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The Blind Leading the Blind in Army Ant Raid Patterns: Testing a Model of Self-Organization (Hymenoptera: Formicidae)

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We present field experiments and analyses that test both the assumptions and the predictions of a model that showed how the swarm raids of the army ant Eciton burchelli *might be self-organizing, i.e., based on hundreds of thousands of interactions among the foraging workers rather than a central administration or hierarchical control. We use circular mill experiments to show that the running velocity of the ants is a sigmoidal function of the strength of their trail pheromones and provide evidence that the swarm raid is structured by the interaction between outbound and inbound forager traffic mediated by the pheromones produced by both of these sets of ants. Inbound traffic is also affected by the distribution of prey, and hence, sites of prey capture alter the geometry of the raid. By manipulating the prey distributions for* E. burchelli *swarms, we have made them raid in a form more typical of other army ant species. Such self-organization of raids based on an interaction between the ants and their environment has profound consequences for interpretations of the evolution of army ant species.*

KEY WORDS: army ants; behavior; pheromones; foraging; self-organization; *Eciton;* mathematical model.

INTRODUCTION

The swarm raids of army ants are one of the wonders of the insect world. The largest raids of neotropical army ants are those of *Eciton burchelli*, which may

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contain up to 200,000 workers raiding in a dense phalanx 15 m or more wide (Franks, 1982; Franks and Bossert, 1983; Franks and Fletcher, 1983). Such a raid can sweep out an area of 1000 m^2 in a single day. The raid system is composed of a swarm front, a dense carpet of ants that extends for approximately 1 m behind the leading edge of the swarm, and a very large system of anastomosing trails. These trails, along which the ants run out to the swarm front and return with prey items, characteristically form loops that are small near the raid front and get ever bigger and less frequent away from it. The final large loop leads to a single principal trail that provides a permanent link between the army ants' raid and their nest bivouac. The complex structure of the raid is dynamic but its basic design features are almost always maintained (see Fig. 1).

The swarm raids of army ants are of general importance in social insect behavior, as they are one of the best examples of totally decentralized control. The hundreds of thousands of army ants that form an *E. burchelli* swarm raid, are virtually blind: their eyes have only a single facet. The complex structure of the raid system appears to be generated literally by the blind leading the blind, without any centralized control.

Recently, Deneubourg *et al.* (1989a) formulated a computer simulation model showing how the characteristic patterns of army ant raids could be self-organizing, i.e., generated from the interactions between many identical foragers, each with simple trail-laying and trail-following behavior. Here we present the results of field experiments designed both to verify the fundamental assumptions of the computer model and to test its predictions.

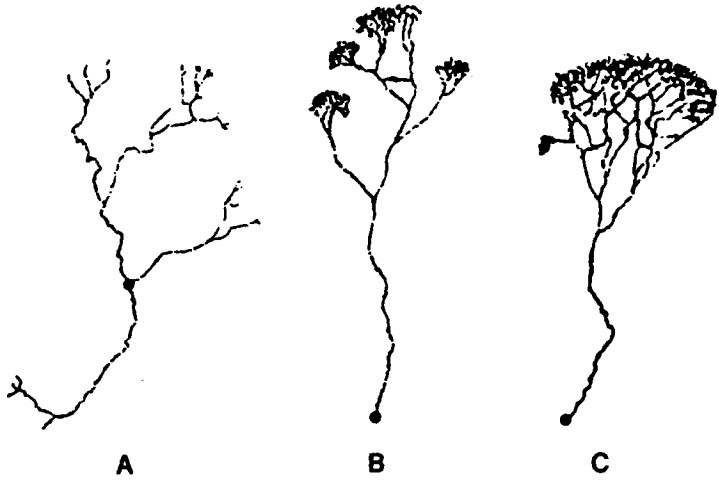


Fig. 1. Foraging patterns of three army ant species, (A) *Eciton hamatum*, (B) *E. rapax*, and (C) *E. burchelli*. Redrawn from Burton and Franks (1985).

THE MODEL

Assumptions

The basic assumptions of the model were as follows.

(a) The ants lay pheromone trails both on the way out to the raid front and on the return journey. Return journeys are initiated by the discovery, capture, and transport of prey. The prey distribution in the model, therefore, controls the distribution of return traffic, which in turn influences future outward traffic.

(b) At the point where a trail bifurcates, an individual ants' choice of the left or right trail is determined by the relative strength of the pheromones on each branch, which is a function of the amount of outbound and inbound traffic flow that has occurred on that trail and the decay rate of the pheromone.

(c) The velocity of the ants increases sigmoidally as a function of the strength of the trail pheromones.

Thus ants should run quickly down the heavily used principal trail and mill about slowly and randomly at the front of the swarm as they proceed into virgin territory. (Hence at the swarm front the ants diffuse outward. This accounts for the density of these slow-moving ants and the cloud-like shape of the raid front; see Fig. 1c.)

(d) The number of ants leaving the bivouac per unit time is relatively constant.

Predictions

The major prediction of the model is that the structure of the raid is influenced by the distribution of the prey the army ants capture. For example, when the computer simulation is run with no prey present (i.e., the model army ants continue to raid outward because they do not encounter prey and therefore have no "stimulus" to turn around and head home), the raid has a swarm front and a principle trail but no branching trails (Fig. 2A). If the exact same model is rerun so that the ants have a relatively high probability of encountering small prey items at any site ahead of the raid, as is the case for *E. burchelli*, the ants return from these sites of prey capture, choosing to turn left or right in response to previously laid pheromones and so trace their way back to the principal trail. It is these returning ants, possibly also laying substantial amounts of trail substances on the homeward journey, and their interaction with outgoing ants that lead to the formation of the branching trail system that further influences the shape and development of the raid (see Fig. 2C).

The prediction that the distribution of prey directly influences the basic design of the raid system in army ants has profound implications. In parts of the neotropics there are three species of army ants of the genus *Eciton* that all raid aboveground. They have species characteristic raid patterns (see Fig. 1).

