J. Indian Inst. Sci.
A Multidisciplinary Reviews Journal
ISSN: 0970-4140 Coden-JIISAD

Check for updates

REVIEW ARTICLE

Recruitment Strategies and Foraging Patterns of Ants: What Shapes Them and Why?

*K. N. Ganeshaiah**

Abstract | The effectiveness of procuring food by any ant colony depends upon the strategies adopted while recruiting the foragers to fetch food and the geometry of paths that these recruited foragers employ for searching and harvesting the food. This paper analyzes these recruitment strategies and search paths adopted by ants, and attempts a synthesis of the possible evolutionary process shaping them. Ants exhibit a wide range of recruitment strategies that differ in the size of the foraging team and the interactions among its members. It is shown that these diverse strategies are strongly associated with the size of the ant colony. Small colonies recruit individual foragers, while large colonies recruit foragers *en mass*; moderate size colonies exhibit a mix of these strategies. This association between the colony size and foraging group is argued to be a consequence of the crisis in processing information in large colonies. While in small colonies, collective decisions to recruit individuals (and small groups) can be easily arrived at, by the ants at the colony level, in large colonies, the tsunami of information flow in space and time creates a crisis for integrating and processing the data. As a result, the task of recruitment is inevitably shifted from the nest level to the foraging paths where individuals are entrusted to self-recruit based on the information gathered by them; this leads to a seamless and spatially dynamic recruitment of workers resulting in an *en mass* foraging strategy. Further, the size of the recruited team is also shown to be shaping the geometry of the foraging paths. While individual foragers search and harvest food in a circular or sinusoidal movement pattern, the *en mass* foragers adopt trails or columns that grow and branch out in a bifurcating system. These foraging paths adopted by different group sizes are shown to be very effective in 'managing' the complex substrates they forage on, and also to be very efficient in maximizing the benefit-to-cost ratios of foraging.

1 Pre-amble

Procuring food is the most basic component of the activities of any species that shape its survival, and hence its fitness. However, the task of fetching food is both energy-demanding and time-consuming (Traniello, 1989;[25]). Therefore, each species can be expected to adopt specific strategies that enhance the efficacy of harvesting the food[3,18–20,30–32].

In ants, procuring food for the colony is contingent upon (a) gathering reliable information on the distribution of food resources around their colonies, (b) accordingly recruiting appropriate numbers of foragers to different sites, (c)

[1] Department of Plant Genetics and Breeding, and School of Ecology and Conservation, University of Agricultural Sciences, GKVK, Bengaluru 560 065, India.
*knganeshaiah@gmail.com

Springer

Table 1: Different strategies of recruitment adopted by ants based on the size of the foraging group and the per cent species exhibiting these strategies.

Foraging strategy/group size	Description	Percent species (***N*** = 105)
Individuals	Individuals recruited; forage independently	24.76
Tandem recruitment	Generally two ants; move one behind the other with tactile communications	15.23
Group/Mass[a] Recruitment	Small groups ranging from few to several hundreds; exhibit certain level of interactions	5.71
Mass recruitment[a]	Recruited in thousands to lakhs	33.33
Trunk trail[a]	Mass of ants move in continually bifurcated trails, generally marked by chemicals	10.47
Group hunting[a]	Entire colony of, up to even a few lakh ants, move as an army or a group	10.47

[a] In this paper these are treated together as *en mass* foragers

method of harvesting the food at those sites, and (d) transporting it efficiently to the colony[26]. Each of these components of the foraging sequence can be expected to be stringently shaped, such that food is procured with the least cost of searching, harvesting, and transporting to the colony. Obviously, depending upon the diet preferred, the needs of the colony, the ecological niche of the species, and the availability and distribution of resources in the habitat, ants can be expected to adopt specific strategies at each of these different stages of foraging. Given that ants live in a wide range of habitats, vary enormously in their colony sizes, and devour diverse food types, the strategies adopted by them would also be highly diverse. Identifying the patterns among, and the factors associated with, such diverse strategies and, tracing the possible continuum among the strategies could help understand the adaptive trajectories and processes involved in shaping them.

This paper attempts to trace the adaptive trajectories among the strategies employed by ants at two discrete stages of foraging, viz., (a) recruitment of the foragers to fetch the food, and (b) searching and harvesting the food. Enlisting the diversity of strategies adopted in recruiting ants for foraging, I trace the possible continuum among those recruitment strategies. Further, identifying the features associated with different recruitment strategies, I attempt to construct the possible adaptive process that has shaped them. Similarly, I enlist the diversity of search paths adopted by ants while foraging and illustrate that all of them could be grouped into two distinct geometries that are associated with specific recruitment strategies. It is argued that these distinct geometries of search paths have evolved as an effective solution to 'manage' the challenges faced by ants while searching and harvesting food on the complex substrates they forage on.

1.1 Recruitment Strategies

Ants exhibit a wide variation in the size of the foraging groups recruited and the levels of interactions among the members of the group[2,10,13,14,25,26,29]. Certain species of ants search and harvest food individually, few do so as 'tandem foragers'; others forage in very small groups, or in large trail forming groups; and some species raid as an 'army of ants'[2,29]. Compiling the wide spectrum of recruitment patterns from 97 species of ants, Beckers et al.[2] distinguished six distinct types based on the size of the foraging group, features of the foraging path, and the interactions among the members (Table 1). While these types are very useful in recognizing the diversity of the recruitment strategies adopted, some of them have a broad range in the numbers of ants recruited and hence may overlap with respect to the size of the foraging group rendering them difficult to differentiate distinctly. This is particularly true among the categories such as 'Mass Recruitment' and 'Group or Mass foragers'; in fact, for the present discussion, all these could be merely treated as *en mass* foragers. Further, it is also not very unusual that some species adopt a mix of these strategies. For example, we have found that colonies of *Camponotus sericius* recruit individuals as well as small groups of 5–15 ants for foraging, though the latter is very infrequent[1]. The data provided

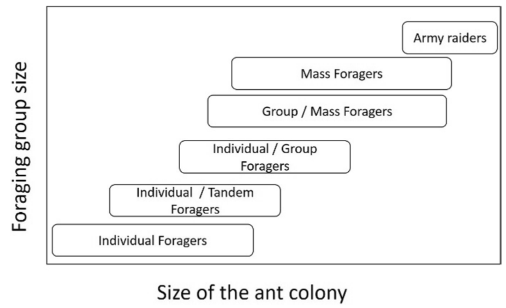


Figure 1: Schematic depiction of the relation between the foraging strategies (foraging group size) and size of the ant colony. This figure is adopted and modified from[2].

by ([29], see their supplement) also show that the same species may adopt more than one strategy.

