Spatial Patterns in Army Ant Foraging and Migration: *Eciton burchelli* on Barro Colorado Island, Panama

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Summary. *Eciton burchelli* colonies alternate bouts of central place foraging with periods of migration according to a set rhythm. When these army ants forage from a central nest site they separate neighbouring raids by using a pattern similar to that used by many plants in spiral phyllotaxis. During the intervening periods of migration, raids and emigrations are orientated to lower the probability that the raid path will cross itself and also to separate the successive bouts of central place foraging. This orientation has been analysed by a series of alternative, analytical models which reveal that the navigation is achieved by each day's raid and emigration being constrained to take roughly the same compass bearing as these activities on the previous day.

An *E. burchelli* colony transferred to the previously *Eciton*-free and prey rich Orchid Island, exhibited temporal and spatial foraging patterns insignificantly different to colonies on Barro Colorado Island.

The predetermined foraging patterns of *E. burchelli* are abandoned only when colonies fail to emigrate on some days and subsequently migrate in a radically different direction. This behaviour may be due to colonies avoiding areas marked by others, and could account for the absence of observed intraspecific collisions. By avoiding their own earlier raid paths and those of conspecifics, colonies of *E. burchelli* increase the amount of new ground they encounter.

Introduction

Selection for efficient foraging is regarded as a major factor in the evolution of army ant behav-

iour (Wilson 1958, 1971). It is believed, for example, that nomadism evolved in army ants because they locally deplete their social insect and large-arthropod, prey populations and must regularly move to new feeding areas (Schneirla 1957, 1971; Wheeler 1910; Wilson 1958, 1971). The foraging and movement patterns of army ant colonies are therefore expected to minimize re-exploitation of recently raided areas. In this paper we report a test of this hypothesis for *Eciton burchelli*. Colonies of this species produce massive raid swarms and are the most polyphagous of neotropical army ants (Rettenmeyer 1963). Although much is known about the structure of individual raids (Schneirla 1940; Rettenmeyer 1963) and organization of colony migration in *E. burchelli* (Schneirla and Brown 1950; Willis 1967; Schneirla 1971; da Silva 1977): this is the first study to generate a broader picture of the search pattern of these predators.

Eciton burchelli colonies are harvesting animals (see Pyke 1978); they do not respond to prey at a distance but simply consume all available prey along their entire life-time's track. Like other harvesting animals, these army ants may forage more efficiently simply by avoiding their own former paths and those of conspecifics (Cody 1971, 1974; Smith 1974a, b; Pyke et al. 1977; Krebs 1978). However, a common assumption is that, unlike territorial social insects (Baroni Urbani 1979; Hölldobler and Lumsden 1980), the foraging patterns of army ants are not constrained by neighbouring colonies (Schneirla 1971; Rettenmeyer et al. 1980). In this paper this assumption is tested through an examination of the movement and foraging patterns of *E. burchelli* colonies for evidence of intraspecific interference which could affect foraging efficiency.

The analysis of the spatial foraging patterns of *Eciton burchelli* is greatly simplified because colonies have an unvarying temporal pattern of activi-

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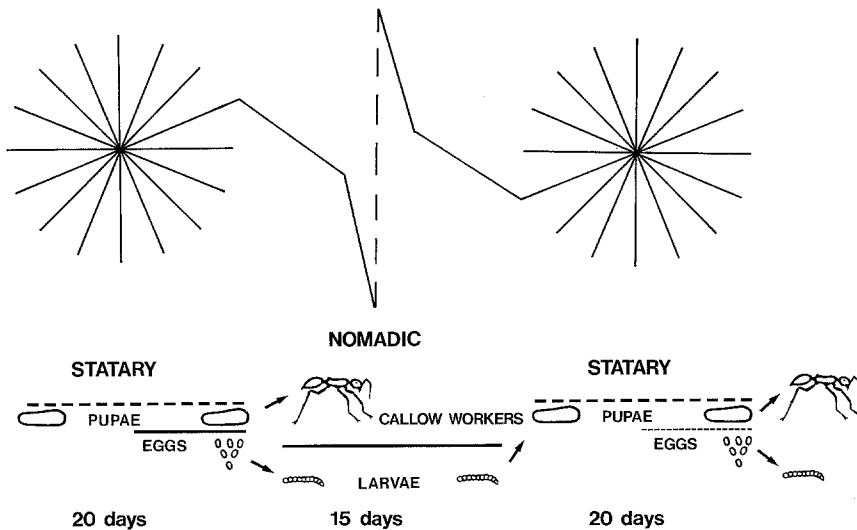
Fig. 1. The 35 day behavioral cycle of *Eciton burchelli*. The foraging and migration pattern is diagramatically represented above an outline of the brood cycle. For further explanation see text