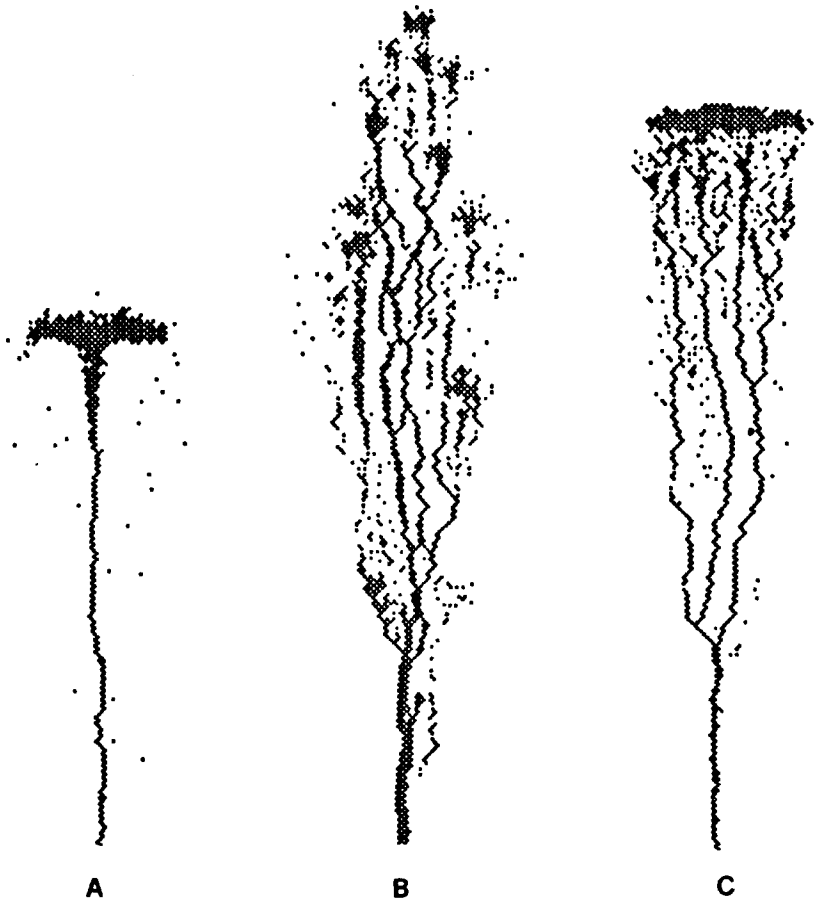


Fig. 2. Three distinct foraging patterns developed by Monte Carlo simulations of the same model with three different food distributions. From Deneubourg *et al.* (1989a). (A) No food. (B) Each point has a 1/100 probability of containing 400 food items (as might be the case for an army ant that is a specialist predator of other social insects such as *E. rapax*). (C) Each point has a 1/2 probability of containing one food item (as might be the case for a generalist predator such as *E. burchelli*).

The model predicts that these species specific patterns may simply be the result, not of different communication systems, but of the different prey distribution patterns of the three species. *E. hamatum* attacks wasp nests that are few and far between, but represent large packets of prey. *E. burchelli* eats both solitary arthropods (rather common but small packets of prey) and certain species of ant colony. *E. rapax* has an intermediate diet, attacking ant and wasp nests and relatively few large arthropods. *E. hamatum* has a dendritic raiding pattern, *E.*

burchelli a large cohesive swarm raid, and *E. rapax* a raid system with many small swarm systems. The model suggests that these different patterns may be created in part as a direct response to the distribution of prey. Widely distributed sites of prey capture cause ants to return along highly separated trail systems and split the raid system; further isolated discoveries are made by these separate swarms, which continue to diverge in response to the prey distributions (see Fig. 2B, showing the same model rerun with "prey" patches that are very dense but rather rare).

If indeed the prey distribution to a large extent controls the structure of the raid, as the model predicts, then it should be possible to manipulate an *E. burchelli* raid to split into subswarms simply by manipulating the distribution of its prey. We now describe a test, in the field, of this major prediction of the model.

METHODS

The fieldwork was conducted in January and in July and August of 1989 on Barro Colorado Island, in the Republic of Panama [see Franks (1989) for a general review of this field site and its army ant populations]. To test the main assumptions of the model, either the raid systems of *E. burchelli* were recorded without manipulation by filming with a video camera-recorder or samples of fewer than 100 workers were taken from such raid systems and transferred to the laboratory clearing on Barro Colorado Island, where the experiments were also video-recorded.

Choices at "Y"-Junctions

In the first series of experiments, the video recordings were made by filming natural branching points along raid systems, for extended periods of time. The natural Y-junctions chosen for filming fulfilled two criteria. First, the trail of ants moving outward branched symmetrically into two: second, the two branches symmetrically reunited. In other words, naturally looping trails were filmed that formed both a Y-junction for those ants moving outbound toward the raid front and a similar Y-junction for inbound ants moving back toward the nest. Suitable loops are common in *E. burchelli* raids and form a natural analogue to the diamond bridge experiments used by Deneubourg *et al.* (1989b). In experiments with *Iridomyrmex* such diamond bridges were physically introduced between the nest and the foraging arena of colonies to determine how the flow of forager traffic determines future traffic flow patterns (Deneubourg *et al.*, 1989b). We did attempt to introduce such physical diamond bridges into army ant trails, but they were always avoided, presumably because the ground surrounding them still had some trail pheromones present (see below) from the

earlier transit of the whole swarm raid. The drawback of analyzing natural "diamond bridges" in *E. burchelli* raids, rather than newly introduced physical bridges, is that the dynamics of traffic flow cannot be studied from the very outset of new trail formation. For the analysis we have used, however, this potential problem has minimal consequences.

The video recordings of *E. burchelli* diamond loops were then analyzed at the University of Bath, by counting the number of ants running outward toward the raid front or returning to the nest along both branches, every minute. In this way the number of ants choosing to take the left or right branch at a Y-junction could be determined as a function of the numbers that had earlier made such decisions or that had returned along these trails in earlier time periods.

Circular Mill Manipulations

The tendency of isolated groups of army ants to form circular mills has been extensively documented by Schneirla (1944, 1971). This process occurs when groups of army ants are isolated from the rest of their society and are deprived of normal cues, so that if they begin to run in a circle, they tend to reinforce their own trail, making it harder for themselves to break out from such a circular mill. The very existence of this phenomenon shows that the army ants must be laying trails when they are exploring new territory and in the absence of any encounters with prey.

We used circular mills for the first time, as a basic bioassay for determining how the ants respond in terms of their running velocity to (a) the amount of traffic and trail laying that has occurred and (b) the decay of the chemical trails over the time that elapsed since the mill was last saturated. An artificial mill-arena was built from the lid of one plastic bucket and the cut-down bottom of another plastic bucket with a larger diameter. The two were put together to form a circular trough, the vertical sides of which were coated with fluon to prevent the ants escaping. The trough was 2 cm wide at its base and had a circumference of 0.75 m. Groups of 40 *E. burchelli* workers were independently introduced to such a mill, and their running behavior was recorded with the video camera.

The running speeds of a particular physical caste of the work force, the submajors, which can run faster than any of their nestmates (Franks, 1985, 1986), were noted in min 0 to 10 and 20 to 30 of four separate mill experiments. In each of these intervals the time taken for 10 submajors each to complete a full lap of the mill was noted.