An analysis of about 105 species of ants (Becker's data updated from our own studies) showed that while about 25% of the ant species recruit individual foragers, about 33% recruit mass foragers. The other two strategies of recruitment, viz., Tandem Runners and small Group Recruitment, that are bracketed by these two major categories are very low in their frequency: while 15% of species deploy 'Tandem Runners', only 5–6% recruit small groups. However, since the size of the 'small group' foragers and 'mass foragers' could heavily overlap, it would be meaningful to combine them as *en masse* (represented by categories GM+MR from[2]). Clearly, '*en mass*' along with the trunk trails and group hunting turn out to be the most abundant (>60%; Table 1). In the following discussion, these categories are treated under '*en mass*' foragers though the very small groups could be treated separately.

Clearly, despite certain subjectivity in the classification of the recruitment categories, it is clear that two types, viz., 'Individual' and '*en mass*', recruitment strategies stand out as the most predominant (Table 1), even if we separate them from others categories such as 'Trunk Trails' or 'Group Hunting' and 'Tandem Runners'. This obviously raises several questions: in particular, why and when do ant colonies resort to recruiting individuals and when do they recruit *en mass* foragers? A close scrutiny of the features associated with the varying sizes of the foraging groups recruited suggests that colony size[2] and the diet of the ants[29] play significant roles in shaping these foraging strategies. In the following, the possible process through which these two factors may have independently and interactively shaped the recruitment strategies is discussed.

1.1.1 Colony Size and the Foraging Group

Beckers et al.[2] suggested that the size of the recruited group increases with the size of the ant colony (Fig. 1). An analysis of the data from 105 species (97 from[2] and 8 from our own sources) shows this association to be very strong [see Table 2 $\chi^2_{(df=4\times3=12)} = 74.67$; $P < 0.01$]. Clearly, there exists a strong positive association between the colony size and the size of the foraging group. The proportion of ant species recruiting 'individuals' drops steeply with the log increase in colony size; none of the colonies with more than 100,000 ants recruit individuals. On the other hand, en *mass* recruitment is adopted only in colonies that have more than 10,000 individuals; frequency of its adoption increases steeply beyond that size. The 'small group' (which includes the tandem runners and very small groups) foragers are recruited by the moderate size colonies (Figs. 1 and 2).

It could be argued that this association between the colony size and the size of the foraging group is merely an inevitable numerical consequence of the colony size, with no specific adaptive advantage. For example, even if the large colonies recruit individuals, the numbers of foragers emerging from the colony at any given moment would be so high that they 'appear' to be recruited *en mass*. Similarly, small colonies by default cannot recruit *en mass* foragers as they do not have as many ants to do so. While this seems a simple and plausible explanation, it does not address other associated features of recruitment in large colonies. For example, some species of ants with very large colonies exhibit trunk trail foraging, or group hunting, both of which could be executed by the small colonies as well. In fact, all of the ants of small colonies could be recruited as one group that hunts for the food or could be recruited in trunk trails for foraging. That these possibilities are not generally seen in very small colonies seem to suggest that there are other independent factors shaping this association between the colony size and the size of the foraging group.

Group versus the individual decision: In general, individual foragers are recruited based on the information shared and or decision arrived at the colony level. Small bits of information brought in independently by the few individual scouts and foragers is passed on to other ants at the colony level either actively (by specific behavioral display to convey the food source) or passively (by chemical trails). Sometimes, such information is also integrated and processed jointly by the ants at the colony level, and accordingly, further recruitment of individual foragers is executed.

Table 2: Number of ants species with different foraging strategies segregated in to three colony sizes (Data source: updated from [2].

Recruitment strategies	Colony size with varying number of ants			
	Small (< 1000)	Medium (1001–10,000)	Large (10,001–100,000)	Very large(> 100,000)
Individuals	22	4	0	0
Tandem Runners	14	2	0	0
Mass Recruiters	14	18	4	5
Trunk Trails	2	0	3	6
Group Hunters	1	0	3	7

The contingency chi square test to assess the independence of the colony size and the group size was highly significant (Chi-square: 74.67; $P < 0.001$) indicating a strong association between them

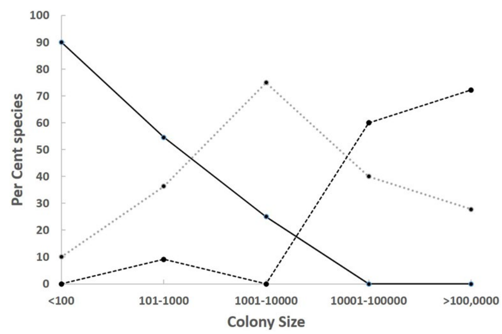


Figure 2: Percent ant species that recruit Individuals or Tandem Runners (solid line), small groups (dotted line) and *en mass* (dashed line) foragers. Data from the updated list (see text).

Once recruited, these individual foragers indulge in their task without any (or with least) interactions with other foragers. In fact, once they leave the nest, they hardly have any opportunity to interact among themselves while foraging. On the other hand, in the *en mass* foraging strategy, though mass recruitment does start from the nest, the members of the foraging team most often make instantaneous decisions 'on the go' by gathering and the processing the information along their search paths[2,6,13]. Thus, in *en mass,* and trail foragers, decisions are mostly taken outside the colony by the individual foragers by interacting with other members encountered on the way: members of the group gather information by interacting with other members on way to foraging, cumulate such bits of information and continually process it to arrive at the decisions on the direction of foraging and, or, sites to be visited. For example in the fan-like terminal part of the trails of *Leptogenys proecessionalis,* ants recruit themselves into new branches based on the food patches they encounter[13]. Further, it has been shown that members along the trails need to make very few contacts with others to arrive at the most appropriate decision[8].

