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Foraging Behavior of Ants: Experiments with Two Species of Myrmecine Ants

Fritz Taylor*

Department of Biology, University of Chicago, Chicago, Illinois 60637, USA

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Summary. 1. Experiments presented in this paper for two species of ants confirm the predictions of models based upon the hypothesis that the animals maximize the net rate of energy intake while foraging.

2. *Solenopsis geminata* in the laboratory recruited at higher rates to patches of sugar solution when the distance to a patch decreased, the diameter of a patch increased, or the sugar concentration increased.

3. *Pogonomyrmex occidentalis* in its natural setting recruited at higher rates to patches of seeds mixed with pebbles when the distance to a patch was decreased, the size of the patch was increased (when recruitment was already at a high level), the density of seeds was increased, or seed size was increased. When presented with a uniform distribution of seed sizes within a patch, this species tended to choose intermediate-sized seeds, but there was no tendency to choose a narrower range of seed sizes as the distance to the patch increased. This last finding was the only one inconsistent with a model based on maximization of net rate of energy intake.

4. The tendency for *Solenopsis* to respond to sugar concentration and for *Pogonomyrmex* to respond to seed size refutes the predictions of models based on minimization of the average time required to obtain each food item.

5. Increased temperature increases running speed. Thus, when the temperature increased during an experimental session for *Pogonomyrmex*, a particular rate of recruitment to a patch was maintained by a decrease in the total number of recruits on the trail to the patch.

6. Further analysis of the *Pogonomyrmex* results reveals that different levels of response to variable changes in the various experiments can be explained in terms of the model. This indicates that interference among recruits to a patch is always important to the level of response.

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* Present address: Department of Biology, The University of New Mexico, Albuquerque, New Mexico 87131, USA

Introduction

In a companion paper (Taylor, 1977), I develop models of foraging behavior for two species of ants based on the hypothesis that they maximize the net rate of energy intake during recruitment to patches of food. These models show what experiments would be necessary to test the often-stated hypothesis that the criterion for performance in foraging behavior is the maximization of net energy intake. I found that quantitative tests of either of the two models presented are critically hampered by the need to obtain values for certain parameters which would be extremely difficult to measure. I also found, however, that qualitative predictions can be tested by an appropriate experimental design. If recruitment occurs simultaneously to experimental and control patches, the values of these difficult parameters will be the same at all patches and, therefore, should not influence the results. For *Solenopsis geminata* to behave consistently with this model, recruitment should increase to a patch of sugar solution as it is moved closer to the colony, as it is increased in size, and as the concentration of the sugar solution is increased. For *Pogonomyrmex occidentalis* to behave consistently with this model, recruitment should increase to a patch of seeds as it is moved closer to the colony, as it is increased in size, as the density of seeds is increased, and as seed size is increased to a point. Also, when presented with a patch containing a uniform distribution of seed sizes over the range they can carry, *Pogonomyrmex* should choose intermediate-sized seeds and as the patch is moved farther from the colony, there should be a tendency to choose a narrower range of seed sizes. Finally, these models can be readily differentiated from simpler time-minimization models. If there is no response to sugar concentration or seed size, the models proposed for maximization of net rate of energy intake must be abandoned in favor of the corresponding time minimization models. This paper reports the results of experiments testing these hypotheses.

I chose ants as my subject not because they are interesting and abundant animals (Wilson, 1971), but because recruitment is easily quantified. *Pogonomyrmex* species typically live in habitats with sparce vegetation (Cole, 1968) allowing experimental manipulation of seed size and abundance. *Pogonomyrmex occidentalis* was most convenient to the Southwest Research Station. *Solenopsis geminata* is a suitable animal for study in a laboratory setting (Wilson, 1962). It was the only species of the genus with large colonies that the USDA would allow to be transferred to Chicago. *Solenopsis* species have considerable caste polymorphism and are active predators and scavengers. *Solenopsis geminata* is specialized to take seeds as a supplement to its diet. The "soldiers" apparently behave as seed millers (E.O. Wilson, pers. comm.). In this it differs from *Pogonomyrmex* species which, except for one, are monomorphic and specialize on seeds (Cole, 1968).

Materials and Methods

Solenopsis geminata

This series of experiments was run on a laboratory colony confined to a table-top arena. The arena was 2 m by 6 m. The colony was housed in plastic boxes, the entire unit having one opening to the outside. In addition to sucrose fed to the ants during experiments, they were fed egg baby food mixed with liquid baby vitamins. During experiments, sucrose solution was placed at designated distances from the colony in what will be called *patches*. Each patch was a 5-cm diameter plastic petri dish with top and bottom glued together. Access to the solution was permitted through a hole cut through the top to 5- or 8-mm diameter. Thus, below the hole, which determined the *patch size*, was a reservoir of solution so that concentration would not change drastically over short periods. As the reservoir became depleted, it was replenished by an eyedropper. This procedure disturbed drinking ants little. The petri dish was placed on top of a 5-cm glass vial. A wooden ramp led from the table top to the edge of the petri dish. If the dish were placed flat on the table, ants that were waiting to drink and running about on and near the patch, would be difficult to distinguish from new recruits.

Each experiment was started by setting out two patches so that a separate recruitment trail would be formed to each. Recruitment rate was measured for 12 min. For the first 50 s out of each minute, I counted the number of ants ascending each ramp. For the last 10 s, I recorded what had been measured. A 3-min running average has been used for graphing the data to filter out very short-term fluctuations in rate. Most of this variation arose from the bottleneck at the colony entrance. Thus, each 12-min period gives a 10-min count. After the recruitment rates had remained constant through two 12-min intervals of recording, the variable of interest was changed in only one of the patches. Ants were removed from *both* patches and *both* petri dishes were replaced by new ones. The colony's response was measured as the change in rate of recruitment to the altered patch relative to the control patch.

Experiments to test *Solenopsis* responses include changes in distance, patch size which alters interference among recruits on the patch, and concentration of the sugar solution which alters the energy content per worker-load. Table 1 outlines the experimental procedures for *Solenopsis geminata.*

Pogonomyrmex occidentalis

This series of experiments was run in the field at the Southwest Research Station near Portal, Arizona. The same two colonies were used for all experiments except for seed-size selection within a patch in which a third colony was used because one of the former two had become satiated. An arena was constructed around each colony to exclude other ants and to confine foraging by the colony to seeds offered by me. An area about 4 m wide and extending at least 9 m from the colony was cleared of vegetation and swept smooth to clear unwanted seeds. Around this a barrier was constructed of grease applied to the surface of plastic strips. The plastic stopped the grease from running into the soil during the heat of the day. The grease was renewed as required.