To examine the decay rates of trails, a group of 40 army ants was given at least 30 min to form and saturate the circular mill trail. These workers were then taken out, and either these ants or a different group of 40 workers, from the same colony, were replaced after intervals ranging from 1 to 840 min, and their running velocity was noted. In this procedure the ants were all rapidly

reintroduced to the trough at one point and the time was recorded for the ants traveling clockwise to meet those running anticlockwise. This method was used so that the behavior of a group of ants could be assessed as they ran over an old trail that they themselves had not influenced. Their meeting point was almost always diametrically opposite to the reintroduction point. Hence, the average velocity of the group of ants, traveling over a trail for the first time since it was saturated, could be calculated from the average distance traveled, i.e., half the circumference of the trough, divided by the time taken for the mill of ants to reform.

This method using 40 ants in the mill at a time was preferred to alternatives using solitary ants because the behavior of these virtually blind army ants may be influenced by cues such as the close contact of their nestmates. Such is the interdependency of these army ants that even the survivorship of small isolated groups is extremely short. The possibility that the trail running behavior of army ants is influenced by the physical contact of their nestmates was investigated in the following way. In another series of circular mill experiments the numbers of ants running clockwise and anticlockwise past a set point in the trough were counted both in the first minute of their introduction to the mill and in another period of a minute after they had been running in the trough for 30 min. We could then determine if the ants have a tendency to run in the same direction as the majority of their nestmates.

Quantitative Observations of General Traffic Flow Within Natural Raid Systems

A long video recording was also made of the behavior of ants running in the principle trail of the raid near their bivouac nest, to determine changes in overall traffic for an extended period. The recording was made from 1134 to 1444 h (local time), filming for 10-min periods, at 10-min intervals, to give a total of 100 min of observations. These were fully analyzed to give data on the number of outbound and inbound ants per minute for the 100 min of sampling in the 190-min period.

Manipulating the Food Distribution in the Path of a Raid

Two methods were used to manipulate the food distribution encountered by *E. burchelli* swarm raids. First, since their arthropod prey are confined mostly to the leaf litter, raking away and redistributing the leaf litter to leave discrete bare patches that are relatively prey-free should make the raiding environment of the army ants much more heterogeneous. Second, since their prey are generally scattered over a large area, placing very large packets of immobilized arthropods ahead of the swarm should effectively swamp the raid so that for a considerable time almost all their prey will come from these packets. Both of

these methods of altering the spatial pattern of their prey were used to examine how prey capture alters the structure of raid systems.

Prey Introduction. Large packets of prey were introduced in front of a swarm raid by using plastic mesh bags (25 × 25 cm with mesh holes approximately 1 cm in diameter), each of which was filled with 100 dead crickets (subadults of *Acheta domesticus*). Dead crickets had to be used because Barro Colorado Island is a nature reserve, so that live animals cannot be introduced. The crickets were killed and preserved by freezing and then thawed out before placing them before the army ants. The fresh weight of crickets in each bag in the pair was the same. In each experiment the total fresh weight of crickets introduced was between 50 and 60 g. In a complete nomadic raid lasting 10 h, an *Eciton burchelli* colony on Barro Colorado Island collects on average about 60 g dry weight of insect matter. Taking fresh weight to be five times dry weight, the prey introduction experiments presented extremely concentrated sources of food totaling one-fifth of a colony's complete daily intake.

Two such cricket bags were placed in front of a swarm raid, one toward either side of the swarm front, in each such experiment. These experiments were used to test the prediction of the Deneubourg *et al.* (1989a) model that *E. burchelli* will produce a raid system more like that of *E. rapax* if it encounters an appropriate prey distribution (see Figs. 2B and C).

Prey Redistribution. A large garden rake was used to redistribute leaf litter and the prey it contained in the swarm's path. In certain experiments a wide belt of the leaf litter of equal width to the swarm itself was raked away and evenly redistributed ahead of a raid, and in others just four or five small patches of leaf litter were raked away evenly in all directions to leave clear patches in a symmetrical distribution ahead of the swarm front (see Fig. 10).

RESULTS

Choices at Y-Junctions

Natural Y-junctions in *E. burchelli* raid systems were filmed until one branch completely dominated the other in terms of traffic flow. We begin by considering one such system, site 1, in some detail. In this case the traffic on a Y-junction was filmed for 67 min and all the traffic flow, i.e., numbers of foragers outbound (moving out from the nest to the swarm front), along both branch A and branch B of the Y-junction, and the total numbers of ants inbound (returning, with and without food on both branches) were determined every minute by repeatedly analyzing the videotape (see Table I). Figures 3a–3d show the cumulative traffic on these trails over time. Figure 3a shows changes in the cumulative numbers of all foragers, i.e., all traffic on trails A and B through time. Clearly, trail B becomes increasing dominant. Henceforth, B is designated the

Table I. Analysis of a Natural "Y"-Junction in an *E. burchelli* Raid[a]

Time (min)	Outbound branch		Inbound with prey		Inbound without prey		Inbound total		Total traffic	
	A	B	A	B	A	B	A	B	A	B
1	56	61	0	67	2	58	2	125	58	186
2	90	101	0	68	1	100	1	168	91	269
3	113	129	0	79	3	68	3	147	116	276
4	97	100	0	74	2	71	2	145	99	245
5	92	73	0	84	8	63	8	147	100	220
6	112	90	0	33	3	69	3	102	115	192
7	67	82	0	48	2	58	2	106	69	188
8	97	60	0	63	1	83	1	146	98	206
9	80	52	0	78	3	71	3	149	83	201
10	76	70	0	86	5	62	5	148	81	218
11	67	71	0	77	7	70	7	147	74	218
12	86	65	0	62	2	75	2	137	88	202
13	107	53	0	64	4	67	4	131	111	184
14	60	56	0	68	3	61	3	129	63	185
15	54	77	0	59	1	63	1	122	55	199
16	77	90	0	45	2	62	2	107	79	197
17	85	73	0	58	6	59	6	117	91	190
18	67	96	0	54	2	63	2	117	69	213
19	98	68	0	39	8	47	8	86	106	154
20	77	92	0	66	12	56	12	122	89	214
21	93	79	0	69	4	72	4	141	97	220
22	60	95	1	44	5	60	6	104	66	199
23	60	115	0	35	5	64	5	99	65	214
24	45	119	0	72	4	36	4	108	49	227
25	49	73	0	44	2	60	2	104	51	177
26	49	75	0	53	2	48	2	101	51	176
27	51	51	0	61	4	67	4	128	55	179
28	66	88	0	32	2	41	2	73	68	161
29	61	69	0	60	5	58	5	118	66	187
30	69	81	1	60	1	63	2	123	71	204
31	64	69	0	70	3	72	3	142	67	211
32	42	75	0	37	2	65	2	102	44	177
33	58	105	0	28	2	35	2	63	60	168
34	43	99	0	32	4	54	4	86	47	185
35	36	112	0	26	3	49	3	75	39	187
36	25	87	0	47	2	52	2	99	27	186
37	29	95	0	27	1	52	1	79	30	174
38	55	86	0	38	2	39	2	77	57	163
39	37	94	0	34	1	39	1	73	38	167
40	3	78	0	41	0	51	0	92	3	170
41	9	31	0	20	0	44	0	64	9	95
42	2	8	0	39	3	55	3	94	5	102
43	3	20	0	30	1	55	1	85	4	105
44	5	18	0	19	4	61	4	80	9	98
45	4	30	0	31	1	63	1	94	5	124
46	7	39	0	49	0	71	0	120	7	159
47	5	69	0	13	1	63	1	76	6	145