In between these two extreme strategies, some ants recruit Tandem Runners or very small foraging groups from the nest similar to that of the recruitment of individual foragers; the members in these small groups do interact among themselves on their foraging trip, similar to those in the mass foraging groups[1]. For example, in tandem runners, the ant that brings the info-bit to the nest itself leads the other ant to the foraging area, sometimes by carrying it on its back. When the recruited foraging group is more than just the tandem runners, e.g., 5–15 ants in *Camponotus sericius*[1], they all move as an interacting, cohesive group till they reach the foraging area[29]. Both in tandem runners and very small group recruiters, once the ants reach the resource patch, the members of the group generally separate, and search and fetch the food to the nest individually.

Thus, there appears to be a continuum in the recruitment strategies among the ant species from individual to mass foragers as if reflecting a gradual path of evolution of these strategies. In the individual and small group foragers, decision to recruit is taken at the colony level, as if it is a consensus activity, while in the *en mass* foraging groups, such decisions are taken mostly outside the nest, i.e., on their go along the foraging path. Individual foragers have limited opportunities to interact and share their experience outside the nest, while the in *en mass* foragers' interactions among the foraging members outside the nest seem to be most active and critical. In the tandem and small group foragers, decisions are made both at the nest and also via interactions among the members outside the nest.

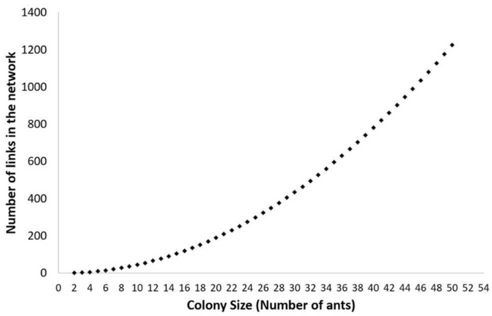


Figure 3: Increase in the number of interacting links or nodes for each ant with increase in the colony size (number of ants).

Despite such a clear continuum, there are no *a priory* arguments about how these diverse foraging strategies could be 'adaptive' in their respective species. Any explanation addressing this, needs to essentially answer the strong, positive relation between the sizes of, the colonies and their foraging teams. Interestingly, the answer seems to lie in the increasing complexity of acquiring, integrating, and processing information among foragers[2,4,7] with increase in the colony size.

a. *Colony size and the crisis of information processing*: Decision for an effective recruitment can be arrived at by compiling, integrating, and processing information on the resource status of the areas sampled by the scouts and, or, foragers. In small colonies, information brought in by the small group of foragers (and scouts), can be easily integrated and processed at the colony level, and accordingly, decisions can be arrived at to recruit appropriate numbers of individuals to different places. On the other hand, in very large colonies, the massive information brought in by the thousands of foragers, cannot be easily and instantaneously integrated[2,5] for two reasons:

i) Information *Tsunami*: In large colonies, the information brought in by the thousands of foragers at any given moment of time is both huge and diverse creating an information *Tsunami* at the colony level. Ant colonies do not have any central processing units where these huge data could be dumped, organized, integrated, and processed instantaneously into meaningful information. Further, arriving at a collective decision at the colony entails that each forager establishes contact with all others to gather data and process it, and, that the information thus gathered and processed by each ant is further exchanged among all others as a network in a pyramidal manner. Clearly, the number of contacts of such a network increases non-linearly with the number of foragers (given by the combinatorial links, $NC_2 = N!{*}2!/(N-2)!$, where N is the number of foraging ants entering the colony at any given moment). The number of links of the network increases at an increasing rate with the number of ants entering the colony (Fig. 3).

Though such huge network of contacts are theoretically achievable, in practice, such a process of information exchange becomes untenable and useless owing to the prolonged time required for any decision to be made. Further, the limited neural system of ants may also impose a constraint on such a possibility. In other words, arriving at a feasible decision-making system based on the information provided by all the foragers is untenable in large ant colonies, due to physical constrains that lead to time delay, and also due to the limited neural system of the ants. In this sense, the very process of evolution of a social system that has favored the increased colony size of ants may indeed pose a severe hindrance to arrive at effective foraging decisions.

Therefore, large colonies need to evolve alternate strategies to resolve this info-crisis. Perhaps, one solution they have resorted to is for the individual ants to be used as local processing units. Individuals are prompted to gather data from as many other foragers as they can, compile and process such data instantaneously on their own, and make independent decisions to self-recruit to the foraging areas. This they can do even while on their way out for foraging and not necessarily in the nest. In other words, in large colonies, self-recruiting seems to be inevitable.

ii) Temporal Pile-Up of Information: While the above shows the difficulty in establishing a comprehensive network among the members of large colonies, the continuous arrival of foragers with time, all with fresh bits of information poses further challenges in utilizing the flowing data. The amount of unused data arriving at the colony begins to pile up with time, posing further difficulty for organizing and processing the information. Such piling up of unprocessed data aggravates the difficulties of processing leading to a breakdown in the recruitment at the colony level.

Thus, unless ant societies address these hurdles, species with large colony sizes face survival problems which in turn may limit their further evolution. However, the fact that more than 25 ant species have evolved to have more than 100,000 ants in their colonies suggests that the species with large colony sizes have overcome this crisis of information processing. Ant societies seem to have resolved these hurdles by adopting alternate behavioral strategies for sharing and processing information and thence to arrive at the decisions on recruiting foragers. One such alternate strategy is a self-organized process of recruitment that involves independent and instantaneous decision-making by the individual foragers[1,21]. This they seem to do by applying a set of simple rules on the data or information gathered by them while on their go[5–7]. Clearly, the extent to which such a self-organized foraging strategy is adopted would be a function of the colony size, with small colonies adopting purely colony-level decisions and very large colonies adopting purely self-organized recruitment of foragers Beckers et al.[2].