A patch in this case consisted of cracked wheat combined with 40 ml of gravel spread flat to cover a 12-cm square of plastic. Both the wheat and gravel had been sifted separately through standard geological sieves to give a particular diameter range. The ants are sensitive to both seed and gravel size (Taylor, 1975). Such patches were placed on square of plywood divided into nine 15-cm squares, three on a side. The plywood platform was raised about 5 cm from the soil and a 10-cm-wide ramp led from the soil to the patch. A patch was renewed by putting down the appropriate wheat–gravel mixture in a square on the opposite side of the board, so that when the platform was lifted and turned 180°, this square ended up where the old patch had been. The foragers already on the platform reversed their direction of return relative to the platform, since these ants use a sun compass for orientation (Hölldobler, 1971), and had little trouble finding the ramp.

At the start of an experiment at least two patches were placed in the arena and separate recruitment columns formed to each. When recruitment rates maintained their relative levels for two recording intervals, the manipulation of a particular variable could be made in one of the patches. Here one could only use relative levels of recruitment because any equilibrium that existed changed during a session as the soil surface temperature, air movement, humidity, and insolation changed. Experiments to test *Pogonomyrmex* responses include changes in distance, patch size, density, and size of seeds. Recording was carried out as with *S. geminata.* Each type of experiment was performed twice on each of two colonies. The conditions of these experiments are presented in Table 2. Note the following convention: the word "variable" will refer to the actual quantities manipulated in an experiment, the word "parameter" will refer to some constant in the models from the companion paper (Taylor, 1977) as used in the discussion of this paper. This should decrease confusion in such cases as the seed-size experiments in which manipulation of one variable influenced more than one parameter.

Certain behaviors are also important within the patch and were recorded in half of the experiments on *Pogonomyrmex*. The timing of three events was measured for ten ants on a patch: first, the time from entering the patch until the forager first found a seed, which was detected by a marked downward movement of the ant's head; second, the time from entering the patch until the forager had secured a seed in its mandibles (this seed was often not the first one found but was usually the one she returned home with); and third, the total time spent on the patch.

In addition to the above experiments, another series tested response to size distribution of seeds within a patch. Cracked wheat was sifted to obtain 1.0–1.4, 1.4–2.0, 2.0–3.0, and greater than 3.0-mm diameter size classes. These were dyed different colors with food coloring and measured out so that a single layer of each size class covered 8.5 cm^2 which required about 75 pieces of the greater than 3.0-mm size. This was an attempt to make it equally probable that an ant would find each size class. If the experimental distribution had been chosen by taking equal numbers of each size, the larger size classes would be far more conspicuous than the smaller. The four classes were mixed and presented without gravel. Two different color orderings were used for possible attraction to particular dyes. In the series labeled Series 1, the seeds were colored blue, red, green, or blue in that order from smallest to largest size. In the series labled Series 2, the seeds were colored green, blue, red, green in the same order.

Results

1. Experiments on Solenopsis

Distance. Figure 1 displays the results of experiments on *Solenopsis* in which distance to a patch was manipulated. It should be noted at the outset that the differences in recruitment rates to the patches cannot be tested for statistical significance because the rates to each patch are correlated through time. A *t*-test, for example, would indicate highly significant effects due to the experimental treatments in every instance (Figs. 1 to 3). I believe, however, that the significance of the responses to the treatments is obvious from looking at the graphs presented. In experiment 1, the experimental patch, *B* at 3.2 m, was first more distant than *A* at 2.4 m and was receiving fewer recruits. At this point the rate of recruitment to *B* was 5.2 per 50 s compared to 14.7 to *A*. When *B* was moved to the same distance as *A*, they both received recruits at the same rate. For the second and third intervals after the change, *B* now received 8.0 and 7.1 recruits per 50 s, while *A* received 6.8 and 7.3. In experiment 2, *A* and *B* were started in opposite directions from the colony at 0.9 m. Just before the experimental change, *A* received 7.0 recruits per 50 s and *B* received 6.2. The experimental patch *C*, at first absent, was inserted twice as far from the colony as either control. Recruitment never reached as high a level for *C* as for *A* and *B*. During the second and third intervals after the change, the recruitment rates to *A* were 9.4 and 9.0, to *B* were 9.3 and 8.7, and to *C* were 1.2 and 1.4 per 50 s. In summary, the rates of recruitment decreased by 8.2 and 8.9 ants per 50 s for each increase of 1 m distance in experiments 1 and 2, respectively.

Patch Size. The amount of interference foragers experience on a patch is related to the rate of recruitment and the size of the patch. In experiment 3 (Fig. 2) both *A* and *B* started at 8 mm diameter and recruitment reached 55.2 and 56.0 per 50 s, respectively. When *B* was reduced to 5 mm, the rate of recruitment to it

Table 1. Conditions of experiments with *Solenopsis geminata*

Variable manipulated	Experiment	Date	Patch	Values before			Values after			Percentage change[a] in total recruitment	Observed slope
				Distance (m)	Size, mm diameter	Sucrose concentration	Distance (m)	Size, mm diameter	Sucrose concentration		
Distance	1	3 VI	A	2.4	5	1.5	2.4	5	1.5	−17.8[b]	8.2
			B	3.2	5	1.5	2.4	5	1.5		
	2	11 VI	A	0.9	5	1.5	0.9	5	1.5	39.8	8.9
			B	0.9	5	1.5	0.9	5	1.5		
			C	–	–	–	1.8	5	1.5		
Patch size	3	9 III	A	1.8	8	1.5	1.8	8	1.5	− 3.9	2.0
			B	1.8	8	1.5	1.8	5	1.5		
	4	3 VI	A	2.4	5	1.5	2.4	8	1.5	− 5.6	1.7
			B	2.4	5	1.5	2.4	5	1.5		
Concentration	5	31 III	A	1.8	5	0.5	1.8	5	1.5	−13.3	5.7
			B	1.8	5	0.5	1.8	5	0.5		
	6	1 IV	A	1.8	5	1.5	1.8	5	0.5	−35.7	8.0
			B	1.8	5	1.5	1.8	5	1.5		

[a] This number is the difference between the average total rate of recruitment during the second and third interval after the experimental change and the total for the interval just before the change as a percentage of the total rate for the interval just before the change