Table I. Continued

Time (min)	Outbound branch		Inbound with prey		Inbound without prey		Inbound total		Total traffic	
	A	B	A	B	A	B	A	B	A	B
48	5	74	0	26	3	46	3	72	8	146
49	5	130	0	21	2	52	2	73	7	203
50	5	150	0	29	2	66	2	95	7	245
51	17	151	0	37	4	59	4	96	21	247
52	25	152	0	37	3	65	3	102	28	254
53	24	141	0	30	2	54	2	84	26	225
54	7	140	0	24	4	54	4	78	11	218
55	26	118	0	18	2	81	2	99	28	217
56	11	96	0	29	4	50	4	79	15	175
57	20	109	0	26	3	58	3	84	23	193
58	29	100	0	28	2	66	2	94	31	194
59	15	90	0	36	1	51	1	87	16	177
60	11	77	0	31	0	69	0	100	11	177
61	9	100	0	42	2	81	2	123	11	223
62	10	94	0	15	2	72	2	87	12	181
63	16	108	0	24	0	53	0	77	16	185
64	8	77	0	56	1	70	1	126	9	203
65	5	93	0	42	0	59	0	101	5	194
66	2	98	0	45	0	64	0	109	2	207
67	4	95	0	37	0	85	0	122	4	217

[a] The numbers of ants running outbound and inbound with and without prey are recorded for each minute on each branch, A and B (see text for further explanation).

winning trail and A the loosing trail. This increasing dominance of B over A is very clearly shown in Fig. 3b, which depicts the proportion of all outbound foragers choosing B as a function of time. The dominance of B over A through time could not be predicted purely in terms of initial outward traffic on these trails. Indeed as Fig. 3c shows, total outward traffic was sometimes higher on A rather than B at the early stages of the competition between these trails: only after 30 min did outbound traffic flow rates diverge. The major difference between trail A and trail B from the beginning was that much more traffic was returning along B; see Fig. 3d. However, since, as we show, the army ants lay trail pheromones on the outward journey and on the inbound journey, it would be wrong to interpret the competition between B and A purely in terms of the influence of inbound traffic. Rather, since inbound traffic positively influences the direction of outbound traffic, which itself can attract further outbound traffic (and indeed further inbound traffic), there can be very strong positive feedback.

The data from the above experiments and those at three other sites were also analyzed to determine whether the choice of trails by outward-bound ants

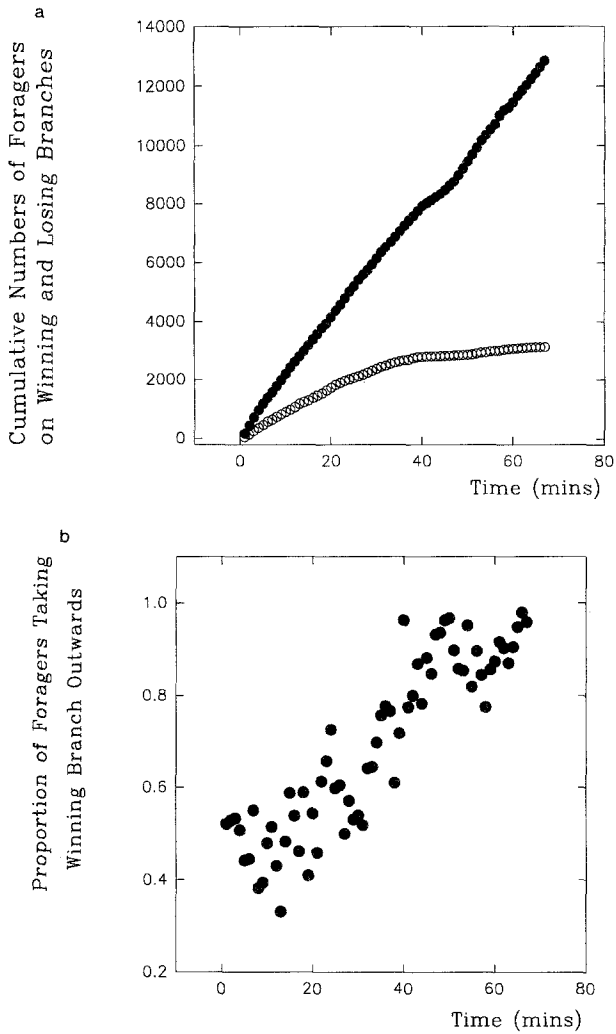


Fig. 3. Analyses of traffic flow at the natural Y-junction at site 1. (a) The cumulative numbers of all foragers, i.e., all traffic on the winning (B) and losing (A) trails changing through time, represented as filled and open circles respectively. Clearly, trail B becomes increasingly dominant. (b) The proportion of all outbound foragers choosing the winning trail B (filled circles) as a function of time. (c) Total outward traffic was sometimes higher on the losing trail A (open circles) rather than the winning trail B (filled circles) during the early stages of the competition between these trails: only after 30 min did outbound traffic flow rates diverge. This shows that the dominance of B over A through time could not be predicted purely in terms of initial outward traffic on these trails. The major difference between trail A and trail B from the beginning was that much more traffic was *returning* along B; see d. (d) Cumulative numbers of *inbound* foragers on the winning (B, filled circles) and the losing (A, open circles) branches as a function of time.