Such self-organized behavior of ants in large colonies is mediated often by chemicals[5,29] or steered by behavioral interactions along trails[13] and results in a collective intelligence[4,11] and an *en mass* recruitment of foragers. Thus, while small colonies recruit solitary foragers, in large colonies, *en mass* foragers are recruited through a self-organized process. However, the critical size of the colony and, the specific drivers, which trigger the shift from solitary to group and mass recruitment, is not yet well understood. Interestingly, it has been shown that medium-sized ant colonies adopt a mixed strategy where a proportion of ants forage solitarily, while others are recruited in small groups[26]. We have shown that, unlike in other group or mass foraging ants, small foraging groups of *Camponotus sericius* behave as independent units with a discrete structure that is locally regulated rather than being completely self-organized[1].

Thus, we do see a clear continuum in the evolution of the foraging strategies driven purely by the crisis of information processing. In small colonies where information arriving at the colony is very limited and 'manageable', ants resort to a collective decision at the colony level. However as the colony size increases up to a few hundreds to thousands of individuals, the crisis of managing the information has led to a shift in the strategy: ants resort to recruiting individuals and also small groups. The latter behave almost as an independent unit with its members interacting among themselves. When the colony size increases beyond few thousands, the crisis of information processing has been resolved by completely resorting to an *en mass* recruitment where the members behave in a self-organized decision-making system.

b. *Diet and foraging group size*: Another factor that seems to be associated with the foraging strategy adopted by ants is their diet. This can be seen at two levels: (i) spatial and temporal distribution of the food, and (ii) the composition of the diet.

i. *Spatio-temporal features of the diet*: Compiling data from over 1400 publications, Lanan[29] assessed the extent of association of different foraging strategies with spatial and temporal features of the diet viz., relative spread of the resources, frequency of occurrence of the resources, size of the resource, and depletability following its harvesting. The study indicated some distinct patterns of association. For example, irrespective of the phylogenetic root, all the species that recruit solitary foragers were found to harvest small resource packs that are distributed unpredictably in space and that do not get depleted due to foraging. Small insects, dead or live (that can be captured by individual ants), grains and honey dew drops are the most common food types representing these features. The tandem and small group recruiters also share similar features. The trunk trail and column foragers are similar to the solitary and group foragers except for one specific feature: the food harvested by them was highly depletable after the harvest. Once they ambush the foraging patch, the entire food source is depleted, forcing the group to search for new food patches and re-lay their trunk trails. A careful scrutiny of the data provided by ([29], supplement) shows that the large foraging groups almost always hunt large animals, while the small groups devour a wide range of diet. In other words, the composition of the diet also seems to be shaping the foraging group.

ii. *Composition of the diet*: Large colonies are almost always associated with hunting prey; they devour large insects and even small mammals. Similarly certain trail forming ants of the large colonies, such as *Leptogenys* sp, harvest termites, other insects and even small animals. On the other hand, individual foragers are associated with a vast range of diets: they harvest nectar from the glands on plants, seeds from and around plants, other plant parts, such as leaves, floral parts, and arils associated with seeds. This is also clear from the data compiled by Lanan ([29], see the supplementary data): almost all raid forming ants devour insects or other animals, while solitary foragers exhibit a wide range in their diet, such as honey dew, grains, plant parts such as fruits, and small insects (dead or alive). Ants of certain species, such as Acacia-ants, seem to bridge this spectrum. They have a modest-sized colonies that occupy the entire Acaica tree, and exhibits a mixed strategy in their diet: they hunt for insects on the host plants and attack them in groups, but as individuals, they harvest *Beltian* bodies on the tips of the leaflets as a protein source, and also visit nectar glands at the base of the leaves as a carbohydrate source.

Thus, there does appears to be a gradual shift in the diet of ants with the size of the foraging group, and hence the colony size. Small colonies that recruit individuals prefer to feed on plant sources, such as nectar and grains, while the large colonies prefer to be carnivorous; some with medium-size colonies that recruit both individuals and groups exhibit a mixed diet. However, this association may not be very strong as evident from several exceptions. For example, individual foragers such as *Camponotus* do harvest small insects as a protein source at least occasionally[28,29]. Similarly, some of the trail forming ants such as *Pheidolegiton* harvest grains and store them in their nests[13]. Unfortunately, whether or not these are indeed exceptions rather than a general pattern cannot be ascertained as there are no large data sets to assess this. Nevertheless, it is logical to expect that the benefit–cost ratios of searching and harvesting food does demand that the large foraging groups prefer to devour highly concentrated, resource-rich patches such as animals or termite mounds. In fact, it does not pay the large groups to visit highly distributed small patches of food such as nectar in plants or randomly spread-out grains on the ground. On the other hand, individual foragers may not be able to 'kill' and harvest insects and animals on their own and hence can be expected to resort to harvesting small, distributed patches of resources such as honey and perhaps opportunistically some (dead) insects.

What shapes the recruitment strategy—diet or the colony size? In summary**,** though the recruitment strategy, in particular the size of the recruited team, seems to be associated with both the colony size and the diet features of the ants, among the two, the colony size seems to be the major or the underlying driver of the recruitment than the diet because of two reasons:

First, increase in the size of the colony imposes a crisis in information processing at the colony level which in turn enforces large colonies to adopt a self-organized *en mass* recruitment. On the other hand, very small colonies are capable of processing information efficiently at the nest and hence recruit individuals to appropriate patches. Moderate-sized colonies adopt a mix of these two strategies.

Second, though diet features do exhibit an association with the foraging group size, there are several exceptions rendering it a less important factor driving the recruitment strategy. Besides, it does appear that once the recruitment strategy is shaped by the colony size, the recruited group size defines the specific diet feature to enhance the efficiency of harvesting: large foraging groups are selected to be carnivorous due to their highly concentrated and rich nutrients and small groups manage with the highly distributed, low rich food systems. In other words, the weak relationship between the diet features and the foraging group size could result merely as a consequence of the colony size shaping the foraging group size.

1.2 Search Patterns

Once the foragers are recruited, they face the most complex challenge while searching for food[13,27]. While foraging, they enter into mostly unknown territory or even if known, a terrain that is likely to be unpredictable with time. This territory, be it a plant or ground, is inevitably a three-dimensional substrate whose surface, structure, and design are complex, highly diverse and also change with time. For example, the design of the plants on which ants forage may vary from a simple, repetitively bifurcating branching system to a completely random and or complex design that cannot be easily visualized or perceived and digested by the limited neural system of the ants. Even though the ground terrain on which most ants forage may appear to be a simple two-dimensional surface, it is indeed not an easily maneuverable plane but a highly complex multi-dimensional structure owing to the unpredictable projections of the ground and also due to the multiple obstructions of vegetation, litter, and other inanimate objects.