[b] In this case, the rate to B before the change was multiplies by 3.2 m/2.4 m to compensate for a difference in distance

Table 2. Conditions of experiments with *Pogonomyrmex occidentalis*

Variable manipulated	Experiment	Colony	Date	Patch	Values before		
					Distance (m)	Size, number of 12 cm squares	ml wheat
Distance	1	1	6 VII	A	4.5	1	4
				B	4.5	1	4
				C	9	1	4
	2	1	10 VII	A	4.5	1	4
				B	–	–	–
				C	9	1	4
	3	2	28 VII	A	–	–	–
				B	9	1	4
				C	4.5	1	4
	4	2	31 VII	A	4.5	1	4
				B	9	1	4
				C	–	–	–
Patch size	5	1	4 VII	A	6	1	3
				B	6	1	3
	6	1	5 VII	A	6	2	4
				B	6	1	4
	7	2	23 VII	A	6	1	4
				B	6	1	4
	8	2	24 VII	A	6	1	4
				B	6	1	4
Seed density	9	1	1 VII	A	6	1	4
				B	6	1	4
	10	1	2 VII	A	6	1	4
				B	6	1	4
	11	2	25 VII	A	6	1	12
				B	6	1	4
	12	2	26 VII	A	6	1	4
				B	6	1	12
Seed size	13	1	12 VII	A	6	1	4
				B	6	1	4
	14	1	15 VII	A	6	1	4
				B	6	1	4
	15	2	8 VIII	A	6	1	4
				B	6	1	4
	16	2	13 VIII	A	6	1	4
				B	6	1	4

Values before		Values after					Percentage change[a] total recruits	Observed slope[b]
Size wheat (mm)	Size gravel (mm)	Dis-tance (m)	Size	ml wheat	Size wheat (mm)	Size gravel (mm)		
1.4	2.0	4.5	1	4	1.4	2.0	6.4	−0.93
1.4	2.0	—	—	—	—	—		
1.4	2.0	9	1	4	1.4	2.0		
2.0	2.0	4.5	1	4	2.0	2.0	3.8	−0.84
—	—	4.5	1	4	2.0	2.0		
2.0	2.0	9	1	4	2.0	2.0		
—	—	4.5	1	4	2.0	3.0	−10.7	−1.02
2.0	3.0	9	1	4	2.0	3.0		
2.0	3.0	4.5	1	4	2.0	3.0		
2.0	3.0	4.5	1	4	2.0	3.0	6.8	−0.51
2.0	3.0	9	1	4	2.0	3.0		
—	—	4.5	1	4	2.0	3.0		
1.4	1.4	6	1	3	1.4	1.4	51.2	0.7
1.4	1.4	6	2	3	1.4	1.4		
1.4	1.4	6	1	4	1.4	1.4	5.6	0.3
1.4	1.4	6	1	4	1.4	1.4		
2.0	3.0	6	2	4	2.0	3.0	− 2.4	29.9
2.0	3.0	6	1	4	2.0	3.0		
2.0	3.0	6	1	4	2.0	3.0	−12.6	10.0
2.0	3.0	6	2	4	2.0	3.0		
1.4	1.4	6	1	12	1.4	1.4	48.3	2.0
1.4	1.4	6	1	4	1.4	1.4		
1.4	1.4	6	1	4	1.4	1.4	—	2.0
1.4	1.4	6	1	12	1.4	1.4		
2.0	3.0	6	1	12	2.0	3.0	0.6	5.8
2.0	3.0	6	1	12	2.0	3.0		
2.0	3.0	6	1	12	2.0	3.0	−14.8	5.5
2.0	3.0	6	1	12	2.0	3.0		
2.0	3.0	6	1	4	2.0	3.0	17.3	6.0
1.4	3.0	6	1	4	2.0	3.0		
2.0	2.0	6	1	4	2.0	2.0	23.8	7.7
1.4	2.0	6	1	4	2.0	2.0		
3.0	3.0	6	1	4	3.0	3.0	−13.6	0.5
1.4	3.0	6	1	4	3.0	3.0		
2.0	2.0	6	1	4	2.0	2.0	−11.8	1.2
1.4	2.0	6	1	4	2.0	2.0		

[a] This number is the difference between the total numbers out in the second interval after the experimental change and the interval just preceding the change as a percentage of the total number out in the interval just before the change

[b] Computed as in Table 1, footnote [b]. Value for Seed Size is computed as change per change in volume (mm^3) of seed. Because sieve sizes used were 1.0, 1.4, 2.0, and 3.0 mm which represented the lowest sieve size allowing the seeds to pass, the mean diameter for each group lies between those values. The 1.4 mm size in the text was set at 1.2 mm; the 2.0 mm and 3.0 mm sizes were set at 1.7 and 2.5 mm, respectively, for these computations

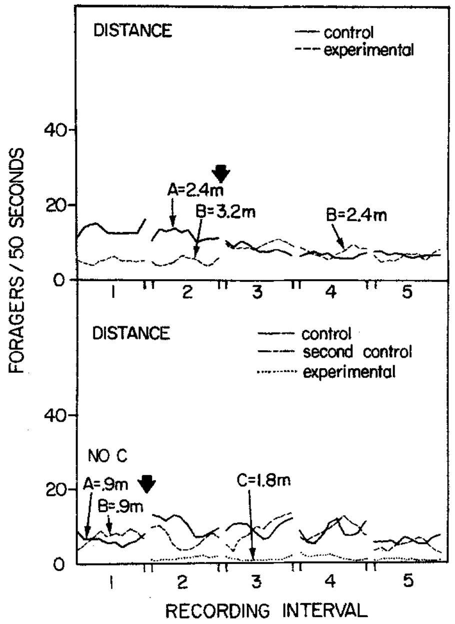

Fig. 1. Distance experiments for *Solenopsis geminata*. Specifications are given in Table 1 for all experiments on this species. *above:* Experiment 1. A convention used in all graphs is that the manipulated patch is represented by a *thin, dashed line;* the control by a *heavy, solid line;* and where there are two controls the experimental by a *dotted line*. The *large arrow* above the graph designates the time when an experimental change was made. Here patch B was moved from 3.2 to 2.4 m. The parameters involved in the manipulation are identified next to the letter of the appropriate patch above the graphs. After the experimental change only that patch which was altered is identified with its new parameter value, the other patch(es) having remained unchanged. Each line segment is ten minutes long. The break between segments represents an interval when the recruitment rates were not recorded. *below:* Experiment 2