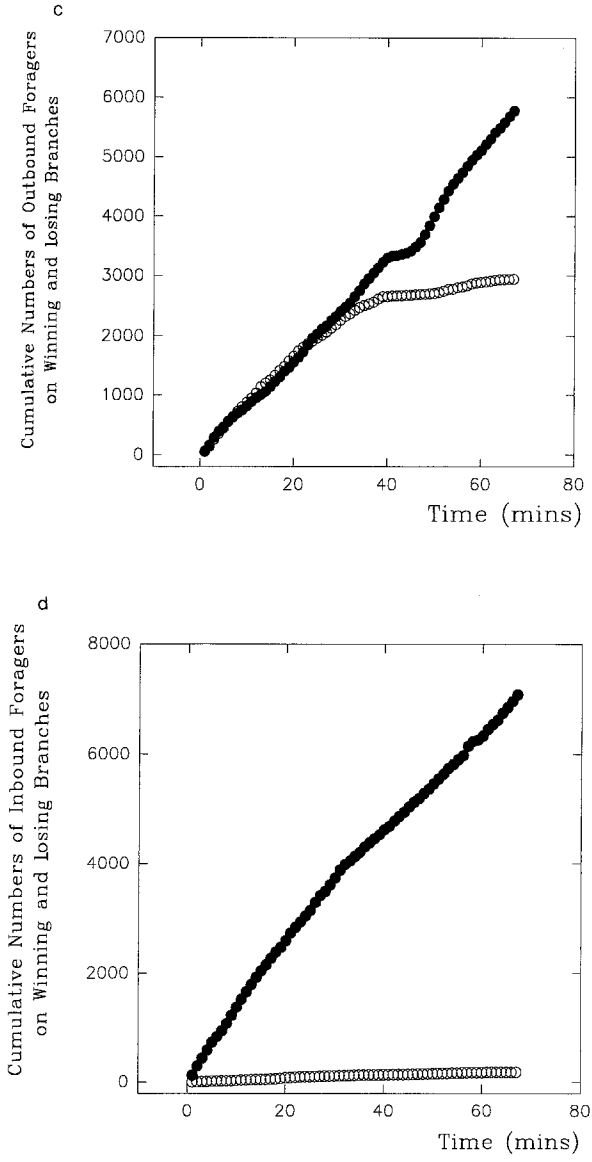


Fig. 3. Continued

is influenced equally by those returning or by those that had been outward bound in a previous time period (see Table II). The results clearly show that both outbound and inbound ants have a significant effect on the proportion of outbound ants selecting each trail.

Circular Mill Manipulations

When workers are introduced to a circular mill they gradually *increase* their running velocity. The lap times for submajors were recorded in four separate mills (see Table III).

Ants reintroduced to a circular mill had initial average velocities that fall exponentially as a function of time since the mill was last saturated with trail pheromones (Fig. 4). The relationship between this initial average velocity (IAV) and the age of the old trail is best described by

$$\ln (\text{IAV}) = -2.77\ (\pm 0.08359)\ -0.00522\ (\pm 0.00095) * \text{age}$$

($r = 0.91$, $n = 8$, $P < 0.001$; the figures in parentheses are standard deviations), where IAV is expressed as meters per second and the age of the old trail ranges from 1 to 180 min. The velocity of the ants responding to trails of 300 and 840 min was, respectively, 0.023 and 0.026 m/s, i.e., only slightly less than the initial average velocity of 0.035 m/s for the ants running on a trail 180 min old.

The model of Deneubourg *et al.* (1989a) assumed a sigmoidal relationship between pheromone strength and running velocity. Such a sigmoidal relation-

Table II. The Proportion of Outward-Bound Ants Choosing the Winning Trail (1), Rather than the Losing Trail (2), at Time t [i.e., $01/(01 + 02)$], Is Regressed as a Function of the Proportion of Ants Returning on that Trail in the Same Time Period [$R1/(R1 + R2)$] and the Proportion of Ants Going Out on that Trail and returning on that Trail in the Previous Time Period.[a]

Site	Constant A	Coefficient B	Coefficient C	Coefficient D	Sample size	Time lag (min)	r
1	−0.653	0.822*	0.870**	−0.066	65	1	0.89***
2	−0.0290	0.528**	0.397*	0.004	20	5	0.83***
3	−0.402	0.133	0.443**	0.178	26	1	0.45**
4	0.0276	0.362*	0.545**	0.270	45	1	0.76***

[a]This time period was 1 min for sites 1, 3, and 4 and 5 min for site 2. The longer interval for site 2 as taken because filming at that site was made for periods of 1 min at 5-min intervals. Thus, $01/(01 + 02) = A + B * [R1/(R1 + R2)] + C * [01/(01 + 02)(t - 1)] + D * [R1/(R1 + R2)(t - 1)]$.

*$P \simeq 0.05$.

**$P < 0.05$.

***$P < 0.01$.

Table III. Velocities of Submajors, as Meters per Second, Running in a 0.75-m-Circumference Circular Mill[a]

	Period of observation						
	0–5 min			20–30 min			
Mill	Mean	SD	*n*	Mean	SD	*n*	*P*
A	0.066	0.005	10	0.074	0.007	10	<0.01
B	0.055	0.009	10	0.072	0.003	10	<0.001
C	0.041	0.006	10	0.051	0.009	10	<0.01
D	0.069	0.008	10	0.063	0.005	10	>0.05

[a]The observation that in only three of the four mills was there an increase in submajor speeds between 0–5 and 20–30 min, and then only by about 20%, is probably due to the mills being almost completely saturated with trail pehromones after the first 1 or 2 min. The initial 5 min had to be considered to provide sufficient submajor laps for the statistical analysis.

ship can be approximated as three straight lines, one for the upper and one for the lower asymptotes and one oblique line for the growing phase in which there is a rapidly changing response. The above observations examine the linear growing phase in such a sigmoidal relationship. It is evident that the ants have both an upper asymptote and a lower limit to their running velocities.

If, for the sake of argument, we make the assumption that velocity is directly proportional to pheromone strength, the above calculations suggest that the trail pheromones of *E. burchelli* have a half-life of approximately 132 min on average (with a standard deviation of 13 min). The half life ($T_{1/2}$) is calculated as $T_{1/2}$ = natural log (2)/k: in the above case, $k = 0.00522$.

Analysis of the number of ants running past a set point in the circular mill in a clockwise or anticlockwise direction shows, in a sizable proportion, 16 of the 44 separate analyses, of the 22 circular mills, a significant tendency for the majority of ants at any one time to be running in the same direction. In eight of the remaining mills the numbers running in either direction were remarkably similar (see Table IV). These findings are not necessarily contradictory. If, by chance, equal numbers of ants were running in both directions, it might take a very long time for one direction to dominate.