Thus, it is imperative that ants develop simple yet effective search strategies that help them

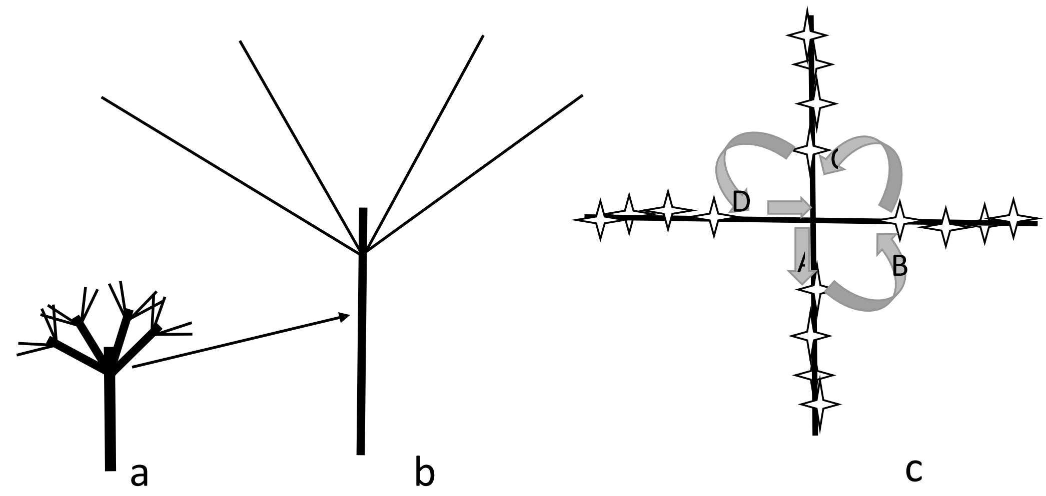


Figure 4: **a** Polycasial branching system of *Croton bonplandianum*. Generally there will be four branches at each node and each of these four branches further lead to a similar four branched system. The pattern repeats up to five in an annual herb. Only two stages are shown here. Each of this branching node is expanded to show the four branches (**b**) and their top view with the fruits subtending the nectarines (indicated by the star shape) is also shown (**c**). The pattern of foraging by the individuals of *Camponotus sps* is also shown: when the individual ant arrives at the base of the inflorescence, it randomly moves on to any one of the branches (say A), forages on it, gets down to the base again and turns right to climb on to another branch (B), forages on it and repeats the process similarly by turning right on to branch C and then to D, after which it exits the entire branch. This rotation could also be in the left direction, but once it turns left, it repeats it, so that it forages always in a circular pattern as shown.

'manage' these complex surfaces. The search paths employed have to be very flexible and adaptive to circumvent the problems encountered on the diverse range of substrates and at the same time minimize their cost of traveling, searching, and harvesting food. For example, ants foraging on the nectar on the diverse species of plants have to adopt strategies that would render them effective on a diverse range of plant designs. Similarly, ants foraging on randomly distributed food sources on vast areas of ground need to develop strategies that reduce the total cost of communication and commutation between the nest and different resource patches. The following presents a cafeteria of such search strategies adopted by ants that forage as individuals, or in small groups and *en mass*. As can be seen, despite the fact that the search paths adopted by ants appear to be highly diverse, they are based on a set of simple and effective rules that would reduce the cost of harvesting while at the same time rendering them capable of 'managing' the complex substrates on which they forage.

a. *Individual foragers*: The individual foragers of *Camponotus* species forage for nectar on a range of plant species that differ widely in their structural design—from a simple repeating branching pattern of *Croton bonplandianum*[13] to a complex racemose inflorescences of Cashew trees[27]. In *Croton* plants, on an average, four branches emerge at each node at almost equal angle to each other. Each of this branch or rachis bears a set of female flowers (2–15 depending upon the stage of the plant) placed linearly at the base. Each of these female flowers subtends a nectary on the rachis which secretes few microliters of nectar following the fertilization of the flower and its maturation into fruit[12]. Ants visit the branches to harvest these nectaries.

Studies have shown that individuals of *C. sericius* foraging on *Croton* arrive at each node and explore the branches in a circular pattern, harvesting one branch after the other either in left or right direction (see Fig. 4 for details). Once all the branches are explored and the yield from them has reduced, the ant leaves the node and proceeds to another node; and the pattern continues. In fact, the circular exploration of branches is repeated at all levels or stages of branching, such that ants explore the entire plant in a systematic pattern[13].

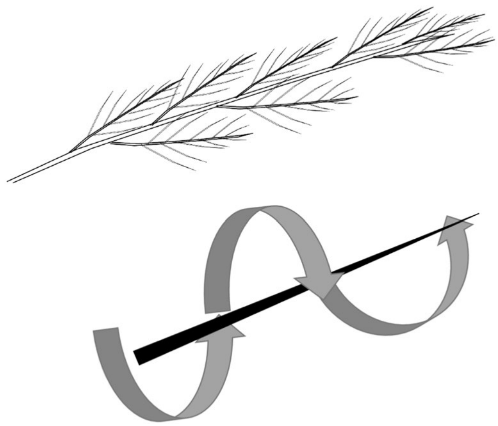


Figure 5: The branching pattern in the racemose inflorescence of cashew (top). Aphids harbor on the flower buds of these branch-lets and secrete honey dew. Individuals of *Camponotus* visit these aphids for harvesting the honeydew, and in doing so, they explore the entire inflorescence in a non-random pattern, they move in a sinusoidal search path (bottom) circling the inflorescence from bottom to top. In the process, as they encounter fresh branch-lets, they explore aphids on them in a similar pattern and then proceed around the rachis acropetally searching in circular path. Once the entire inflorescence is explored they depart.