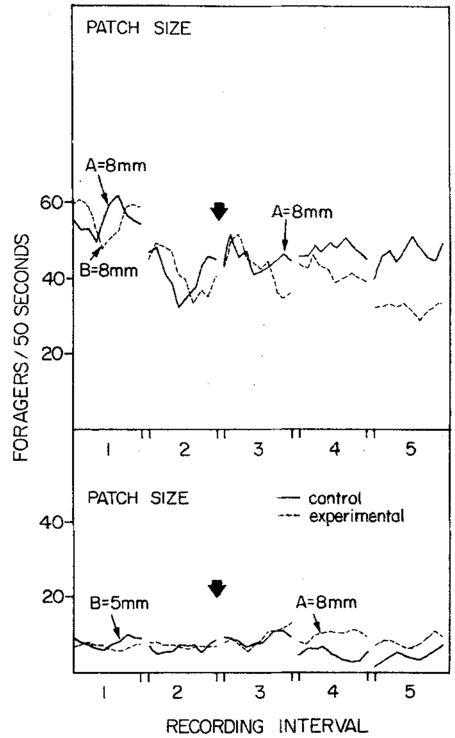

Fig. 2. Patch size experiments for *S. geminata*. See Figure 1 for explanation of figure. *above:* Experiment 3. *below:* Experiment 4

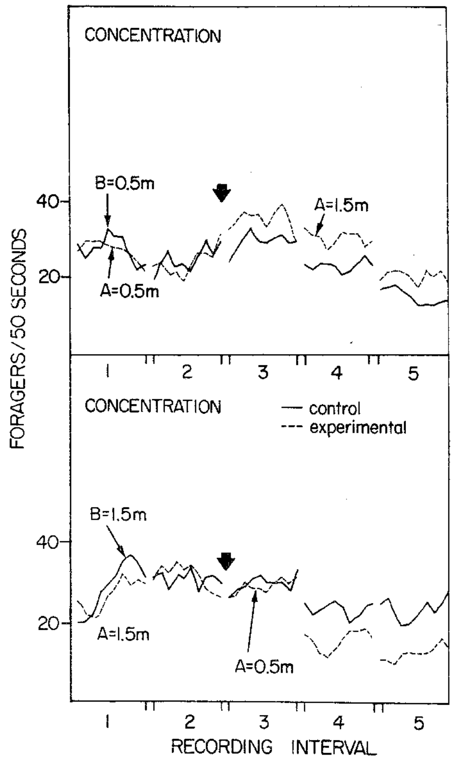

Fig. 3. Concentration experiments for *S. geminata*. See Figure 1 for explanation of figure. *above:* Experiment 5. *below:* Experiment 6

decreased, so that after 75 min, recruitment to *A* was 46.5 per 50 s, while that to *B* was 32.0. In experiment 4, both patches started at 5 mm and recruitment reached 7.3 for *A* and 7.1 for *B*. At this point, *A* was increased to 8 mm. It was recruited to at 9.0 per 50 s compared to 4.9 to *B* in the second interval after the change. In summary, the rates of recruitment increased by 2.0 and 1.7 ants per 50 s for each 1 mm increase in patch diameter in experiments 3 and 4, respectively.

Concentration. The responses of *Solenopsis* to changes in sugar concentration are given in Figure 3. In experiment 5, both patches started with a 0.5 *M* solution and recruitment rates were close at 24.8 per 50 s for *A* and 25.7 for *B* just before *A* was increased to 1.5 *M*. After this, *A* increased relative to *B*, being 28.6 and 22.9, respectively, two intervals after the change. In experiment 6, both patches started with 1.5 *M* solution and again recruitment rates were very similar with 32.0 per 50 s to *A* and 31.0 to *B*. In the second interval after the change, *A* was 16.2 per 50 s and *B* was 24.2. In summary, the rates of recruitment increased by 5.7 and 8.0 ants per 50 s for one-molar increase in sugar solution concentration in experiments 5 and 6, respectively.

2. Experiments on Pogonomyrmex

Manipulation of Variables in Different Patches. The results when graphed for experiments in which distance, patch size, density, and seed size were varied appear similar to those for *Solenopsis* as presented in Figures 1 through 3. Again statistical tests cannot be made of the significance of the responses to treatments. However, the graphs are presented elsewhere (Taylor, 1975) and the interested reader may refer to them to see that the significance of the responses to the experimental manipulations is obvious in every case in which I claim it is below. These results have been summarized in Table 3. Table 4 presents data on search

Table 3. Responses to doubling of variable value for *Pogonomyrmex*
Observed rates of recruitment with variable change in effect, $\dot{n}$, and temperature (in parentheses) where appropriate. See text for further explanation. Computed from data presented in Taylor (1975)

Variable	Experiment	Colony	Responses to doubling	$\dot{n}$
Distance	1	1	−4.2	9–55 (31° C)
	2	1	−3.8	13–56 (36)
	3	2	−4.6	15–66 (34)
	4	2	−2.3	2–28
Patch size	5	1	0.7	31–32
	6	1	0.3	38–38
	7	2	29.9	65–95
	8	2	10.0	88–98
Density	9	1	8.0	17–33
	10	1	8.0	16–32
	11	2	23.2	59–106
	12	2	22.4	56–100
Seed size	13	1	7.2	14–33 (35° C)
	14	1	9.3	13–38 (30)
	15	2	0.6	14–20 (39)
	16	2	1.5	26–30 (38)

Table 4. Ratios of search times on experimental to control patches

Variable	Experiment	Ratio before			Ratio after		
Patch size	7	1.03	0.91	1.01	0.91	1.05	–
	8	0.99	0.95	0.96	0.91	0.95	1.05
Density	11	0.53	0.88	0.90	0.93	1.23	–
	12	–	0.62	0.69	1.03	0.99	1.12
Seed size	15	1.05	1.54	1.93	0.94	1.07	–
	16	1.09	0.95	0.97	1.05	0.83	–

Computed from data presented in Taylor (1975) times which will be used later for comparison to the material in Table 3 in the discussion of relative levels of response to variable changes. The response to doubling is a simple statistic describing response to a change in the value of some variable. First, the slope is computed. It is the difference in rates of recruitment between the control and experimental patches when the parameter change, e.g., 4.5- and 9-m distances to patches, is in effect, divided by the difference between the values of the variables. Units are thus the number of ants per 50 s per unit variable. Then the slope is multiplied by the lower value of the variable to give a number which tells by how much recruitment would change if the value of the variable were doubled, assuming a linear response. Notice that the rate of recruitment has been taken for convenience to be the mean value for the 12-min interval of interest. In the later discussion where responses to doubling of a variable are taken to be different, the difference is usually striking. From Table 3 we can see that within a class of experiments, the direction of response was always consistent. Rate of recruitment decreased when distance to patch was increased. It increased when patch size was increased if recruitment was high, when density was increased, and when seed size was increased. The differences among levels of response within a class will be discussed later.

