm intervals. The intervals on the thick rod were thus the same height as those on the standard substrate, but twice the circumference (50 mm versus 25 mm); the intervals on the long rod were identical in height and area to those on the standard, but there were twice as many of them. Eighteen animals were subjected to three successive, unrewarded searches, one on each of the three rod types. The order of presentation was varied systematically in a 3 × 3 Latin square design. Other than assuring that the animals were reasonably well motivated, however, the level of hunger was not controlled.

Results

Mean values of the primary search measures for each rod treatment and successive position are displayed in Table III. Two-way analyses of variance (Rod Shape × Location and Position × Location) were performed on the dwell time and pause time variables; analysis of the pattern of vertical movement did not include the location factor. The only significant, effect of rod shape on dwell time was the interaction term ($F(2,34) = 3.52, P < 0.05$), apparently reflecting a disproportionate enhancement of the dwell time at the rod tip in both experimental treatments and a reduction in the stem dwell time on the long rod. There was some suggestion of a lower pause duration on the long rod, but the trend was not statistically significant ($F(2,34) = 2.77, P = 0.08$). As in the previous experiments, dwell time was significantly higher at the tip than on the stem ($F(1,17) = 484, P < 0.0001$).

The mean number of reascents was lower on the thick rod, in accordance with the prediction, but the difference failed to achieve significance ($F(2,34) = 0.42, P > 0.2$); there was also a strong suggestion of

Table III. Mean Search Measures from Geometry Experiment

A. Treatment effects						
Rod shape	Location	Total search time (s)	Dwell time (s)	Pause time (s)	Duration of descents (s)	No. of reascents
Standard	Tip	90.54	7.83	12.07	46.25	2.833
	Stem		1.88	13.31		
Long	Tip	123.99	17.91	5.18	67.66	2.667
	Stem		2.39	5.56		
Thick	Tip	89.63	12.07	9.38	40.08	1.722
	Stem		1.83	10.73		
B. Position effects						
Position	Location	Total search time (s)	Dwell time (s)	Pause time (s)	Duration of descents (s)	No. of reascents
First	Tip	105.25	13.44	14.38	51.52	2.611
	Stem		2.02	13.45		
Second	Tip	95.03	11.96	9.43	47.80	2.389
	Stem		2.08	11.02		
Third	Tip	103.89	12.41	2.82	54.68	2.222
	Stem		2.01	5.13		

a higher incidence of subterminal reversal of ascent on the thick rods, again qualitatively supporting the notion that curvature plays a role in channeling vertical movements. Search duration was not perceptibly affected by the change in radius. The duration of descending runs was significantly longer on the long rod ($F(2,34) = 4.46$, $P < 0.025$), reflecting a generally longer total search time ($F(2,34) = 2.81$, $P = 0.07$); the number of reascents did not appear to be affected by rod length. As a result of these effects, the probability of reascent was lower for both experimental treatments (0.039 for long; 0.043 for thick; 0.061 for standard), though the difference was only significant for the long rod ($z = 2.11$, $P < 0.04$, binomial test; Cox & Lewis 1966). The only significant effect of sequential position was to reduce pause time ($F(2,34) = 3.34$, $P < 0.05$). In contrast to the repeated trials experiment, serial forced searches of different rods had no signifi-

cant impact on the number of reascents or the search duration ($F(2,34) < 0.85$, $P > 0.3$).

Discussion

Doubling the radius of curvature was clearly not sufficient to tempt the larvae into extensive lateral movement, though there was good qualitative evidence of an increased tendency to circumnavigate, rather than ascend, the thick rods. The absence of a significant effect on stem dwell time may only indicate that the increase in mean distance moved per interval was too small to make itself felt statistically. The increase in tip dwell time on the thick rods suggests that the animals do compensate for an increase in surface area when turning is relatively unconstrained.

Doubling the length of the rod increased the search duration, but by only about 25%. The reduction in the probability of reascent apparently offset the effects of

increased stem length to some degree. The enhanced dwell time at the tip of the long rod was not directly predicted by the inhibition hypothesis, but it could represent a rebound effect (Kennedy 1966), in which the more protracted inhibition of turning during the longer ascent induces a much higher level of turning at the tip when the constraint is finally released.