Individual ants of *Campnotus sericius* also forage on the honey dew secreted by the aphids feeding on the inflorescences of cashew trees[27]. Each of these racemose inflorescences has a main rachis that is highly branched (Fig. 5). The number of aphids on the entire inflorescence represents its resource status and the aphids are uniformly distributed across the branches, such that sampling any of the branches indicates the resource status of the entire inflorescence. Accordingly, the ants visiting an inflorescence sample the honey dew available on one or two branches and then decide to abandon the inflorescence (if the aphid density is poor) or, continue to forage on it (if the resource status is good).[A] Once decided to continue, they face the challenge of systematically exploring the aphids located on the complex racemose inflorescence[27]. And how they accomplish this again suggests a simple adaptive rule they employ.

Our study showed that ants do not move randomly on the inflorescence; rather, they exhibit a non-random foraging pattern that leads to a systematic exploration of the inflorescence. In particular, they move around the rachis of the inflorescence in a sinusoidal (circular) pattern from the bottom toward the tip. In the process, as they encounter a new branch, they explore the aphids on it and, once the honey dew from them is harvested, they move back to the main rachis, and continue their sinusoidal exploration till they find a new branch. Thus, the entire inflorescence is explored 'completely' and also 'efficiently'. 'Completely' because the sinusoidal movement on the rachis leads them to explore all the branches and, 'efficiently' because of two reasons: (a) Compared to a random search, the sinusoidal movement avoids revisiting the same branch thus avoiding wasteful searches. (b) Having invested time and energy to travel all the way to the inflorescence, their benefit–cost ratio of foraging by the ants would be maximized only when they explore all the available aphids on the entire inflorescence[30–32]. Sinusoidal movement ensures that the ants visit all the branches of the inflorescence. Thus, the benefit-to-cost ratio of foraging would be maximized by this pattern of searching and foraging.

Rules adopted by individual foragers: Studies on both Croton plant and cashew tree show that ants exploring and foraging on complex substrates, such as plants, do not exhibit a random search path. Instead, they seem to adopt certain simple movement rules that renders a systematic exploration of the plants. Irrespective of the level of complexity of the design of the host plant, ants seem to adopt a circular or sinusoidal exploration of the plants, such that resources are explored completely and harvested effectively. It is not clear and, it would be interesting to analyze, if this circular movement pattern could indeed be a universal solution for all kinds of complex plant designs. However, the fact that vastly differing designs such as the repetitive simple branching design of Croton and the complex racemose branching pattern of cashew could be effectively addressed through a circular movement pattern seems to suggest that it could indeed be a potentially effective movement rule that could be applied in general.

But does this rule of circular exploration by the individual foragers could lead them to an efficient search pattern on the ground also. While it may be difficult to visualize how such a simple

[A] Our studies have shown that once an ant has harvested honey dews on an inflorescence, the new ants arriving immediately on to it do not generally proceed to forage as extent of honey dew available would be very less; they abandon it and move on to another inflorescence. However, ants arriving later (the critical interval of time not studied), sample a few branches, and if the harvest on them is 'good', they continue to forage.

rule may help individual foragers to explore the (almost) two-dimensional terrain of the ground (but often multi-dimensional, owing to obstructions; see above), a few studies do indicate that ants adopt such simple rules even while searching on the ground. In unknown terrains, insects are known to exhibit an ever-expanding spiral and loop patterns[15,16]. For instance, Lai et al.[16] have observed that in *Solonopsis geminate*, ants search in expanding loops and circles turning almost always in one direction. Such circular patterns of movement lead to an effective exploration of unknown territories. Thus, circular exploration seems to be ingrained in the foraging strategy of the individual ants.

b. *Group foragers*: Similar to the individually foraging ants, group foraging ants also face challenges while foraging on the complex designs of the substrates ([10, 13,17]). The substrate could be the ground, or the highly complex designs of plants and, occasionally it could be sub-terranean also. For example, on the ground, while the ants of *Pheidolegeiton* sp. forage in long, branched trails for grains, those of *Leptogenys* sp. search for insects and termites via their highly branched trails[13]. On the other hand, *Oecophylla* foragers search for insects and other carnivorous food on the plant surfaces via a network of trails; foragers of *Dorilinae* hunt for insects sometimes even under the ground, again forming branched trails. Most often, such mass foragers employ chemical cues along their trails, to keep track of their paths[26,29]. These trails generally occur as bifurcated branching systems as in *Leptogenys* or as a complex network of interconnected path trails as in *Oecophylla*. Both the networks and the branching patterns are shown to be highly non-random with varying degrees of branching and connectivity[13].

Though several categories or patterns have been identified among the search paths of the *en mass* foragers, they all seem to have one common feature: they move in trails or long columns that branch either at the growing tip or, all along the trail. At the growing tips, the branching pattern may not often be very distinct, perhaps due to the high density of branches that overlap, creating a plume-like (see Fig. 1b in[29]) or a fan-like structure[13]. In fact, it has been shown that the fan-like growing tips eventually branch out when they encounter food items, that are separated by a critical distance[13]. The trails or columns branch along their path, generally in a bifurcating manner ([13], also see Fig. 1 in[29]). However, when the spatial frequencies of such branches intensify, they begin to merge resulting in a network. In other words, ants that forage in large groups (*en mass*), or trails and in growing columns, seem to adopt one common feature or pattern: they branch in a bifurcating system while searching and harvesting the food.

Rules adopted by group foragers: Clearly, one important rule that the ants of large colonies seem to be adopting while foraging is to explore, search, and forage in columns or trails that grow and branch out. This geometry can be argued to be the most efficient rule adopted as an inevitable consequence of the recruitment strategy adopted by the ants in large colonies.