Quantitative Observations of General Traffic Flow Within Natural Raid Systems

Total traffic flow in the video-recorded principal trail declined over the 190-min observation period (Fig. 5) as best described by TTF = 261 − 0.311 * (time), where TTF is total traffic flow and time is in minutes ($r = 0.53$, $n = 100$, $P < 0.001$). There is a weak but significant negative correlation ($r = 0.446$, $P < 0.001$, $N = 100$) between outbound and inbound forager numbers

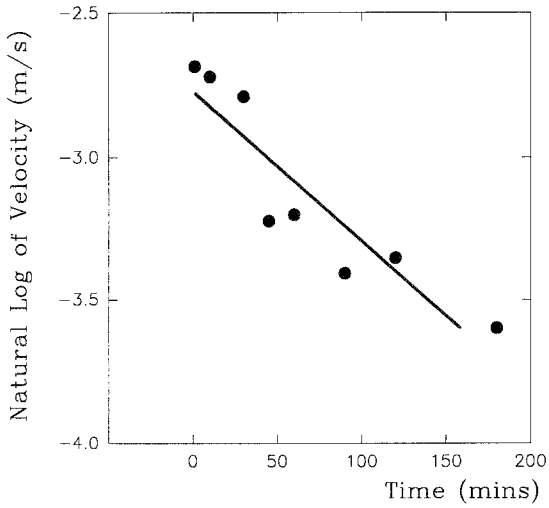


Fig. 4. The natural log of the velocities of ants reintroduced to a circular mill as a function of time since the mill was last saturated with trail pheromones. The initial average velocities fall exponentially as a function of time. The relationship between this initial average velocity (IAV) and the age of the old trail is best described by ln (IAV) = −2.77 (±0.08359) − 0.00522 (±0.00095) * age ($r = 0.91$, $n = 8$, $P < 0.001$; the figures in parentheses are standard deviations), where IAV is expressed as meters per second and the age of the old trail ranges from 1 to 180 min.

per minute (Fig. 6), such that outbound numbers = 132 − 0.435 * (inbound numbers).

Manipulating the Food Distribution in the Path of a Raid

Prey Redistribution Experiments

The first three experiments involved creating a number of small bare patches in the leaf litter in front of swarm raids. In the first two experiments, the swarms broke up into subswarms and in the third experiment the swarm remained intact but its entire course was changed.

Experiment 1. The introduction of five circular (1-m-diameter) areas raked free of leaf litter at 2-m intervals across the path of a swarm raid resulted in the splitting of the swarm front into two smaller fronts, which took divergent paths, avoiding the bare patches. The subsequent behavior of the smaller swarm fronts was similar to the behavior of the primary swarm. The two divergent paths remained distinct for as long as observations were maintained, a period of more than 2 h (see Fig. 7).

Table IV. The Number of Ants Running in Opposite Directions in the 1st and 30th min of 22 Different Circular Mills[a]

Ants running			
1st min		30th min	
Clockwise	Anticlockwise	Clockwise	Anticlockwise
20	9*	17	19
24	18	12	11[b]
51	50[b]	32	20
47	62	14	13[b]
34	23	27	21
44	42[b]	43	21**
26	33	16	5
44	23	18	98***
16	18	25	25[b]
60	26**	18	24
22	50**	13	23
35	34[b]	18	29
29	23	10	9[b]
35	52*	29	33
24	40*	62	38*
101	2***	90	11***
16	12	15	10
12	4*	7	8[b]
16	19	5	10
13	28*	20	40*
11	44***	11	13
17	13	17	21
697	625*	519	502

[a]The data are treated, for simplicity, as for 44 separate trails. The numbers running in each direction were tested against a 1 : 1 ratio for each mill, within each time interval.
[b]Extremely small chi-square value, equivalent to $P > 0.90$.
*Significant chi-square value, $P < 0.05$.
**Significant chi-square value, $P < 0.01$.
***Significant chi-square value, $P < 0.001$.

Experiment 2. Five circular raked areas were introduced in the swarm's path (exactly as in experiment 1). This resulted in the splitting of the swarm front into five distinct trails. One of the trails went up a tree and the other two pairs converged to form distinctly divergent swarms. The ants did not cross the prey free patches.

Experiment 3. Four circular (1-m-diameter) raked areas were introduced into the path of the swarm's front. This diverted the whole swarm to the left so that it completely avoided the clear patches.

In the next two experiments leaf litter was redistributed away from the entire width of the swarm raids. In one experiment the swarm broke up into

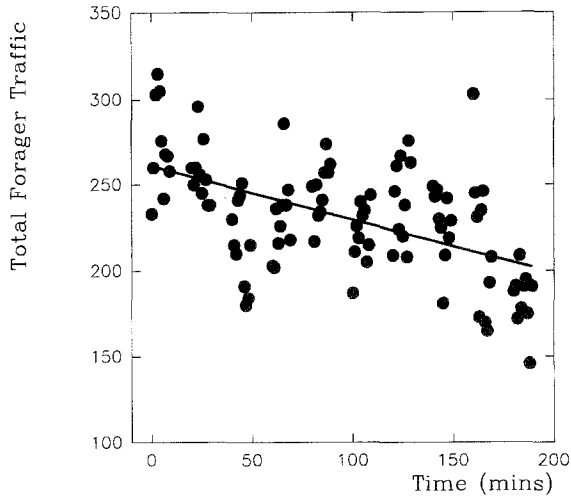


Fig. 5. Total forager traffic, the number of ants passing a set point per unit time, as a function of time for the principal trail of a raid near the bivouac nest. The recording was made from 1134 to 1444 h (local time), filming for 10-min periods, at 10-min intervals, to give a total of 100 min of observations. Total traffic flow in the video-recorded principal trail declined over the 190-min observation period (Fig. 3) as best described by TTF = 261 − 0.311 * (time), where TTF is total traffic flow and time is in minutes ($r = 0.53$, $n = 100$, $P < 0.001$).

divergent subswarms, and in the other, where the leaf litter-free band was so wide that it could not be avoided, it was crossed by the swarm, with no long-term effects on its structure or direction.

Experiment 4. A rectangular band (4.4 * 0.66 m) was raked free of leaf litter in the path of a swarm front. Again, the swarm front was divided into two smaller fronts, which remained distinct and divergent.

Experiment 5. An 8.8 * 1.1-m band was raked free of leaf litter ahead of a swarm raid. In this case the prey free band caused the swarm to become narrower but had no long-term effect on the behavior of the ants.

Prey Introduction Experiments

Experiment 6. Two bags of 100 crickets each were introduced into the swarm's path. The swarm split into two smaller swarm fronts, each of which eventually continued to the left of each bag of food. The progress of the trails was interrupted by the bag since the ants returned to the nest with food items: 200 crickets were retrieved in total. Any trails not encountering food packets continued in the normal way. The two divergent fronts eventually converged.

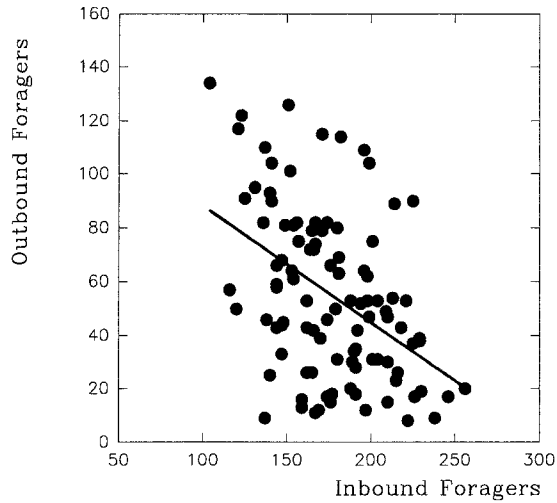


Fig. 6. Outbound forager numbers as a function of numbers of inbound foragers from the analysis of the video recording also represented in Fig. 5. There is a weak but significant negative correlation ($r = 0.446$, $P < 0.001$, $n = 100$) between outbound and inbound forager numbers per minute, such that outbound numbers = 132 − 0.435 * (inbound numbers).