ty which is based on an endogenous rhythm governed by the growth of discrete generations of workers (Schneirla 1971). Colonies alternate bouts of central place foraging called statary phases with periods of nomadism (Fig. 1). During a statary phase a colony has a brood of pupae and eggs, so the adult ants have to feed only themselves. A statary colony uses the same nest site for a period that lasts between 19 and 24 days with an average duration of 20 days, and raids usually occur on only 13 days during this phase ($n=51$, data from Willis 1967; re-analysed in Schneirla 1971). At the end of this bout of central place foraging the eggs and pupae hatch. The subsequent nomadic phase is the period of larval development and ranges between 12 and 19 days with an average length of 15 days ($n=42$) (Willis 1967; Schneirla 1971). To feed its voracious larvae the colony raids on every day and usually at dusk all members of the colony join the emigration to the next nest. On 14.1% of nomadic days (121 of 860 observed; Willis 1967) the ants do not emigrate but remain at the same nest site, then on the next day they raid and emigrate in a new direction. The average 15 day nomadic phase thus has only 13 emigrations. The larvae all pupate at the end of the nomadic phase and the colony enters another statary phase. These behavioural cycles are maintained through-out the lives of colonies and are asynchronous among colonies (Schneirla 1971).

Colonies of *Eciton burchelli* hunt a wide variety of leaf litter invertebrates, though they mostly prey on other ant species (Rettenmeyer 1963; Franks 1980, 1983). Foraging is qualitatively similar in colonies of different size – all raid only during daylight with swarms averaging 6 m wide and containing up to 200,000 ants (Willis 1967). Swarms raid

an average distance of 105 m per day (Franks 1982a). Generally, only one swarm is produced per colony per day and the raiding ants are continously linked to the nest by a principal trail of workers returning with prey, while others move out to join the swarm. The emigration follows exactly the principal trail of the nomadic raid – so the migration of colonies is constrained and determined by their foraging patterns.

Study Sites and Methods

This study, in common with the majority of work on *Eciton burchelli* (Rettenmeyer 1963; Willis 1967; Schneirla 1971), was conducted on Barro Colorado Island (BCI), Panama. This island supports 1,560 ha of moist lowland tropical rain forest. Observed foraging patterns of 20 colonies on BCI are compared first with null hypotheses based on randomness and then with a series of alternative adaptive hypotheses. In addition, the fixity of the foraging patterns of these army ants was tested by transferring an *E. burchelli* colony from BCI to Orchid Island, and *Eciton*-free but similarly forested neighbour of BCI. Both islands were isolated when Gatun Lake was formed between 1911 and 1914 by the damming of the Rio Chagres to form the Panama Canal (Croat 1978). This investigation took place between December 1977 and December 1979.

The raid systems of nomadic and statary colonies were mapped daily by recording the position of each swarm's principal trail. As the swarm sweeps forward it often abruptly changes direction; the principal trail provides a record of these movements (Schneirla 1940). This trail can be depicted as a series of straight lines between the points at which these changes of direction occurred. A 100 m tape was laid along each trail and the length and compass bearing of each straight section was recorded. To estimate the average compass bearing of each day's raid, a line was fitted, by the least-squares method, through a map of the points at which the swarm changed direction. The angles between raids of successive days were calculated from these average compass bearings to determine the overall pattern of raiding in complete statary and nomadic phases.

In July 1978 an *Eciton burchelli* colony of 296,000 ants was transferred from BCI to Orchid Island. The colony was moved in the nomadic phase because at that time its queen was not physogastric and was therefore less prone to injury. The pendulous bivouac, a nest formed as a basket of living workers, was scooped into a plastic bucket, whose rim was coated with Fluon GP-1, a dry lubricant that ants cannot climb over. The ants were collected at dawn; a time when they are most torpid and almost all are within the bivouac. The number of ants collected was determined by weighing both the colony and counted subsamples. To prevent the ants dying of heat stress, the bucket was transported with its base in a chest containing ice and water. The ants were tipped-out at a suitable site on Orchid Island where they quickly formed a bivouac. Very few dead army ants were later found at this site. The progress of this colony was examined at intervals over the course of a year. Similar mapping techniques were used on both BCI and Orchid Island.

Results

During a day's raid in either phase the swarm proceeds in a zig-zag fashion: a turn to the left tends to be followed by a turn to the right and vice versa, as was the case in 314 of 452 successive turns. ($\chi^2 = 62.26$, $P < 0.001$). Due to this compensatory behaviour there is little change in the average direction of the swarm through the day, and over-all progress tends to be in a straight line.