The difference between this experiment and the previous one in the effects of sequential searching trials suggests that recognition of the substrate could play a role in the inhibition of reascent. The delay between successive trials was slightly longer in the rod geometry experiment, owing to the necessity of exchanging the substrates, and this might also have played a role. If substrate recognition is involved in the inhibition effect, it would be interesting to know whether it depended only on general features of the topography, or whether it might also be influenced by the gradual accumulation of adhesive-gland secretion. The hypothesis that the secretion may function as a kind of trail pheromone, indicating areas that have been heavily searched and dissuading the animal from returning to them, is certainly a tenable alternative, one that is susceptible to systematic exploration and testing. The reduction in pause time, at any rate, is clearly a consequence of some other factor, possibly the increase in the amount of handling and manipulation suffered by the animal in successive, repeated trials.

Experiment 4: Post Hoc Analyses of the Behavioral Mechanism

The distribution of foraging effort in these experiments is consistent with a two-tiered decision hierarchy, in which the decision to leave the tip interval is causally distinct from the decision to leave the rod as a whole. The functional separation is suggested by the disproportionately greater dwell time at the tip, but the strongest evidence is provided by the differential response of stem and tip searching measures to experimental treatment. Searching on the stem, as reflected by stem dwell time, number of reascents, and the search time variables, was strikingly affected by repeated forced trials on the same rod, but was not perceptibly influenced by prey contact at the tip. Conversely, tip dwell time and pause time were amplified subsequent to prey contact, but no effect on tip dwell time was produced by repeated trials. Manipulation of other variables yielded effects at both lev-

els, but only in the case of food deprivation were they clearly similar in magnitude and direction. To examine these decision processes in greater detail and to begin to unravel the underlying behavioral mechanism, a post hoc analysis was conducted of foraging behavior in the two regions.

A. The Decision to Leave the Rod

One common feature of all three experiments was the responsiveness of the dwell time measure to experimental manipulation. It is, therefore, paradoxical that it was actually the number of visits, rather than the mean dwell time, that exerted the strongest influence on the total duration of the search. On all searches of the standard 10-cm rod, pooled across experiments, the number of visits accounted for 78.1% of the variance in total searching time, while differences in mean dwell time accounted for only 14.1%. The number of visits, in turn, was determined almost entirely by the number of reascents: the number of reascents per trial accounted for 92.4% of the variance in the number of visits, while the mean length of descending runs accounted for only 4.6%. It appears that a more detailed analysis of the pattern of vertical movements may be required to illuminate the decision process for the rod as a whole.

A coherent model of rod-searching has never been advanced in the literature, but a simple hypothesis that appears generally consistent with their reported results can be gleaned from the writings of Dixon (1959) and Bänisch (1964). The model proposes that larvae are negatively geotactic during their initial ascent, but that a period of searching at the tip initiates a reversal in their preferred orientation, and they begin to descend the rod. At some point in their descent, they may again reverse the geotaxis and return to the tip. The probability of recurrence of a negative geotaxis is postulated to decrease with time, allowing the animal to descend further down the rod in each successive run. Finally, one descent reaches into the basal interval, and the animal leaves the rod.

There appear to be three components of this hypothesis that are subject to test. The first is that the probability of reascent is independent of the animal's position on the rod. The second is that this probability gradually decreases over the course of the trial, generating progressively longer downward runs. The third is that the larva's direction of movement on the rod is determined with reference to the gravitational field. Evidence bearing on all three components can be obtained from data gathered in this study.