Unlike the individual foragers of small ant colonies, foragers of large colonies invariably indulge in an 'on the line' communication along the trail (see section above) and the recruitment thus occurs outside the nest, based on the information gathered by ants while moving along the trails. Therefore, in the mass foraging ants, the efficiency of foraging depends on how they communicate information on the quality of the food patches (availability and richness) in different places and, the cost of harvesting the food (defined by the travel distance, disturbances, and hurdles, etc.,) in those places. Such communication among the members could occur either directly via physical contact, or indirectly via the composition and intensity of pheromones laid along the trails. It is also likely that the members of the trails integrate the information based on the frequency of food being transported by other members of the team from different directions of the foraging path. Using such direct and or indirect cues, individual ants evaluate the relative resource values of different places in different areas[21], and accordingly reorient on their own to different paths of the trails. Thus, the efficiency of the group foragers in harvesting the food depends crucially on (a) the speed with which the information is transferred among the members so as to recruit them to new areas, and, (b) the travel cost of the recruited workers to new areas[13]. Clearly, mass foragers are selected to adopt search paths that (a) minimize the average distance between any two points along the search path, such that the cost of travel for the new recruits is minimized and, (b) minimize the total length of the foraging trails, such that the ratio of area explored (benefit) to the length traveled (cost) is maximized. It has been argued that this can be

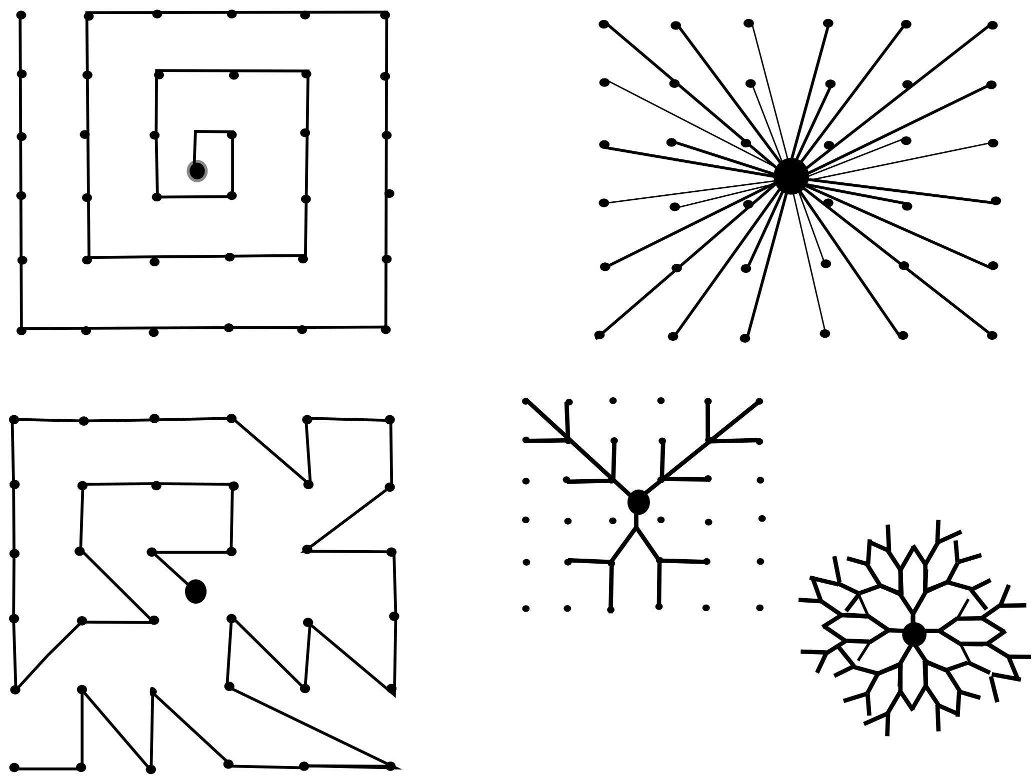


Figure 6: Different paths connecting the nest (central large circle) with the food patches that are evenly distributed (shown here by the black dots). These figures are redrawn based on those from Stevens[22]. The expanding spiral (top left) and the random meandering design (bottom left) shall have the highest average distance between any two points though the total distance of the path is less (see Table 4 in Stevens[22] for values). The exploding or radiating pattern (top right) shall have highest total path length though the inter point distance would be minimal. The branching patterns (bottom right) connecting all the points serve as a good trade off between inter-point distance and the total length of the path. The inset shows both the bifurcating and tri-furcating branching pattern. Among these however the bifurcating branching pattern (shown here but not to scale) is the best trade off (see Table 4 in Stevens[22]). Please note that these topologies are only representative as they are modified from Stevens[22].

better attained by adopting the trail network system than any other strategies ([13,22,23]; Fig. 6).

Considering several alternate architectural topologies such as a spirally growing trail, randomly meandering path, a star shaped or radiating trails of foragers from the nest and a branching pattern, it can be shown that while spiral and meandering architectures minimize the total path length, explosive architecture minimizes the average path length (Table 3). However, comparatively, the branching pattern is shown to be a good trade-off in minimizing both the total path length and also the average path length between any two randomly chosen points. Further, among the different branching patterns, a bifurcating system is shown to be the most efficient compared to the tri-furcating branching architecture (Table 3, [9,13,22,23]). Thus, the rule of a bifurcating system of branching trails, adopted by the mass foraging ants, appears to be the most efficient strategy that maximizes the benefit–cost ratio of harvesting the food that is widely and evenly distributed in an area.

1.3 Conclusion

Ants exhibit a wide range of recruitment patterns that are shaped mostly by the size of the colonies. While small colonies recruit individual ants from their nests, very large colonies that forage '*en mass*' recruit foragers 'on their go' via a self-organized process where individual members of the foraging teams make decisions and reorient themselves to the most productive

Table 3: Total path length that connects all the points in an octagon with the center and average distance between any two randomly chosen points in different topologies.

Topology (shown in Fig. 4)	Total path length (units)	Average distance between any two points (units)
Spiral	90.00	45.00
Meandering	90.00	45.00
Explosion	331.00	3.37
Branching (trifurcating)	90.00	3.67
Branching (bifurcating)	77.90	4.42

The values are from Stevens[23]. Representative topologies corresponding to these five types are shown in Fig. 4 of this article[23]

areas. Ant species with moderate size colonies adopt a mix of these two strategies. Further, these recruitment patterns, in turn seem to have shaped the search paths that ants adopt to overcome the challenges they face while foraging on complex substrates. The individual foragers that cannot exchange information on their foraging trips seem to adopt entirely different rules of foraging compared to group foragers that have ample opportunity to exchange such information. Individual foragers adopt a circular or sinusoidal search paths that helps them circumvent the complex designs of the substrates, while the *en mass foragers* adopt bifurcating branching patterns as the best trade-off architecture that minimizes both the total cost of harvesting and the travel cost between any points in the foraging area.