A completed statary phase has on average 15 (Willis 1967), 89 m long (S.D. = 41, $n = 25$) (Franks 1980) raids radiating out from its central nest site: this includes the nomadic raids leading to and from the statary bivouac. Such raids, for simplicity, can be considered as uniformly straight and 6 m wide (Willis 1967). If these raids were systematically arranged around the statary bivouac with the maximum angles between all neighbouring raids, 100% of the area around the nest would be covered out to a distance r at which the total front of swarms, 15×6 m, equals the circumference of a circle of radius r centered on the bivouac; i.e. where $r = 90/2\pi$. Beyond this, raids will approximately cover 15, 450 m² rectangles. In such systematic raiding 100% of the area around the bivouac will be swept out to 14.3 m and there will be 30% coverage out to 89 m. By contrast, the percentage of the available area escaping 15 randomly separated raids would be on average:

$$100 \left(1 - \frac{6}{\pi r}\right)^{15}$$

where r is the distance from the bivouac. Hence if these raids were at random angles from their neighbours, 88% and 27% coverage would occur on average up to 14.3 m and 89 m, respectively, from the statary bivouac.

Thus a clear advantage would be gained in the statary phase by systematic foraging and just such a distinct pattern of raiding has been observed during these bouts of central place foraging. In the statary phase, colonies rotate their successive raids around their central nest site. Seven statary, BCI colonies were observed: two tended to place each new raid in a clockwise direction from the previous raid, the other five had anti-clockwise foraging patterns; both trends were significant ($\chi^2 = 5.56$, $P < 0.05$, $n = 2$; $\chi^2 = 11.6$, $P < 0.001$, $n = 5$). The mean angle between successive statary raids is 123° (S.D. = 40, $n = 41$) significantly different ($t = 5.28$, $P < 0.001$) from a mean of 90° expected if raids were at random.

There is also evidence of systematic raiding and navigation in the nomadic phase as indicated by the separation of successive statary bivouacs which is greater than could be achieved by a random walk in the nomadic phase. If each nomadic raid (and subsequent emigration) was in a random direction relative to the previous one, colonies would be performing a random walk of, on average, 13 steps. The average step length is 80.9 m (S.D. = 43, $n = 395$) which is the average emigration distance measured as straight line between successive nomadic bivouacs (Willis 1967). The direct distance between the ends of a large number of such random walks would be normally distributed about a mean of $80.9 \times 13^{\frac{1}{2}} = 291.6$ m (Pearson 1906), and this would be the average distance between successive statary bivouacs. On BCI, the direct distances between 38 successive statary bivouacs were normally distributed with a mean of 529 m (S.D. = 267) (Franks 1980; in a further analysis of original data summarized in Willis 1967). Thus the army ants are achieving a significantly ($t = 5.48$, $P < 0.001$) greater separation of their statary bivouacs than they could by raiding in random directions in the nomadic phase.

There are three techniques by which this navigation could be achieved (Fig. 2).

(1) The colonies navigate by 'choosing' a direction for the entire nomadic phase and then raids oscillate about this preferred direction, compensating for deviations from the chosen line.

(2) The army ants do not raid in random directions but tend to follow the same compass bearing in each day's raid as they did during the previous one.

(3) The colonies increase the step length and decrease the number of steps in an otherwise random walk. This could occur if they occasionally maintain straight lines to avoid walking into unsuitable areas, such as those swept out around
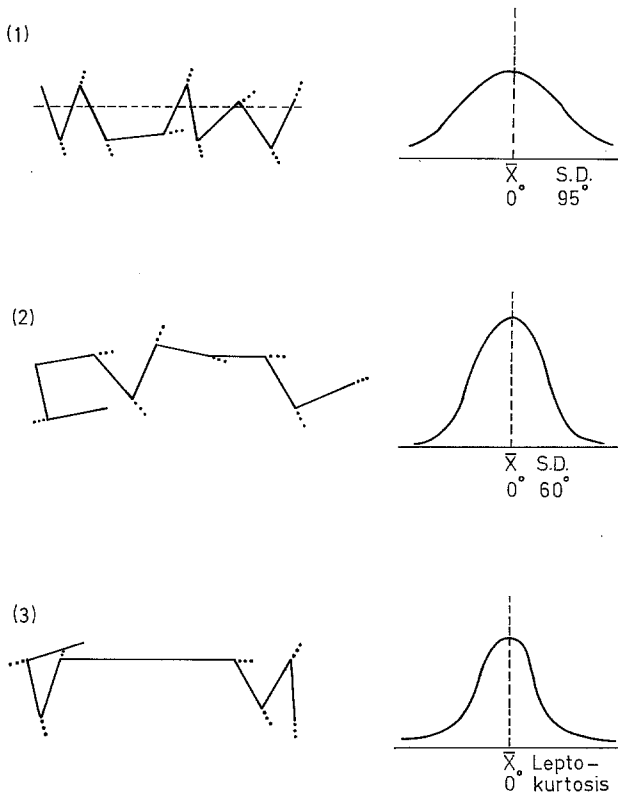
(1)

X̄   S.D.
0°   95°

(2)

X̄   S.D.
0°   60°

(3)

X̄₀ Lepto –
0°   kurtosis

Fig. 2. Three models for nomadic navigation in *Eciton burchelli*. An illustration of each type of walk appears to the left of the distribution of angles between raids that each walk would be expected to generate. *1* Oscillations about a direction chosen for the whole nomadic phase. *2* Directional change between each day's raid and the next constrained to be less than random. *3* Occasionally the same raid direction is taken on successive days; due, for example, to topographical constraints, other raid directions are at random. For further explanation see the Appendix and text

statary bivouacs, or if their movements are sometimes constrained by topographical features.