Pupal cases were present near the army ants' nest, which indicates that the swarm was ready to start its nomadic phase; however, the following day the swarm was found in the same area. The main nest had disappeared, and instead the ants had formed several small nests along their trail. There were two swarm fronts instead of one and they both showed normal behavior. Observation of the swarm was maintained for another 15 days and the same behavior continued. A main nest was never found and the small group of nests was moved every day along the trail. Observations were not made at night so that it is not known whether the ants reconstituted one main nest after nightfall.

Experiment 7. As above, the bags of crickets were introduced into the swarm's path. Again, the swarm front was split into two main trails, each one heading in the approximate direction of a bag (see Fig. 8). Small branches linked the main trails to the bags. The branches stopped at the bags. A total of 116 crickets was retrieved by the army ants, and as before, the swarms eventually converged.

Experiment 8. Following the introduction of the food bags the direction of the main swarm changed and broke into two subswarms, neither of which moved directly toward the bags. However, small trails were formed between the main trail and the bags. In this experiment the ants retrieved 134 crickets.

Experiment 9. The introduction of the food bags, in this case, had no diver-

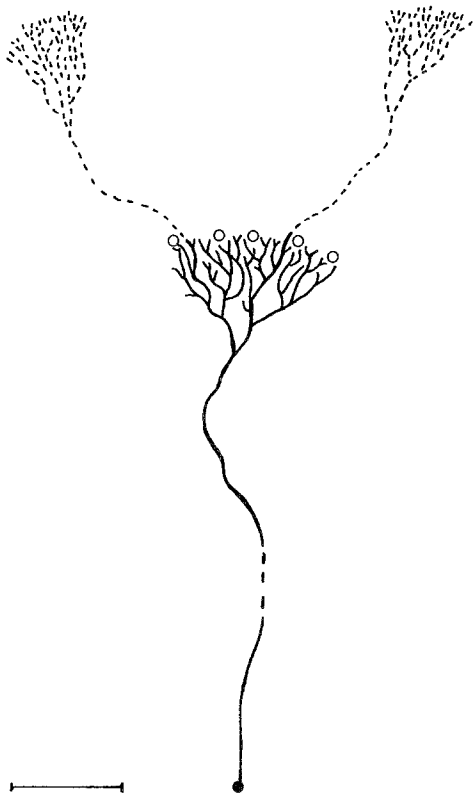


Fig. 7. The progress of an *E. burchelli* swarm raid before (solid lines) and after (dashed lines) five patches of leaf litter, represented by small open circles, were raked clear. The scale bar represents 10 m. [See the description of experiment 1 under Prey Redistribution Experiments (Results) for further details.]

gent effect, however, the swarm front continued to move in the direction of one of the bags, from which the ants retrieved 100 crickets. The other bag was not recognized as a source of food, possibly due to the poor condition of the defrosted crickets it contained.

DISCUSSION

Our field experiments and analyses provide tests and support for all the fundamental assumptions and key predictions of the model of army ant raiding by Deneubourg *et al.* (1989a).

The choice of branch trails by outgoing foragers in the raid system is influ-

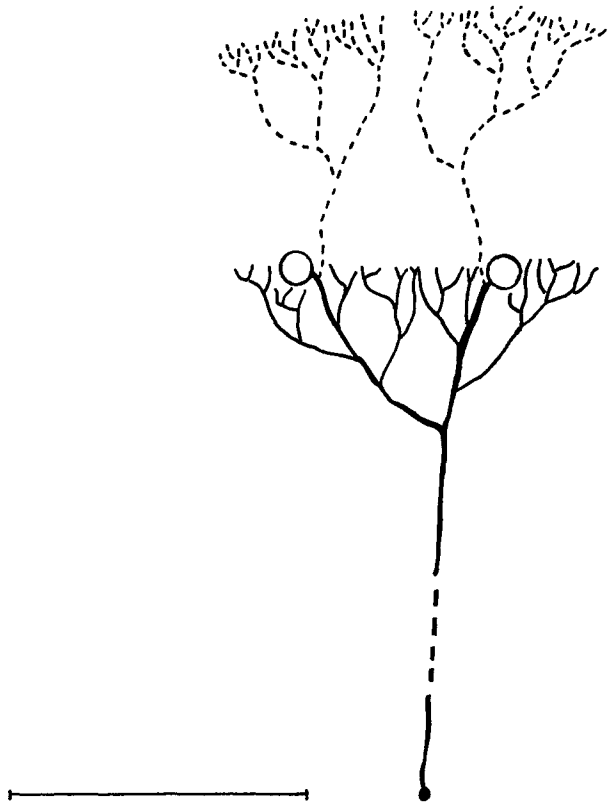


Fig. 8. The progress of an *E. burchelli* swarm raid before (solid lines) and after (dashed lines) two large bags of crickets, represented by the two large open circles, were introduced. The scale bar represents 10 m. [See the description of experiment 7 under Prey Introduction Experiments (Results) for further details.]

enced by the amount of both outbound and inbound traffic on such trails. Our analyses suggest that the quantities of trail substances laid by outbound and inbound foragers per ant per unit distance may be rather similar or at least not radically different.

The circular mill experiments show (1) that the ants speed up as they saturate their own trail and (2) that, for the intervals we investigated, the velocity of the reintroduced ants declines exponentially as such trails decay through time. The Deneubourg *et al.* (1989a) model actually assumes a sigmoidal relationship between the velocity of the ants and the strength of their pheromone trails. This is a logical necessity given the upper and lower limit set by a maximum running speed and a minimum rate of walking by the ants. The circular mill experiments

examined intermediate running speeds in which an exponential curve gives a reasonable description of this part of the sigmoidal relationship.

The half-life of the ants' running velocity as a function of trail age is between 2 and 2.5 h. It is, of course, unlikely that running velocity will be directly proportional to pheromone strength. Nevertheless, calculations based on this assumption may have some value as guidelines. For example, if the pheromone itself had a half-life of 2 or 3 h, this would be consistent with the behavior of these army ants. It is known that *E. burchelli* workers can recognize their own trails, especially their principal trails, that are days or even a week or more old (Franks and Bossert, 1983). This is clearly possible with a trail half-life of 2.5 h if the quantities of pheromone laid are very large, as expected with colonies of 500,000 workers, all of whom participate in emigrations along the same principal trails. Furthermore, the estimated exponential rate of trail decay is fast enough that maintained trails will almost always be stronger than recently abandoned ones [see Hölldobler and Wilson (1990) for a recent review of pheromone dynamics]. The assumption of the Deneubourg *et al.* (1989a) model that velocity is a sigmoidal function of trail pheromone strength is therefore a reasonable one and explains why workers run at about 3 m/min in a large principal trail but the swarm front proceeds at only 14 m/h (Franks, 1985, 1986, 1989). The low velocity of the swarm front, as a whole, is due in part to individuals running slowly in virgin territory and in part to them looping back toward the swarm after running forward only a few centimeters (Scheirla, 1971).