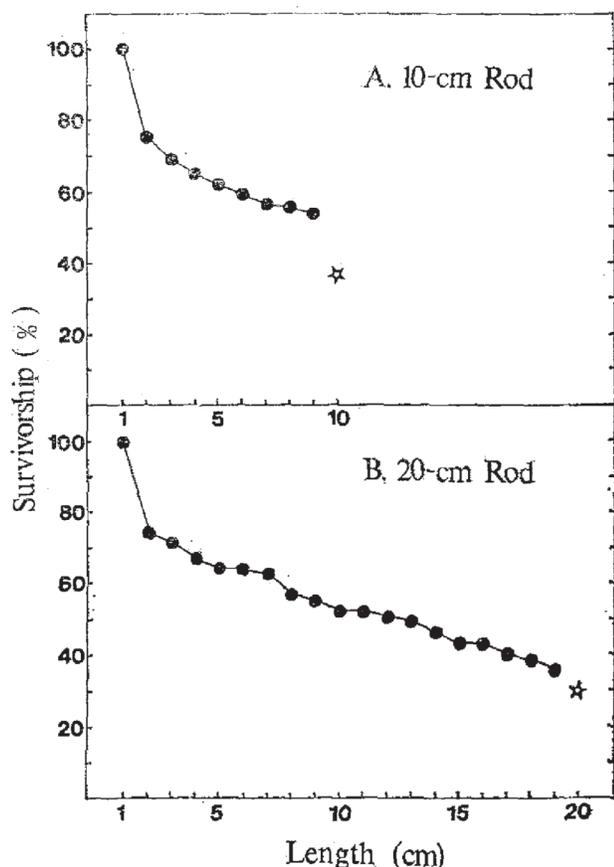


Figure 2. Survivorship curves of descending runs, pooled across experiments. Asterisks indicate the proportion of descents that terminated in exit from the rod.

The probability of reascent. When climbing the rods, chrysopid larvae almost invariably ascend all the way to the tip. Descending runs are more indeterminate, their end-points being distributed throughout the length of the rod. The pattern of vertical movement can therefore be viewed as a projection of the spatial probability distribution of the terminations of descending runs. The simplest null hypothesis is that the larva behaves as if it were unaware of its position on the rod, implying that the probability of reascent should be essentially constant, and that the length of descending runs should approximate a Poisson variate. This prediction is testable.

If the probability of a reascent is essentially constant and independent of the animal's position on the rod, the survivorship curve for descending run should display a logarithmic decline with increasing distance from the tip. The searches on standard rods in the deprivation and rod geometry experiments were pooled with the first two searches for each an-

imal in the repeated trials experiment, generating a total of 333 descents, of which 122 terminated in exit from the rod. The survivorship distribution for these descending runs (Figure 2A) was analyzed for significant deviations from a log-linear null hypothesis, using Durbin's modification of the Kolmogorov-Smirnoff statistic (Cox & Lewis 1966). A similar analysis was performed on 67 descending runs from the searches on 20-cm rods in the rod geometry experiment (Figure 2B).

The descending runs from the standard rods showed a significantly concave survivor function ($D^+ = 0.133$, $P < 0.001$), suggesting a disproportionately higher probability of reascent from the basal interval. To confirm this inference, the distribution was analyzed using only descending runs that terminated in intervals 2-9 (a total of 154). The survivorship function from these data was not statistically distinguishable from the log-linear hypothesis ($D^- = 0.057$; $P > 0.1$).

A similar pattern seemed to hold for the 19 intervals on the long rod, with an excess of reascents from the basal portion ($D^+ = 0.229$, $P < 0.005$). In this case, however, the anomaly extended further up the rod, since removal of reascents from the basal interval did not alter the pattern or greatly reduce the significance ($D^+ = 0.197$, $P < 0.025$). The region of deviation was limited, however; the survivorship distribution for the 10 terminal intervals on the long rod was indistinguishable from that for the entire standard rod, and tests performed on reascents from intervals 11-19 showed no deviation from the log-linear hypothesis ($D^- = 0.106$, $P > 0.1$).

Trends in the length of descending runs. The results of the survivorship analysis suggest that the probability of reascent is independent of the animal's position over most of the rod, though there does seem to be a disproportionate enhancement of reascent from the basal intervals. It is still possible, however, that this probability is not constant with time, but decreases systematically in the course of a searching trial, generating downward runs that become progressively longer, finally culminating in departure (Dixon 1959). To test this hypothesis, a sample of 38 searching trials was extracted from the pool of observations on standard rods described above. The criterion for selection was the occurrence of at least two descending runs of differing length, other than the final descent and exit from the rod. By Dixon's

hypothesis, whenever two incomplete descents occurred in succession, the second member of the pair should, on the average, be longer than the first. In the 38 searches in the sample, there were 115 such pairs of sequential descents (excluding ties). In 64 of these (56%), the second run was longer than the first. This was not sufficient to infer an increasing trend ($B^* = 1.21$, $P > 0.1$; Fisher's sign test; Hollander & Wolfe 1973). Similar results were obtained on the 20-cm rod. There were 35 pairs of descending runs recorded, of which 15 (43%) accorded with Dixon's hypothesis. Again, the hypothesis of an increasing trend was not supported ($B^* = -0.68$, $P > 0.7$; Fisher's sign test; Hollander & Wolfe 1973).