The army ants could be using any of these three techniques to keep their bivouacs apart by an average of 530 m. However, a unique distribution of angles between emigrations would be associated with each technique. These distributions have been calculated (Appendix). All techniques include the assumption that raid directions and emigrations are no more biased to the right ($+$) than to the left ($-$) of the previous raid and emigration direction, or vice versa. Hence all techniques predict symmetrical distributions of angles about means of $0°$. However, the three hypothetical distributions have significantly different variances.

The angles between successive emigrations of *E. burchelli* colonies on BCI have a mean of $+6.22°$ and a standard deviation of $51.73°$ $(n=32)$. This mean is insignificantly different from zero degrees $(t=0.68, P<0.5)$. The distribution of these
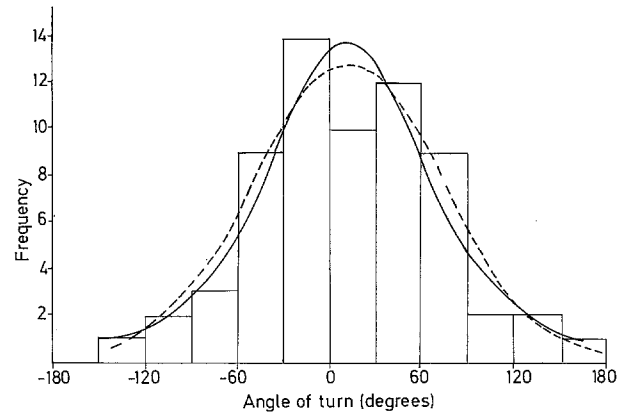

Fig. 3. Frequency distribution of angles between nomadic emigrations. Combined data from Barro Colorado Island and Orchid Island; $\bar{x}= +11.75°$, S.D. $=60.19$ $(n=65)$. The dotted line indicates the expected frequency distribution based on a normal distribution and the solid line represents a circular normal distribution: both of these are insignificantly different from the data $(\chi^2=4.27, df=4, P>0.1$ and $\chi^2=6.26, df=5, P>0.1$ respectively). The circular normal is similar to the wrapped normal (Batschelet 1965). The fit of these distributions justifies the use of the analyses in the Appendix and the statistics in the text

angles is normal, which is in agreement with technique (1) and (2) but discriminates against (3) which predicts a highly leptokurtotic distribution. The variance about the mean predicted by technique (1), 94.61^2, is significantly different from that observed, 51.73^2 $(F=3.31, P<0.002)$. However, the variance predicted by (2) is 60^2, and this is insignificantly different from that observed $(F= 1.33, 0.5>P>0.2)$. Thus technique (2) appears to describe the organization of migration in these army ants – each nomadic raid and emigration is constrained to follow roughly the same compass bearing as that taken by these activities on the previous day.

The *E. burchelli* colony transferred to Orchid Island showed an almost identical form of nomadic navigation to colonies on BCI. The Orchid Island colony distributed the angles between its nomadic emigrations normally about a mean of $+17.2°$ with a S.D. of $67.77°$ $(n=33)$. These data from both islands do not differ significantly from each other (comparison of means, $t=0.74, P>0.4$; comparison of variances, $F=1.72, P>0.1$), and are combined in Fig. 3. The Orchid Island data are also not significantly different from technique (2) $(t=1.46, P>0.1; F=1.28, P>0.5)$ and significantly different from techniques (1) $(F=1.95, P<0.05)$ and (3) (see Fig. 3).

These data for angles between emigrations include data from immediately successive emigrations and also data from those occasions when col-

onies fail to emigrate on one nomadic day and emigrate on the next. Immediately successive emigration angles have a mean of $+8.29°$ and a standard deviation of $52.11°$ ($n=56$); and delayed-emigration angles have a mean of $+33.33°$ and a standard deviation of $98.53°$ ($n=9$). The variance of the latter is significantly greater than that of the former ($F=3.58$, $P<0.01$). That is, a failure to emigrate on one day tends to cause a colony to abandon the direction its whole nomadic migration had taken up to that point. This behaviour can be attributed to colonies avoiding collisions with one another.

Discussion

Throughout the behavioural cycle, the raids of single days are approximately straight (Schneirla 1940); within a day's raiding colonies do not seem to be responding, in their search pattern, to any patchiness in their prey populations. Swarms simply proceed in tight oscillations about the direction chosen for that day. This simple daily raiding pattern greatly simplifies the interpretation of the overall foraging patterns of colonies.