Publisher's Note

Data availability

The work is based on past studies.

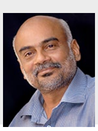
Received: 11 April 2023 Accepted: 22 June 2023
Published: 20 September 2023

References

1. Ashwathi P, Puspita B, Ganeshaiah KN (2020) Structural organization and cohesiveness of foraging groups in *Camponotus sericius* (*Fabricius*) (*Hymenoptera*: *Formicidae*): locally regulated or self-organized? BMC Zool 5(13):1–9. https://doi.org/10.1186/s40850-020-00062-6
2. Beckers R, Goss S, Deneubourg JL, Pasteels JM (1989) Colony size, communication and ant foraging strategy. Psyche 96:239–256. https://doi.org/10.1155/1989/94279
3. Cody ML (1971) Finch flocks in the Mohave desert. Theor Popul Biol 2:142–158
4. Davidson JD, Gordon DM (2017) Spatial organization and interactions of harvester ants during foraging activity. J R Soc Interface 14:20170413. https://doi.org/10.1098/rsif.2017.0413
5. Deneubourg JL, Aron S, Goss S, Pasteels JM, Duerinck G (1986) Random behavior, amplification process and number of participants: how they contribute to the foraging properties of ants. Phys D 22:176–186
6. Deneubourg JL, Goss SS, Franks N, Pasteels JM (1989) The blind leading the blind: modeling chemically mediated army ant raid patterns. J Insect Behav 2:719–725
7. Detrain C, Deneubourg JL (2006) Self-organized structures in a super-organism: do ants "behave" like molecules? Science direct. Phys Life Rev 3:162–187
8. Falcon-Corte's A, Boyer D, Ramos-Ferna'ndez G (2019) Collective learning from individual experiences and information transfer during group foraging. J R Soc Interface 16:20180803. https://doi.org/10.1098/rsif.2018.0803
9. Farji-Brener AG, Chinchilla F, Natalia UM, Ocasio-Torres ME, Chauta-Mellizo A, Acosta-Rojas D, Marinaro S, de Mónica Torres C, Amador-Vargas S (2015) Branching angles reflect a trade-off between reducing trail maintenance costs or travel distances in leaf-cutting ants. Ecology 96(2):510–7. https://doi.org/10.1890/14-0220
10. Franks NR, Fletcher CR (1983) Spatial patterns in army ant foraging and migration: *Eciton burchelli* on

Baro Colorado Island Panama. Behav Ecol Sociobiol 12:261–270

11. Franks NR (1989) Army ants: a collective intelligence. Am Sci 77:138–145
12. Ganeshaiah KN, Uma Shaanker R (1988) Evolution of unique seed maturity pattern in *Croton bonplandianum* Baill strengthens ant-plant mutualism for seed dispersal. Oecologia 77:130–134
13. Ganeshaiah KN, Veena T (1988) Plant design and non-random foraging by ants on *Croton banplandianum,* Baill (Euphorbiaceae). Anim Behav 36:1683–1690
14. Ganeshaiah KN, Veena T (1991) Topology of the foraging trails of *Leptogenys processionalis*—why are they branched? Behav Ecol Sociobiol 29:263–270
15. Hassel MP, Southwood TRS (1978) Foraging strategies of insects. Ann Rev Ecol and Syst 9:75–95
16. Lai LC, Chao TY, Chiu MC (2022) Searching behavior in the tropical fire ant *Solenopsis geminate* (Hymenoptera: Formicidae). Zool Stud 61:e26. https://doi.org/10.6620/ZS.2022.61-26
17. Mirenda JT, Topoff H (1980) Nomadic begaviour of army ants in a desert-grassland habitat. Behav Ecol Sociobiol 7:129–135
18. Pyke GH (1978) Optimal foraging: movement patterns of bumble bees between inflorescences. Theor Popul Biol 133:72–98
19. Pyke GH (1978) Are animals efficient harvesters? Anim Behav 26:241–250
20. Stephens DW, Krebs JH (1986) Foraging theory. Princeton University Press, Princeton
21. Stickland TR, Britton NF, Franks NR (1999) Models of information flow in ant foraging: the benefits of both attractive and repulsive signals. In: Detrain C, Deneubourg JL, Pasteels JM (eds) Information processing in social insects. Birkhäuser, Basel. https://doi.org/10.1007/978-3-0348-8739-7_5
22. Stevens PS (1973) Space, architecture and biology. Syst Zool 22:405
23. Stevens PS (1974) Patterns in nature. Little Brown, Boston
24. Sudd JH, Franks NR (1987) The behavioural ecology of ants, a tertiary level biology series. Blackie, Glasgow, London
25. Traniello JFA (1977) Recruitment behavior, orientation and organization in the carpenter ant *Camponotus pensylvanicus*, degeer (Hymenoptera: Formicidae). Behav Ecol Sociobiol 2:61–79
26. Traniello JFA (1989) Foraging strategies of ants. Ann Rev Entomol 34:191–210
27. Veena T, Ganeshaiah KN (1991) Non random search patterns of ants foraging on honeydew of aphids in cashew inflorescences. Anim Behav 41:7–15
28. Veena T, Kumar ARV, Ganeshaiah KN (1989) Factors affecting ant (Formicidae: Hymenoptera) visits to the extra floral nectaries of *Croton bonplandianum* Baill. Proc Indian Acad Sci (Animal Sci) 98(1):57–64
29. Lanan M (2014) Spatiotemporal resource distribution and foraging strategies of ants (Hymenoptera: Formicidae). Myrmecol News 20:53–70
30. Zimmerman M (1979) Optimal foraging: a case for random movement. Oecologia 43:261–267
31. Zimmerman M (1981) Optimal foraging, plant density and the marginal value theorem. Oecologia 49:148–153
32. Zimmerman M (1982) Optimal foraging: random movement by pollen collecting bumblebees. Oecologia 53:394–398



Professor K. N. Ganeshaiah is INSA Senior Scientist at University of Agricultural Sciences, GKVK, Bengaluru. He has been working on evolutionary ecology of plants and insects. He also works on assessing mapping and conservation biodiversity and bio-resources. Besides, he writes science and historical fiction in Kannada language.