Seed Size within a Patch. The results for selection of seed sizes within a patch are presented in Table 5. In all cases the smallest size class was relatively neglected. There was no significant preference for any other size class. Nor was there a tendency to concentrate more on a particular size class at more distant patches.

3. *Total Available Foragers*

It is possible that the total number of available foragers acts as a constraint on allocation to recruitment. If at the beginning of an experiment all available foragers are mobilized in recruitment, the total number on all trails will not increase subsequent to enhancement of a patch. To increase the rate to the enhanced patch, recruits must be withdrawn from other patches. This will cause different optimal rates of recruitment from those if the patches were presented separately. This would also call for a more complicated mathematical treatment (Taylor, 1977).

Table 1 provides the percentage change in total recruitment after manipulation of the variable of interest for *Solenopsis*. Since the table-top temperature did not vary significantly during the course of an experiment, we can use recruitment rates themselves to estimate the total numbers of recruits on the trails. Only in experiment 2 was there an increase in the total number of foragers after the experimental manipulation. In all other experiments the total number decreased. In experiments 3 and 6, the manipulation caused decreased recruitment, so the constraint does not enter. Thus, in three out of four experiments, an upper limit was established for available foragers, which in turn set an upper limit on the recruitment rates.

Computation of the number of recruits on all trails for each interval was more involved for *Pogonomyrmex*. Figure 4 shows how $1/v$, the time to run 1 m,

Table 5. Seed size selection within a patch for *P. occidentalis*

Distance (m)	Series	°C	Number taken of each seed size (mm)			
			1.4	2.0	3.0	>3.0
Colony II						
1.5	2	34.0	3	31	13	13
1.5	1	36.5	9	18	20	13
1.5	2	38.5	6	20	24	10
1.5	1	39.5	1	20	18	21
		Mean	4.75^{b}	22.25^{a}	18.75^{a}	14.25^{a}
7.5	2	42.0	2	20	19	19
7.5	1	45.0	3	17	19	21
7.5	2	32.6	5	19	15	21
7.5	1	35.0	7	17	18	18
		Mean	4.25^{b}	18.25^{a}	17.25^{a}	19.75^{a}
Colony III						
1.5	1	48.0	10	9	13	28
1.5	2	48.0	12	16	16	16
1.5	1	48.0	3	13	13	21
1.5	2	48.0	8	9	23	20
		Mean	8.25^{ba}	11.75^{ab}	16.25^{ab}	21.25^{a}
7.5	1	47.8	8	20	18	14
7.5	2	48.5	3	12	16	29
7.5	2	49.0	4	16	22	18
		Mean	5.0^{c}	16.0^{ab}	18.67^{a}	20.33^{a}

For a set of experiments on one colony, means with the same supercript do not differ significantly at the 5% level using two-tailed *t*-test

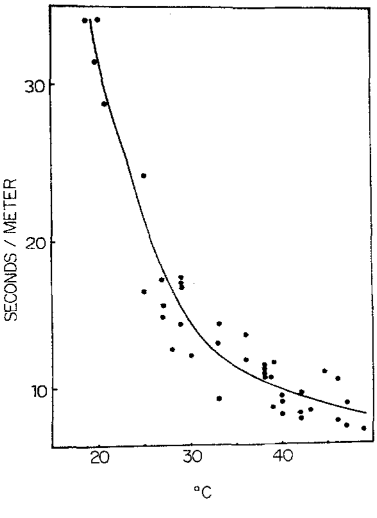

Fig. 4. Time to run 1 m as a function of temperature for *Pogonomyrmex occidentalis* workers on the way *to* a patch without a load. *Each point* represents the mean for ten different running foragers. Curve is fitted by eye

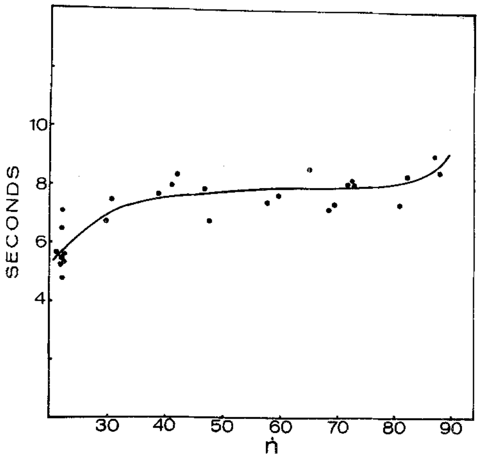

Fig. 5. Time to secure a seed as a function of recruitment rate $\dot{n}$. *Each point* represents the mean of ten individuals which were timed from entering the patch until they had a seed in their mandibles. Seed size was 1.4 or 2.0 mm. Gravel size was 2.0 or 3.0 mm. Soil surface temperature range was 29–35° C. Curve is fitted by eye

varies with temperature. Figure 5 shows that there is little interference over a wide range of recruitment rates. Addition of quadratic and cubic terms in a polynomial regression demonstrate significant contribution to the fit over simple linearity using an F-test ($p < 0.001$). The inflection upward at $\dot{n}$ above 80 is quite understandable because at this recruitment rate there are many ants on a patch. The inflection downward at low $\dot{n}$ is, perhaps, more difficult to explain. In general, the points on the graph were collected on several different dates, but of the eight points above $\dot{n}$ about 22, seven were collected on the same day. The second from the top was collected at another time. Of the six lower points, two were collected on one patch and four on the other, giving some independence to the results. If this lower inflection point is real, its explanation differs from the one at high $\dot{n}$. In my observations, the foragers seemed to spend more time "recognizing" each other at relatively low recruitment rates. This means interference could rise quickly at some $\dot{n}$ in the low twenties. At higher rates very little time was spent in recognition, as though claim on the patch was established and the likelihood of intruders from other colonies was low. The data in Figures 4 and 5 were used to estimate the total time for one roundtrip to patch i.

$$a_i \doteq \frac{2D_i}{v(T)} + t_p \tag{1}$$

to compute the curves in Figure 6. Here the total time spent on the patch, t_p, was taken to be constant at 11 s. The distance to patch i is D_i, T is temperature in °C, and the time to travel 1 m, $V(T)$, is a function of temperature (Fig. 4). These curves have been used to estimate the total numbers of recruits out by:

$$\sum a_i \bar{\dot{n}}_i = \sum \left(\frac{D_i}{v(T)} + \frac{D_i}{v(T)} + t_p \right) \bar{\dot{n}}_i, \tag{2}$$

where $\bar{\dot{n}}_i$ is the mean recruitment rate for the interval.