In the average statary phase if swarms were to leave the bivouac in directions that maximized the angles between all neighbouring raids, 100% of the available area would be covered out to 14.3 m from the bivouac. If raids were produced in random directions only 88% of the available area would be covered out to 14.3 m from the bivouac. Clearly, there is a significant advantage to be gained by systematic raiding in the statary phase.

The simplest possibility would be for *E. burchelli* to rotate each successive raid $24°$ from the last. For example, colonies of *Veromessor pergandei*, which harvest seeds by group foraging, rotate successive raids by small fixed angles of $15°$ to $20°$ (Bernstein 1975; but see also Rissing and Wheeler 1976). However, such a simple scheme may not be the most efficient for these army ants because (a) the arthropod prey of *E. burchelli*, excluding social insects, recolonize foraged areas and recover their normal densities within a week (Franks 1980), and (b) some overlap of raid paths is inevitable up to 14 m from the bivouac. Therefore an efficient foraging pattern might separate neighbouring raids in time and space by maximizing the angles both between successively produced and actually neighbouring raids – thereby allowing time for some recovery of prey populations. The central place foraging of *E. burchelli* is analagous

to a plant growing leaves from its vertical stem. To minimize self-shading a plant with between 14 and 17 leaves can maximize the angles between both successively produced and actually neighbouring leaves in its shadow, by spiralling each new leaf at $126.4°$ from the last (Leigh 1972). Like such leaves, statary raids are not at random; they are rotated around the hub of the statary bivouac and the mean angle between successive raids is $123°$ (S.D. $=40$, $n=41$).

Thus, *E. burchelli* to increase its raiding efficiency appears to use a similar design to that used by many plants to circumvent the problem of self-shading. Many plants execute their spiral designs with much greater accuracy than these arms ants (Leigh 1972); however, the army ants' raids are analagous to extremely thin and very long leaves whose placing does not have to be so exact to avoid overlap.

By navigating in their nomadic phases the army ants have solved two potential problems in their search patterns, first, wasted foraging effort due to the nomadic raid path crossing itself and second, reduced foraging efficiency due to overlap in the areas swept out in successive statary phases. In 38 complete phases followed by Willis (1967) only one colony crossed its own nomadic path (Willis, personal communication), and furthermore, successive statary bivouacs have been significantly separated. On BCI, the probability that raids of average length from successive statary bivouacs will cross is approximately 0.1: if the army ants were to do a random walk the probability of such overlap would be approximately 0.35. The technique that the army ants use to achieve this navigation is simply to constrain each new raid and emigration to take roughly the same compass bearing as these activities on the previous day (Fig. 2). The army ants probably take their cue from the pheromonally marked route (Schneirla 1971) of the previous day's raiding. New bivouacs are situated towards, but not at, the end of the day's raid. A small amount of redundant foraging over the marked ground in front of the bivouac could set the raid direction for the rest of the day.

In all aspects of the search pattern of *E. burchelli* hitherto reported, there is no evidence of any response by these predators to the patchiness of their prey. To test for such responses, an *E. burchelli* colony was transported to the different foraging environment provided by Orchid Island. Prior to this transplant no colonies of this species were living on Orchid Island. Possibly some *E. burchelli* colonies were marooned on Orchid Island when it was isolated more than 60 years ago, but

it is highly unlikely that this small island could have maintained a viable population of these army ants for many years. Orchid Island is less than 1/80th of the area of BCI, and the larger island supports only about 50 colonies of *E. burchelli* (Franks 1982a). Furthermore, doryline queens are never winged (Schneirla 1971) so that army ants cannot invade islands. Orchid Island therefore represented a long-term exclusion experiment. Colonies of the ant prey of *E. burchelli* were more than twice as common on Orchid Island as they were on BCI (Franks 1980), and the populations of these prey would not have been rendered spatially patchy by the previous activities of these army ants.

The *E. burchelli* colony introduced to Orchid Island was within the size range of colonies on BCI (Franks 1980), and throughout a year it maintained behavioural cycles of a similar periodicity to colonies on BCI (Franks 1980). The Orchid colony had a predictably and significantly different composition of prey items in its diet: 86% of prey items carried in its principal trails were social insects, compared with 55% for *E. burchelli* colonies on BCI (Franks 1980, 1982b). Nevertheless, the Orchid colony did not respond to its different raiding environment by changing from the standard, stereotyped, foraging pattern.

This analysis of the geometry of *E. burchelli* foraging suggests that each colony's new raid direction is determined almost exclusively by its own previous raid directions. However, each colony must also be responding in its selection of raid directions to the presence of conspecifics; otherwise colonies would collide at a much higher frequency than occurs on BCI. The avoidance of collisions would be advantageous because intraspecific contact between colonies would probably cause combat and the death or injury of workers. A small number of workers manually transferred from one colony to another elicit an attack response from the recipient that far surpasses even the violence of normal raiding (Franks, personal observations).