Geotactic orientation. A set of rough observations was performed to test Bänisch's (1964) hypothesis of alternating positive and negative geotaxes. A 20-cm rod was held vertically by the tip and a larva was placed about 3 cm up from the base. As the animal climbed toward the midpoint of the rod, its orientation was gently reversed by turning the rod end-for-end. The larva was scored as showing a geotaxis if it compensated for the change in orientation by reversing its direction of movement on the rod within 5 s of the treatment. Five animals were tested several times in this fashion during their initial ascent and again after they had spent some time in searching the tip. After a 30-min recovery period, each animal was subjected to a second round of testing.

The results of the experiment appeared to depend strongly on whether the larva had previously searched and abandoned the tip. Out of 28 reversals performed during the initial ascent, the animals compensated for the change in 22 of them. On the other hand, 42 rod reversals performed after the larva had had the opportunity to search the tip and begin its descent yielded only nine compensatory turns. This difference was highly significant ($\chi^2(1) = 22.2$, $P < 0.01$).

Discussion. The assumption that the pattern of vertical movement is generated by a Poisson process, a probability of reascent that is invariant in time and space, is an attractive simplification. It appears to account for most features of the survivorship function of descending runs (Figure 2), as well as explaining the high variance in the search duration data and the indications, described in an earlier paper (Bond 1981), that the decision to leave the

rod is not time-dependent. There was no evidence of a systematic decline in this probability of reascent with searching time. Neither in these experiments on chrysopids nor in those of Banks (1957) on coccinellid larvae did Dixon's (1959) postulated sequence of descending runs emerge. There were suggestions, however, that some aspects of the substrate configuration may be influential in altering the probability of reascent. The survivorship data indicate that the larva may be aware of its approach to the base of the rod and may alter its behavior accordingly. In addition, changes in rod geometry in the third experiment proved to be the most effective treatment, overall, in inducing a change in the mean probability of reascent.

The response to a reversal in the orientation of the rod showed clear evidence of negative geotaxis only during the initial ascent; no evidence of positive geotaxis was found at any point in the search. It is possible that the decline in geotactic compensation with repeated reversals was simply a consequence of habituation. An alternative interpretation, however, is that the discovery and search of the rod tip frees the larva from the influence of the geotaxis, allowing subsequent searching to be directed more by the configuration of the substrate than by its orientation to gravity. This suggests that vertically oriented branches in a ramified structure should be followed in the initial ascent, while horizontal or descending branches should be searched only after the animal has reached an apex and begun its descent. Bänisch's (1964) description of searching on model plants appears to be open to this interpretation.

B. The Decision to Leave the Tip

If departure from the tip interval is determined by a functionally separate decision process, it is reasonable to inquire whether it also operates as a Poisson process, or whether the decision is arrived at on the basis of some fixed criterion. Foraging theorists have argued that any fixed criterion would most probably be correlated with the elapsed time since the last prey contact (Krebs et al. 1974). To ask whether the larva is employing a decision criterion is thus roughly equivalent to asking whether there is any evidence that the duration of a tip visit is timed. If the animal is timing its exploration of the tip, the log survivorship curve for the individual tip dwell times should be convex, indicating an underlying central tendency or mean duration (Bond 1981). If there is no set criterion, but

only a constant, random probability of departure, tip dwell time should be indistinguishable from a Poisson process, and the log survivorship curve should be effectively linear.

If departure from the tip results from a decision, in even the most tenuous sense of the word, the occurrence of repeated ascents seems anomalous. Once the larva has decided that further search of the terminus is unprofitable, it ought logically to leave the rod: returning to reexamine the same region appears to be wasted effort. Either the larva must be unaware that the tip it enters in subsequent visits is the same one it has encountered previously, or the animal's criterion of profitability alters with successive encounters. The latter hypothesis is not wholly unreasonable: the fact that many larvae in the deprivation experiment required repeated visits to the tip interval to discover a single aphid suggests that their initial search is by no means comprehensive or thorough. There is thus some residual probability of the occurrence of prey at the tip, even after the larva has searched and abandoned the area. This residual chance could conceivably suffice to tempt the animal to re-examine the tip at a later stage in the search. If this were the case, however, we would expect successive tip visits to be of progressively shorter duration; since the prior exploration should have reduced the a priori likelihood of additional prey encounters. The hypothesis of a changing criterion of profitability is, therefore, open to test.