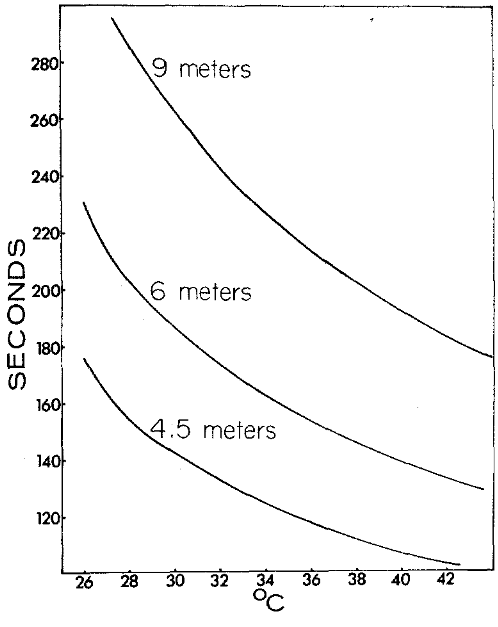

Fig. 6. Total time for a roundtrip to patches at various distances as of functions of temperature. The wheat: pebble ratio is 1:10. The wheat is 2 mm and the gravel is either 2 mm or 3 mm. Calculated from data given in Figures 4 and 5

Of the fifteen experimental changes for *Pogonomyrmex* where data on total numbers of foragers on the trails are available, fourteen involved experimental changes that would cause an increase or no change in recruitment rates. Only experiment 1 caused a decrease after the experimental alteration. Table 2 provides percentage change in total recruits after the experimental manipulations. Considering change in the total number of foragers at the 10% level, four increased, five decreased, and five stayed the same. Of the five that decreased, the total number of foragers after the manipulation of the resource four of these decreases occurred during times when the soil surface temperature increased markedly (Taylor, 1975) thus causing the recruits to run faster so that recruitment rates could be maintained or increased even when the total number of recruits had been decreased. (In the fifth of these, experiment 15, where the total number out decreased by 13.6% at the same time there was a 5° C decrease in temperature, this large decrease in numbers out coincided with a general reduction of activity by the colony.) One must conclude from this, in contrast to *S. geminata* under laboratory conditions, that the upper limit to available foragers in *P. occidentalis* was adjustable to the resources presented during a foraging session. It is of interest that in the four experiments where recruitment from Colony II was unusually high, either no change or a decrease in recruits occurred indicating that the upper limit of mobilization may have been reached (experiments 7, 8, 11, 12).

These findings justify the use of the model for *Pogonomyrmex* that assumed recruitment was generally not near the limit of available recruits. On the other hand, the model taking such a limitation into account is required for *Solenopsis* (see Taylor, 1977).

Discussion

Levels of Prediction

It would be desirable to predict absolute magnitudes of response from the models presented in a companion paper (Taylor, 1977); but as our ability to measure certain parameters now stands, this is quite impossible. In the two-patch model for *S. geminata*, values are missing for parameters representing the energetic value of the resource, the energetic costs of running and drinking, and the total number of available recruits as a function of all other activities in the colony. The energetic value of the resource depends upon its distribution to various castes and life stages as well as the utilization efficiencies of each of these. As a possible way to circumvent part of this difficulty, one might use information on relative efficiencies for metabolism of various sugars to compare choice among them as related to energetic efficiency. I have assumed in the sugar concentration experiments that higher concentrations of sucrose yield more energy for the colony. In considering the energetic costs of running and drinking, one would have to make very fine measurements of metabolic rates during these activities. The parallel problem of estimating parameter values for *Pogonomyrmex* appears even more difficult. Unlike solutions of one type of sugar, seeds provide energy sources from all the classes of lipids, carbohydrates, and proteins which they contain. In evaluating the energetic value of a seed, one must know which components are used as energy sources and which members of the colony use them and with what efficiency. My simple assumption has been that more seed of the same type provides more energy. Estimating the energy cost of running without a seed or with seeds of various sizes would entail the same technical problems of fine measurement of metabolic rates as for *Solenopsis*. Future work in this direction might prove very rewarding in relation to species range and competitive interactions among species.

Despite these problems of measurement, I have been able to make qualitative tests of the models. As predicted by the model based on maximization of net rate of energy intake, *Solenopsis geminata* increased its rate of recruitment in response to decreased distance to a patch size (experiments 1 and 2) to decreased interference due to increased patch size (experiments 3 and 4), and to increased sugar concentration (experiments 5 and 6). As pointed out in Taylor (1977), the fact that the colony responded to a change in sugar concentration requires that we discard the analogous time-minimization model, which postulates that the colony recruits to resources so as to minimize the average time necessary to acquire a load of resource. Thus each load would be given identical value; but apparently *Solenopsis* values a load according to its energy content.

Pogonomyrmex occidentalis also behaved in accord with predictions of a model of its behavior based on the hypothesis of maximization of the net rate of recruitment (experiments 5 through 8), when seed density was increased (experiments 9 through 12), and when seed size was increased (experiments 13 through 16). Again the last experiment on response to seed size leads to the refutation of an analogous model based on a hypothesis of time minimization. The colonies valued pieces of cracked wheat according to their size. Foragers responded to uniform size distributions of cracked wheat by selecting larger sizes. The only result not fitting the qualitative predictions was a lack of tendency under our experimental conditions to select a narrower range of seed sizes as the patches were moved farther from the colony.