There is good evidence that such collisions either do not occur at all or occur at a very low frequency on BCI. *Eciton burchelli* has been under almost constant study on BCI from 1929 (Schneirla 1933) to the present; and Willis (1967) alone, observed more than 1,300 raids. Nevertheless, there have been no recorded observations of queen-right *E. burchelli* colonies making contact. By contrast, harmless collisions between *E. burchelli* and colonies of the other common epigaeic army ant on BCI, *Eciton hamatum*, have been commonly seen and reported (Schneirla 1949, 1971; Rettenmeyer 1963; Franks, personal observations).

To estimate collision frequencies, Franks and Bossert (1983) have developed a computer simulation model that incorporates all aspects of the foraging patterns of *E. burchelli* reported in this paper. The model colonies were programmed to miss emigrations on a random selection of 14% of nomadic days. With a density of model colonies in the simulation similar to that of real colonies on BCI, collisions occurred at a frequency of approximately once per colony per 250 days. If collisions were occurring at that rate on BCI it is highly likely that they would have been observed.

This suggests that colonies are exhibiting mutual avoidance on BCI, and this would require colonies to temporarily depart from their stereotyped foraging patterns. The only occasions on which *E. burchelli* abandons its predetermined path is when colonies fail to emigrate in the nomadic phase. If they fail to emigrate on one nomadic day, then on the next day they raid in a different direction and emigrate down the new raid path. In this way they tend to abandon the general direction taken by the nomadic phase up to that point. The frequency of days without emigrations does not correlate with the stage of the nomadic phase in which they occur, in spite of large sets of data on this behaviour (23 complete nomadic phases were examined, including 55 days without emigrations; from a further analysis of data summarized in Willis 1967; Franks 1980). The absence of this relationship suggests that failures to emigrate may be a response to environmental factors that a colony may encounter at any point in its nomadic phase.

A possible explanation for the absence of some of these emigrations and the low frequency of collisions is that colonies are rejecting areas that still bear the trail pheromones of other *E. burchelli* colonies. This possibility is supported by Willis's (1967) observation that one colony withdrew its raid from an area just foraged by a conspecific colony. Franks and Bossert (1983) incorporated such behaviour into their simulation model, to investigate the possibility that it helps colonies to avoid one another. The model colonies were programmed to stop raiding when they encountered areas raided by other army ants within the last 20 days. Furthermore if a nomadic colony encounters such an area it fails to emigrate that day, and then raids and emigrates in a new direction on the next day. The new raid direction is selected to mimic the directions taken by real colonies when

they also failed to emigrate in the nomadic phase. With this refined behaviour, the model colonies collided at a greatly reduced frequency of only once per colony per 600 days and missed nomadic emigrations on approximately 14% of nomadic days.

This hypothetical avoidance behaviour is based on entirely reasonable assumptions about the colony specificity and longevity of trail pheromones. For example the collision-avoidance hypothesis is a realistic possibility only if trail pheromones are persistent, and this appears to be the case. The trail pheromones of *Eciton hamatum*, a close relative of *E. burchelli*, are photostable, thermostable and water-insoluble (Blum and Portocarrero 1964) and they are known to last at least 31 days in the field (Schneirla and Brown 1950). The hypothesis also requires that the trail pheromones of *E. burchelli* are colony specific, so that the raiding ants do not mistake the trails of alien colonies for their own. At least one component of the trail pheromones of *E. burchelli* would need to be functionally analagous to the colony-specific territorial pheromones of the African weaver ant *Oecophylla longinoda* (Hölldobler and Wilson 1977) and the trail pheromones of *Lasius neoniger* (Traniello 1980). Intriguingly, part of the trail pheromone complex in *Eciton* originates in the hind-gut (Blum and Portocarrero 1964; Hölldobler and Engel 1978) which is also the source of the colony-specific pheromones of *Oecophylla* and *Lasius* (Hölldobler and Wilson 1977; Traniello 1980).

By avoiding areas recently raided and marked by conspecifics, *E. burchelli* colonies will be maintaining a spacing system (Brown 1975). In effect they will have pheromonally mediated individual distances (Price 1970; Wilson 1975; Shorey 1976). In the postulated scheme these army ants will not be strictly territorial because areas are avoided rather than defended. However, the mechanism of avoidance would be strikingly similar to that used by some truly territorial mammals (Leyhausen and Wolff 1959; Wemmer and Scow 1977). The postulated 'exclusive areas' of *E. burchelli* are continually on the move and thus resemble, for example, the spatio-temporal territories of cheetahs (Eaton 1970).