Survivorship analysis of tip dwell time. The distributions of the durations of all tip visits by 2-h and 8-h animals from the deprivation experiment were analyzed for significant deviations from a log-linear null hypothesis. A similar analysis was performed on tip visits from the repeated trials experiment. All three distributions were slightly convex, but the deviations from linearity failed to achieve significance (2-h: $D^- (61) = 0.081, P > 0.1$; 8-h: $D^- (132) = 0.068, P > 0.1$; Repeated Trials: $D^- (135) = 0.086, P > 0.1$). Tip dwell time was not, therefore, statistically distinguishable from a Poisson variate, and there was no evidence that the duration of a visit was determined by a time-dependent decision criterion.

Trends in the duration of successive visits. The hypothesis of a decreasing duration of successive tip searches was tested on the 78 trials from the pool of observations on standard rods that contained two or more tip visits. By the hypothesis, for any pair of, suc-

cessive visits within the same trial, the dwell time for the first should, on the average, exceed that for the second. There were 231 such pairs of visits in this sample of trials; in 119 of them (52%), the second visit was shorter than the first. There was therefore no evidence of a decreasing trend ($B^* = 0.46, P > 0.3$; Fisher's sign test; Hollander & Wolfe 1973).

Discussion. The absence of a fixed time criterion for the duration of a tip visit accords with previous evidence that decision processes in these animals do not rely on the continuous assessment of short-term indicators of foraging success (Bond 1981). In contrast to the exclusive and discrete choices postulated by foraging theorists (Charnov 1976a), lacewing larvae appear to generate their decisions by a kind of random walk. The repeated ascents to the same tip are, presumably, an artifact of the depauperate geometry of the apparatus, which more closely resembles the fictional organisms of parallel botany (*Tirillus vulgaris*; Lionni 1977) than the structure of any naturally occurring plant species. Chrysopids, these results would argue, are preadapted to foraging on complex, highly ramified and interdigitating plant structures, in which the chances of returning to a previously-searched terminus by chance are negligible. Banks' (1957) observations of the searching behavior of coccinellid larvae in the field seem to provide some support for this notion.

General Discussion

When chrysopid larvae were released near the base of a vertical rod, their initial ascent was rapid, apparently directed by a strong negative geotaxis. Upon first entering into the tip interval, the larvae performed a high-density, thorough search, similar to the "intensive searching" described in open-field foraging (Bond 1980). The duration of this search was increased by deprivation and by prey contact, for at least the first visit of the trial. Whether the increase was a result of changes in velocity or in the rate of turning could not be determined, but the results of the open-field study suggest that velocity may be more important, at least in the deprivation effect. The duration of the tip search was also clearly affected by the area of the tip interval and the length of the stem below it.

Eventually, the animals left the tip and began to descend the rod. To all appearances, relinquish-

ing the search of the tip was not discriminable from a Poisson process: there was no evidence that the tip search was timed. The duration of the first tip visit following prey discovery was significantly enhanced; otherwise, there was no indication that successive visits to the tip interval tended to be of shorter duration. The persistence of the animals in descent also appeared to be governed by a random walk process: a constant probability of reversal of direction. Reversal was not perceptibly affected by position on the rod, except toward the base, where the frequency of reascents was significantly enhanced. Subsequent to the initial ascent, all vertical movement appeared to be more influenced by the configuration of the rod, its orientation and diameter, than by the direction of the gravitational vector.

The probability of reversal was affected by the substrate configuration, but was not altered by prey contact, hunger, or repeated trials. Animals at higher deprivation levels produced more reascents in the course of a trial, while those subjected to repeated forced trials produced fewer. Both effects appear to have been due to the interaction between a change in dwell time per interval on the stem and a constant probability of reascent. High levels of hunger slowed the descent, increasing the frequency of turning back before reaching the base; repeated trials had the opposite effect. A similar mechanism regulated the distribution of effort in open-field searching, in which a constant turning probability interacted with a velocity that varied with hunger level to yield a differential density of searching (Bond 1980).

The resulting investment of searching time corresponds surprisingly well to optimal values derived from a knowledge of the levels of deprivation applied (Bond 1980, 1981). The actual decisions, however, appear to be hierarchically nested and approximate, involving a combination of variable control factors interacting with a generally constant, random probability of change or reversal of direction. That chrysopid larvae can, by this means, generate a pattern of investment that simulates the result of a more informed system of discrete decisions is strong testimony to the power of semi-random, hierarchical processes.

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