Explanation of Relative Levels of Response

Even though exact predictions of sensitivity to variation in variables cannot be made, much can be said about relative levels of response observed in the above experiments on *Pogonomyrmex*. In fact, as it turns out, within a type of experiment (distance, patch size, density, or seed size) one can explain all of the observed differences within and between colonies in levels of response to a doubling of the variable and get some insight into what parameters of the model are most important to the ants. It is hazardous to compare between types of experiments because the change in number of recruits per 50 s for a *unit* change in a variable depends upon the scaling of these units. The method used is to differentiate the function for the optimal rate of recruitment with respect to the parameter affected by change in the experimental variable. This tells what parameters are expected by the model to influence the level of response to a change in that particular parameter. By looking at the relative conditions of these parameters during the experiments, one can determine if they account for qualitative differences in levels of response between experiments. As pointed out above in the results for Total Available Foragers, the model for *Solenopsis* must consider recruitment at the limit of available foragers. The appropriate expression for the optimal rate of recruitment in this case [Eq. (14), Taylor, 1977] is too full of parameters to derive anything from this kind of analysis without having better estimates of some of these parameters. The analogous equation giving the optimal rate of recruitment, $\dot{n}^*$, for *Pogonomyrmex* is more tractable:

$$\dot{n}^* = \left[\frac{E}{c_r} - \left(\frac{D}{v} + \frac{c_r' D}{c_r v'} + d + t_1\right)\right] \Big/ 2b \tag{3}$$

The parameters have the following interpretations. E is the energy content of a seed; D is the distance to a patch of seeds; v is the speed at which an ant runs without a seed; v' is the speed she runs with a seed; c_r is the energetic cost per unit time of running without a seed; c_r' is the energetic cost per unit time of running with a seed. The time from entering a patch until a seed has been secured is t_s which has been approximated at $\dot{n}^*$ by $d + b\dot{n}$. So d is a measure of the time to secure a seed at a recruitment rate of $\dot{n}^*$ and b measures the degree to which t_s is sensitive to changes in recruitment rate around $\dot{n}^*$. t_1 is the time from securing a seed to leaving the patch. The value of t_1 was found to be independent of $\dot{n}$.

The first step in the argument is to determine what parameters were affected by each experimental manipulation. The experiments at high recruitment rates (experiments 7 and 8) can be interpreted as influencing the t_s curve in Figure 5. Even though recruitment rate increased with a doubling of patch size (Table 3),

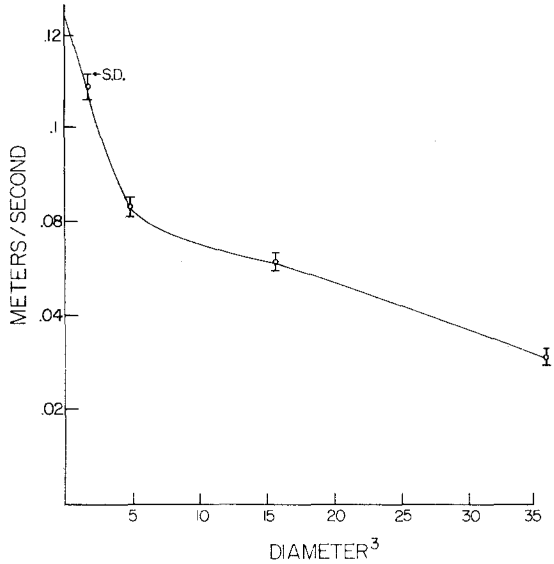

Fig. 7. Speed of running as a function of seed volume in a narrow temperature range. The *four points from left to right* are mean running rates for 29, 38, 29, and 34 foragers respectively at 48° C. *Length of bars* indicate standard deviation. Curve is fitted by eye

the search times on the control and experimental patches stayed the same (Table 4). The change reduced the interference effect at the observed recruitment rate to the control, thus, decreasing b and increasing d. The interference effect due to high recruitment rate is shifted to a higher $\hat{n}$ when the patch is enlarged. The effect of density experiments can be interpreted in two ways. The recruitment was higher to the patch with a greater density of seeds (Table 3) and the time to secure a seed was also higher (Table 4, note that the experimental patch had a lower density than the control at the start). The effect of increased density can be taken as a downward shift in the t_s curve (Fig. 5), i.e., a decrease in d. Alternatively, it can be interpreted as a decrease in the slope, b, of t_s because the recruits need not run around so much on the patch and, therefore, do not meet as often. An increase in seed size can be interpreted as altering three parameters. Certainly the gross energy content, E, is increased. Figure 7 shows that v' will decrease. The energetic cost per unit time of carrying the seed, c'_r, should also increase.

The second and last step in the argument is to use the equations which indicate sensitivity of recruitment to parameter changes in an attempt to explain the observed difference in sensitivity between experiments. These equations were prented by Taylor [1977, Eqs. (30–32)]. The observed levels of sensitivity we desire to explain are the response to doubling of a variable value as listed in Table 3. These are computed as the product of the slope for the experiment from Table 2 times the smaller value of the parameter. Table 3 also presents the observed equilibrial rates of recruitment, $\hat{n}$, since these are important to the developing argument, and soil surface temperature (in parentheses) where these are relevant. Remember that the general level of recruitment is taken as a given which cannot be predicted by our present level of understanding.

In the case of the distance experiments there is not much to explain. The responses to a doubling of distance in experiments 1 and 2 are very close. Experiment 3 is close enough to experiment 1 not to worry about. Experiment 4 could not be as large as experiment 3 given the low level of recruitment, even if there were zero recruitment to the more distant patch. So we need not use our method to explain differences in response among the distance experiments.

Consider an increase in patch size at high levels of recruitment as an immediate decrease in b. From Equation (3),

$$\frac{\partial \dot{n}^*}{\partial b}=\frac{-\dot{n}^*}{b}. \tag{4}$$

In experiments 5 and 6, recruitment was low enough that b was probably not affected by a doubling of patch size; accordingly the response was very low. In experiments 7 and 8 recruitment and response were high. The difference between experiment 7 and 8 can be explained due to differences in levels of recruitment. Referring to Figure 5, b was much greater at $\hat{\dot{n}}_8=88$ than at $\hat{\dot{n}}_7=65$ overriding the effect of $\dot{n}$ in the numerator of Equation (4) and, thus, producing a lower response in experiment 8.