The avoidance of conspecifics may also occur in other army ant species. For example, this type of behaviour may partly explain the erratic emigration behaviour of *Neivamyrmex nigrescens* in New Mexico and Arizona (Mirenda and Topoff 1980). As in *Eciton burchelli*, days without emigrations occurred with approximately equal frequency at all points in the nomadic phase of *Neivamyrmex*.

Furthermore, Mirenda and Topoff (1980) state that 'different colonies were ... restricting one another's foraging activities'. However, there are several anecdotal records of army ant colonies following the old trails of other army ant colonies of the same or different species; though conspecific trail following has not been observed in *E. burchelli* (Schneirla and Brown 1950; Schneirla 1971). In *Neivamyrmex* attraction to older trails could be advantageous because it may lead a colony to a suitable bivouac site or to rich prey areas (Mirenda and Topoff 1980). Possibly, some species of army ants respond to the trail pheromones of other colonies in quite different ways which depend upon the age of the trail they encounter: old trails may be followed and young trails may be avoided.

The analyses of *Eciton burchelli* foraging patterns in general, and the Orchid Island experiment in particular, suggest that colonies do not exhibit area restricted searching (Murdie and Hassell 1973; Krebs 1978) on encountering rich prey patches, but rather they respond solely to their own previous raids and those of conspecifics. This suggests that prey are patchy on a fine scale relative to the size of *E. burchelli* foraging systems, and prey are distributed unpredictably. These hypotheses are consistent with the available data on the patchiness of the leaf litter fauna in general and ants in particular on Barro Colorado Island (Franks 1980; Levings and Franks 1982). The new foraging directions of *E. burchelli* colonies are, most likely, orientated merely to avoid their own earlier raid paths, because the only reliable information the army ants have on the availability of prey is the certainty that prey are most rare in recently raided areas.

Harvesting animals with restricted foraging ranges can also increase the percentage of new ground they encounter by having slight asymmetries in their movement patterns (Cody 1971, 1974; Pyke 1978). *Eciton burchelli* colonies have just such asymmetries; their successive nomadic raids tend to be biased clockwise, and this right-handedness is even more pronounced in raids that follow days without emigrations. Thus the army ants may also use this additional technique to increase their foraging efficiency.

Appendix

Technique 1

For each nomadic phase there is some overall 'preferred' direction. Progress is made in this direction, although somewhat inexactly. In polar coordinates, consider $\theta = 0$ as the preferred direction, with the step of the 's'th day being at angle θ_s to this. If the θ_s's have a wrapped-normal distribution (Batschelet 1965), the probability, $P(\theta)d\theta$, of any value of θ to $\theta + d\theta$ occurring is given by:

$$P(\theta)d\theta = \frac{1}{\sigma\sqrt{2\pi}} \sum_{n=-\infty}^{\infty} e \frac{-(\theta + 2n\pi)^2}{2\sigma^2}.$$

If $\sigma \leq \pi/4$ progress is highly directional; if $\sigma \geq \pi$ it is scarcely directional. The mean directionality may be expressed by the mean of $\cos\theta$, since $\cos\theta$ represents the directional component of 'a', one step of the walk:

$$\overline{\cos\theta} = \int_{-\pi}^{\pi} \cos\theta P(\theta)d\theta.$$

This has been calculated numerically (Franks 1980). The overall 13 step walk is described by A_n, whose modulus $|A_n|$ defines the magnitude of progress independent of direction. For technique 1:

$$|A_n|^2 = a^2 n + a^2 \sum_{s=1}^{n} \left(\cos\theta_s \cdot \sum_{\substack{j=1 \\ j \neq s}}^{n} \cos\theta_j \right)$$
$$+ a^2 \sum_{s=1}^{n} \left(\sin\theta_s \cdot \sum_{\substack{j=1 \\ j \neq s}}^{n} \sin\theta_j \right).$$

If there is no tendency to walk in the preferred direction, then the last has an average value of zero. However, with a truely preferred direction,

$$\overline{\cos\theta_j} > 0.$$

Thus,

$$\sum_{\substack{j=1 \\ j \neq s}}^{n} \cos\theta_j = (n-1)\overline{\cos\theta}$$

on average.
    Therefore,

$$a^2 \sum_{s=1}^{n} \left(\cos\theta \cdot \sum_{\substack{j=1 \\ j \neq s}}^{n} \cos\theta_j \right) = a^2(n-1) \left(\cos\theta \cdot \sum_{s=1}^{n} \cos\theta_s \right).$$

On average, this can be equated to:

$$a^2 n(n-1)(\overline{\cos\theta})^2,$$

because on average,

$$\sum_{s=1}^{n} \cos\theta_s = n(\overline{\cos\theta}).$$

    Thus:

$$|A_n| = a[n + n(n-1)(\cos\theta)^2]^{\frac{1}{2}}.$$

If $\overline{\cos\theta} = 0$, then $|A_n| = a \cdot n^{\frac{1}{2}}$ (Random walk).