The density of the ants and physical contact between them may also help to structure the raid as indicated by the results of the circular mills, showing that these ants sometimes have a distinct tendency to run in the same direction as the majority of their nestmates. The circular mills of *E. hamatum*, shown as photographic plates by Schneirla (1971), show almost all of the ants running in the same direction. These may have been unusual examples, but it is possible that *E. hamatum* workers have a greater tendency than *E. burchelli* workers to follow one another. Alternatively, Schneirla's samples could have been ants taken from the bivouac rather than the raid system. It is possible that the ants that remain in the bivouac and do not forage have an even greater tendency to run in the same direction as the majority of their sisters. This could be an important mechanism that serves to organize the extraordinarily efficient emigrations of these ants.

The analysis of all long-term traffic flow on a principal trail shows that, over the period of observation, traffic flow per unit time changes very slowly. There was a small but significant *negative* correlation between the outbound forager numbers and the numbers of ants returning to the nest per unit time. Thus, it seems clear that incoming foragers do not directly recruit others to join the raid. A more likely explanation, first put forward by Schnierla (1933, 1938, 1971), is that forager activity is stimulated by a shortfall between incoming prey

and the colony's own energy requirements, especially that of the army ants' voracious brood within the bivouac. The pioneering work of Topoff and Mirenda (1980a,b) has experimentally verified this idea for the army ant *Neivamymex*. The more prey-laden incoming foragers, the *fewer* outbound foragers will leave the nest. This could be an important form of negative feedback that helps to regulate foraging activity.

This hypothesis would also help to explain how the bivouac population of a colony in a nomadic phase is able very quickly to switch into a full emigration at the end of a day's raiding. Nomadic raids are extremely long, and as dusk approaches, food captured at the swarm front is likely to be taken to the new bivouac site situated toward the front of the raid system rather than taken to the old bivouac. The amount of food returning to the old bivouac is likely to drop over a period of some hours. As the workers in the old bivouac become more and more hungry, they may start quite suddenly to join the raid system in large numbers, but the food they seek will be available only at the new bivouac site, which will divert this new traffic from the raid system. A cycle of positive feedback may ensue, with less and less food arriving at the old bivouac and more and more ants leaving it. Preliminary support for this hypothesis comes from the prey introduction experiments in which one of the colonies, presented with large and extremely concentrated amounts of surplus food, seemed to have its entire emigration pattern disturbed.

The food manipulation experiments were carried out to test the prediction that the differences in the patterns of the raids of *Eciton burchelli*, *E. rapax*, and *E. hamatum* might be generated by the spatial pattern and density of those items that they recognize and capture as prey. By manipulating the food distribution in front of *E. burchelli* raids, so that their normal prey now occurred in a few dense discrete packets, it was possible to make these colonies raid with separate subswarms like those of *E. rapax*. The social insect prey of *E. rapax* or *E. hamatum* have such a distribution. Their prey colonies are few and far between but, once located, are large dense packets of prey.

This is the first time the prey distribution of *E. burchelli* colonies has been manipulated, and although in some experiments the expected results were not obtained, the food manipulation did have a strong effect in all of them. In three experiments of five, a cohesive single swarm raid was split into two divergent paths by manipulating the distribution and density of the food encountered by raking the leaf litter. In the remaining two experiments the swarm front did not split as the result of the removal of prey, however, in experiment 3 the direction of the swarm was altered, and in experiment 5 the swarm front was narrowed down. In three of the four experiments involving the introduction of prey in bags, the original single cohesive swarm front was split in two. In the fourth experiment one of the introduced bags was not recognized by the ants as a

source of food, but the retrieval of prey from the other bag clearly influenced the design of the swarm raid.

These manipulations are open to the criticism that appropriate controls were not used. Unfortunately, it is not possible to subject the same colony, on the same day, to both experimental treatments and controls. In addition, the extreme heterogeneity of the tropical rainforest environment makes both replicated controls and experiments very difficult. Nevertheless, it seems clear that by manipulating the distribution of its prey, which in turn manipulates the directions from which foragers return with food items, an *E. burchelli* raid can be transformed into one with a design more characteristic of *E. rapax*.

Our experimental observations support the hypothesis that the differences in the raiding patterns of *E. rapax*, *E. burchelli*, and *E. hamatum* may be based on their response to their foraging environment, rather than differences in their communication systems. We are not suggesting that there are no differences in their communication systems. Such differences are bound to exist but may even be of only minor importance in terms of the evolution of these patterns.

The self-organization that appears to be the basis of the construction of the foraging systems of army ants implies that large differences in this type of phenotypic expression may be initiated by small changes in the response of the organism to their environment. As a result, phenotypic diversity can occur in these kinds of system without prior genetic change.

Consider a primitive *Eciton* species, possibly one with a raid system like that of *E. rapax*, as a possible ancestor of *E. burchelli* and *E. hamatum*. If parts of this ancestral population migrated into areas where the only prey were in large packets that were few and far between, i.e., like social insect colonies, it would automatically start to raid like *E. hamatum*, the specialist predator of neotropical wasps. In contrast, if another subpopulation moved into an area in which there were only large arthropods that represented relatively small but common packets of prey, it would apparently inevitably begin to raid like *E. burchelli*, the most polyphagous of neotropical army ants. It is further possible that these separate subpopulations might change genetically as a result of specializing on social insects or general arthropods and thence ignore other prey. If these now genetically distinct, and reproductively isolated, populations then became sympatric, they would have fundamentally different foraging patterns that would help initially to limit intraspecific competition between them. Such competition might then not lead to exclusion but be a selection pressure, which would further refine the differences in their foraging patterns.

Once an army ant raid system becomes so dense that its trails collide to form a network of loops, as is the case in *E. burchelli*, the new raid system is different both qualitatively and quantitatively from the dendritic system that gave rise to it. Such looping trails may serve as a dragnet behind the swarm

front that helps to catch fleeing prey, but as our work suggests they are a by-product of the ants' interaction with their environment and may not necessarily be directly coded for in the ants' communication system. For these reasons, there may be only small differences in the communication systems that these various species of army ants use in foraging.

The combination of modeling and experimentation upon which this recent work on army ant foraging is based highlights the importance for evolutionary interpretation of examining the mechanisms that underlie adaptations in insect behavioral ecology.

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