The effect of increasing seed density can be taken as an immediate decrease in d, i.e., a shift downward to the t_s curve. From Equation (3),

$$\frac{\partial \dot{n}^*}{\partial d}=\frac{-1}{2b}. \tag{5}$$

So we should be able to explain observed differences between experiments solely on the basis of different slopes of the t_s curve. The results within a colony (experiment 9 vs. 10 and 11 vs. 12) are so close that no explanation is required. If the downward inflection in the t_s curve at low $\dot{n}$ can be accepted as valid (see section on Total Available Foragers), b was higher for experiments 9 and 10 than for 11 and 12 so the response is expected to be lower in experiments 9 and 10 as observed. If the effect of increased density is also taken to decrease b, Equation (4) pertains. Now supposing the downward inflection in t_s at low $\dot{n}$ not to exist (i.e., taking the harder case) and to be the same for $\hat{\dot{n}}_9=17$ and $\hat{\dot{n}}_{11}=59$, the fact that $\hat{\dot{n}}_9<\hat{\dot{n}}_{11}$ leads again to the expectation that the response in experiments 9 and 10 would be less than that in experiments 11 and 12, as observed.

Seed size has been interpreted as influencing three parameters, increasing E and c_r' and decreasing v'. The results of experiments 13 and 14 are close enough not to need explanation, but as will be seen below, the higher temperature in 13 does lead to the expectation of a lower response, as observed. Results from experiments 15 and 16 are also close. However, the very low response in 15 can be explained as being due to the 3.0-mm seeds in the control patch in this case as compared to 2.0-mm seeds in the others. Computation of the slope of $\dot{n}^*$ as a function of a parameter using the observed responses to two values of the parameter assumes at least a monotonic change in the function connecting the two points. It is likely from Figure 7 that $\dot{n}^*$ as a function of seed size peaks between 2.0 mm and 3.0 mm; thus the slopes of the line connecting n^* (1.4) to h^* (2.0) would be greater than that for the line connecting it to $\dot{n}^*$ (3.0), as observed. This effect should be able to override the decreased time to secure a 3.0 mm seed compared to a 1.4 mm seed vs. the time to secure a 2.0 mm compared to a 1.4 mm seed as shown in Table 4 for experiments 15 and 16. The difference in response between experiments 13 and 14 and experiments 15 and 16 needs explaining. Since the levels of recruitment were all similar, the parameter b will be considered to be the same for all. The equation describing sensitivity of recruitment rate to a change in seed size, s, is:

$$\frac{\partial \dot{n}^*}{\partial s}=\frac{1}{2bc_r}\left(\frac{\partial E}{\partial s}+\frac{c'_r D}{v'^2}\frac{\partial v'}{\partial s}-\frac{D}{v'}\frac{\partial c'_r}{\partial s}\right). \tag{6}$$

We shall work from left to right through the parameters in the right hand side. The cost of running without a seed, c_r, with units energy per unit time should increase with temperature. Thus, c_r in the denominator should influence sensitivity in the direction observed of experiments 13 and 14 being greater than experiments 15 and 16. The cost of running with a seed, c'_r, should also increase with increasing temperature, leading to the opposite influence of c_r since c'_r is in the numerator. The speed of running with a seed increases with increasing temperature as seen in Figure 4. For the second term in parentheses to have a negative influence with increasing temperature, the effect of v'^2 must outweigh that of c'_r. Distance, D, was the same for all experiments. In the third term, v' in the denominator will again influence the expression in the observed direction. From the foregoing, we can conclude that the speed of running with a seed which could be easily perceived by the individual forager is relatively important in influencing the sensitivity of the equilibrium rate of recruitment to seed size.

In summary, the model for *Pogonomyrmex* [Taylor 1977; Eq. (3) above] explains all of the differences in magnitudes of response between the experiments presented in this paper. The degree to which interference depends upon the level of recruitment (the parameter b) is always important. In discriminating between patches containing different sizes of seeds, the speed of running with a seed (the parameter v') seems to be particularly important to the ants.

Related Literature

In the major paper to date concerning optimal foraging behavior, Schoener (1971) considered long-term patterns in behavior referred to as strategies rather than short-term patterns studied in this paper referred to as tactics (Holling, 1968). Nonetheless, he set the scene for emphasizing energy as the overriding currency in foraging behavior. He distinguished two extreme types of strategies as *time minimizers* (not to be confused with the above use of this term), "whose fitness is maximized when time spent feeding to gather a given energy requirement is minimized," and *energy maximizers*, "whose fitness is maximized when net energy is maximized for a given time spent feeding" (pp. 376–377). In relation to the present work note that these definitions set rules for how much of the time and at what times an animal feeds. They also imply that both types should maximize the net rate of energy intake when they decide to forage; so they cannot be distinguished here. Pyke et al. (1977) provide an update on the literature on optimal foraging. Carroll and Janzen (1973) have reviewed the literature on ant foraging.

The findings of this paper agree, for the most part, with results presented in a recent paper by Hölldobler (1976), who found that *Pogonomyrmex rugosus* and *barbatus* recruited more heavily to patches placed closer to the colony. In 12 out of 17 experiments for *P. rugosus* and in seven out of nine experiments for *P. barbatus*, these species showed higher recruitment rates to patches of higher density at the same distance from the colony. Controls were not run in which baseline recruitment rates are established to the patches before modifying seed density. Therefore, we cannot be sure that extraneous factors were not affecting the experiments, in particular those where recruitment was not greater to the denser patches. In experiments in which the colonies were presented patches with different sized seeds, both *P. rugosus* and *barbatus* chose the patches with smaller seeds. At first this may seem to be at variance with the results presented in this paper. However, his smallest size class (2.1 × 1.1 mm) corresponded to my second largest class (2.0–3.0 mm). If his colonies had been given the choice of yet smaller seeds, they may have still preferred the 2.1 × 1.1 mm size class. Thus, they would have appeared to prefer intermediate-sized seeds. From Cole's (1968) data on ranges of head width, *barbatus* (2.05–2.70 mm) and *rugosus* (1.75–2.70 mm) are larger than *occidentalis* (1.44–2.13 mm). Measurements on running speed as a function of seed size for Hölldobler's two species (as in Fig. 7) would have helped in interpreting the importance to them of the various seed sizes.

In a simulation of choice from a log-normal distribution of prey lengths, Schoener (1969) found that animals should choose a positively skewed distribution of prey sizes and tend to choose larger prey at greater distances to minimize the time needed to fill their food requirements. He cited evidence for these trends in nature for fish, lizards, and birds. For insects, Rabb and Lawson (1957) observed that *Polistes* wasps would kill and eat all sizes of tobacco hornworm larvae but tended to return to the nest only with larger instars.

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