If $\overline{\cos\theta} = 1$, then $|A_n| = a \cdot n$ (Straight progress).

    The observed values $n = 13$, $a = 80.9$, and $|A_n| = 530$ give $\overline{\cos\theta} = 0.4379$. This corresponds to variation about a preferred direction with a standard deviation of 66.9°. This describes the distribution of angles between single days' steps and the 'chosen line.' The standard deviation of directional change between successive days' steps would be $(2)^{\frac{1}{2}}\sigma$ or 94.61°.

Technique 2

An alternative is that the nomadic phase path is straighter than a random walk, because each raid and subsequent emigration is constrained to follow roughly the same compass bearing as on the previous day. The angles between successive emigrations are not distributed at random. In this case, the axis of coordinates can be set from the first step, so $\theta = 0$. The second day's step is at an angle δ_2 to the first, the third at an angle δ_3 to the second, and so on. The position of a point along the planar walk is represented by a complex number $(x + iy)$ where $i = (-1)^{\frac{1}{2}}$. Then the "s"th step may be described by:

$$a \cos\theta_s + ai\sin\theta_s,$$

where:

$$\theta_s = \sum_{k=2}^{s} \delta_k.$$

    The overall 13 step walk is described by A_n where:

$$A_n = \sum_{s=2}^{n} a\cos\theta_s + \sum_{s=2}^{n} ai\sin\theta_s + a.$$

    Hence:

$$|A_n|^2 = a^2 \left(\sum_{s=2}^{n} \cos\theta_s + 1 + i\sum_{s=2}^{n} \sin\theta_s \right)$$
$$\cdot \left(\sum_{s=2}^{n} \cos\theta_s + 1 - \sum_{s=2}^{n} \sin\theta_s \right).$$

    So:

$$|A_n|^2 = a^2 \left(1 + 2\sum_{s=2}^{n} \cos\theta_s + \sum_{s=2}^{n} \cos\theta_s \cdot \sum_{s=2}^{n} \cos\theta_s \right.$$
$$\left. + \sum_{s=2}^{n} \sin\theta_s \cdot \sum_{s=2}^{n} \sin\theta_s \right)$$
$$= a^2 \left(n + 2\sum_{s=2}^{n} \cos\theta_s + \sum_{s=2}^{n} \left(\cos\theta_s \cdot \sum_{\substack{k=2 \\ k \neq s}}^{n} \cos\theta_k \right) \right.$$
$$\left. + \sum_{s=2}^{n} \left(\sin\theta_s \cdot \sum_{\substack{k=2 \\ k \neq s}}^{n} \sin\theta_k \right) \right).$$

With θ_s given as above, if the δ's between each step are distributed with the same probabilities at each new departure, then this is equivalent, on average, to:

$$|A_n|^2 = a^2 \left(n + 2\sum_{k=1}^{n-1} (n-k)\overline{\cos\theta_k} \right),$$

which may be rewritten:

$$|A_n|^2 = a^2(n + n(n-1)\lambda),$$

where λ is an index of the straightness of the walk, which varies from 0 to 1 (with 1 representing an absolutely straight path) and is defined by the expression:

$$\lambda = \frac{2}{n(n-1)} \sum_{k=1}^{n-1} (n-k)\overline{\cos\theta_k}.$$

λ has been calculated for $n=13$, assuming that the δ's are normally distributed about zero with a standard deviation σ, using the relationship evaluated (as for technique 1), between $\overline{\cos\theta}$ and σ. With the observed values, $n=13$, $a=80.9$, and $|A_n|=530$ we find that $\lambda=0.1918$, and the standard deviation of directional change between successive days' steps is 60°.

Technique 3

The army ants could achieve a greater separation of the ends of their nomadic marches if they were to increase the effective step length and decrease the number of steps.

If, on average, they spend q days travelling in a straight line, then for a total of n days, colonies would make a total of n/q steps, each being $q \cdot a$ long. A random walk of such steps will cover, on average, a distance of $qa(n/q)^{\frac{1}{2}} = a(nq)^{\frac{1}{2}}$, which is denoted by $|A_n|$. The index of straightness of the walk, λ, is defined as in technique 2.

Now:

$$|A_n|^2 = a^2(n+n(n-1)\lambda) = a^2 nq,$$

so,

$$q = 1 + (n-1)\lambda$$

and:

$$\lambda = \frac{q-1}{n-1}.$$

With $\lambda=0.1918$, as above, and $n=13$, we find that $q=3.3016$. This means that the army ants can produce the observed separation of the ends of their nomadic migration if they do a random walk with (effectively) a step length that has changed from being one day to over three days long. This would require 2/3 of the angles between emigration per phase to be constrained towards zero, if the rest were at random. Technique 3 requires a very highly leptokurtotic distribution of these angles, symmetrical about a mean of zero degrees.

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