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A REVIEW ON: THE ANT FORAGING AND COMMUNICATION

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ABSTRACT: Ants show a wide range of foraging strategies and this activity is tightly regulated irrespective of the mode of recruitment used. Individual foragers base their decision to forage on information received from nestmates (social information). Transmission of information can be in the form of direct physical interactions such as antennation or indirect exchange of information such as laying of pheromone trails. Foragers also rely on information from their internal states or experience (personal information). The interaction between these two sources of information gives rise to plasticity in foraging behaviour. Recent studies have examined the role of personality (consistent inter-individual variation in behavioural traits) during ant foraging. Since colonies differ from each other in the distribution of personalities of their members, colonies may consistently differ in behavioural traits, giving rise to colony level personality. However, the interaction between information use and personality, especially at the individual level, remains unexplored. Here, we briefly summarize the literature on the Foraging system evolution, Foraging behaviour, different types of foraging strategies, regulation of foraging & will discuss various experiments related to foraging & try to make a review of them.

Keywords: Ant Foraging, Foraging Models, Ant Communication, a review.

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1.INTRODUCTION

Animals live in complex and heterogeneous environments with fluctuating resource availability. Effective decision making in different contexts is critical to their survival and fitness. In group-

living species, including humans, collective decisions emerge from the actions of individual group members. The behaviour of each individual is modulated by the behaviour of others and affects the group as a whole. Social insects such as ants live in colonies which consist of tens to millions of individuals and function as self-organized systems without central leadership. This is possible due to exchange of information among nest mates which allows individuals to coordinate their activities, thus maximizing colony efficiency. Ant foraging is a collective process composed of the activities of individuals as well as behaviourally integrated groups. Ants performed a lot of complicated task ranging from nest building with various floors and compartments to waste management. Ants interact with one another through various chemicals, called 'pheromones' and these chemicals may vary from one species to another. Especially in case of foraging they navigate on the basis of pheromone concentration in the arena. Once they found the food they leave a pheromone trail while bringing it back to the nest which is sensed by other and that in turn leads to the food source. The behaviour of a forager is roughly as follows: the ant leaves the nest and searches in a more or less random manner for food (appetitive behaviour), collects the food either by drinking or by grasping it in its jaws, searches in a more or less random manner for the nest (appetitive behaviour), and distributes the food in the nest by regurgitation or by depositing solid booty among its nest mates. Each of the activities in this be havioural sequence would be expected (in the ethological view) to involve specific patterns of movement, each released by particular and specific stimuli and guided by the same or other stimuli. Therefore, a great challenge in the - of foraging is to explain how the behaviour of such a potentially large and complex system as an ant colony emerges as a function of the properties of its individual components. The task of studying foraging in ants in simplified by the fact that foragers, owing to their sterility, may do little more than forage during their tenure as food harvesters.

❖ **Systematic Position of Ants:**

Kingdom: Animalia

Phylum: Arthropoda

Class: Insecta

Order: Hymenoptera

Infraorder: Aculeata

Superfamily: Formicoidea

Family: Formicidae

1. About Ants:

1.1. Distribution and diversity:

Ants have a cosmopolitan distribution. They are found on all continents except Antarctica, and only a few large islands, such as Greenland, Iceland, parts of Polynesia and the Hawaiian Islands lack native ant species. Ants occupy a wide range of ecological niches and exploit many

different food resources as direct or indirect herbivores, predators and scavengers. Most ant species are omnivorous generalists, but a few are specialist feeders. There is considerable variation in ant abundance across habitats, peaking in the moist tropics to nearly six times that found in less suitable habitats. Their ecological dominance has been examined primarily using estimates of their biomass: myrmecologist E. O. Wilson had estimated in 2009 that at any one time the total number of ants was between one and ten quadrillion (short scale) and using this estimate he had suggested that the total biomass of all the ants in the world was approximately equal to the total biomass of the entire human race. More careful estimates made in 2022 which take into account regional variations puts the global ant contribution at 12 megatons of dry carbon, which is about 20% of the total human contribution, but greater than that of the wild birds and mammals combined. This study also puts a conservative estimate of the ants at about 20×10^{15} (20 quadrillion). Ants range in size from 0.75 to 52 millimetres (0.030–2.0 in), the largest species being the fossil *Titanomyrma giganteum*, the queen of which was 6 cm (2+½ in) long with a wingspan of 15 cm (6 in). Ants vary in colour; most ants are red or black, but a few species are green and some tropical species have a metallic lustre. More than 13,800 species are currently known (with upper estimates of the potential existence of about 22,000; see the article List of ant genera), with the greatest diversity in the tropics. Taxonomic studies continue to resolve the classification and systematics of ants.

Black Carpenter Ant

Red Carpenter Ant

Bullet Ant

Pharaoh Ant

Fire Ant

Banded Sugar Ant

Bull Ant

Dracula Ant

Green Head Ant

Electric Ant

Ghost Ant

Yellow Crazy Ant

Whited footed Ant

Acrobat Ant

Meat Ant

Army Ant

Asian Needle Ant

Dinosaur Ant

(Fig 1: Different Species of Ants)

Morphology:

Ants are distinguished from other insects by the following traits: elbowed antennae; the presence of a meta-pleural gland; a strongly constricted second abdominal segment forming a distinct node-like petiole; and a narrow waist between their mesosoma (thorax plus the first abdominal segment, which is fused to it) and gaster (abdomen less the abdominal segments in the petiole). The petiole can be formed by one or two nodes (only the second, or the second and third abdominal segments can form it).

Ant bodies, like those of other insects, have an exoskeleton, meaning their bodies are externally covered in a protective casing, as opposed to the internal skeletal framework of humans and other vertebrates. Ants do not have lungs. Oxygen passes through tiny valves, the spiracles, in their exoskeleton—the same holes through which carbon dioxide leaves their body. They have a primitive heart and their blood is colorless, rather than red. Their nervous system is much like a human spinal cord in that it is a continuous cord, the ventral nerve cord, from head to rear with branches into each extremity.

The three main divisions of the ant body are the head, the thorax, and the metasoma or gaster.

The **head** of an ant has many important parts. Ant eyes include the compound eyes, similar to fly eyes: numerous tiny lenses attached together, which enables them to see movement very well. They also have three small ocelli on the top of the head, which detect light and dark. Most ants have poor to mediocre eyesight; some are blind altogether. A few have exceptional vision though, such as the bulldog ants *(Myrmecia species)* of Australia. Also attached to the head of an ant are two antennae ("feelers"). The antennae are special organs that help ants detect chemicals, including those used in communication, as well as a sense of touch. Ants release pheromones to communicate with each

(Fig 2: Electron Microscopic image of An Ant)

other and the antennae pick up these chemical signals. The head also has two strong jaws, the mandibles, which are used to carry food, manipulate objects, construct nests, and for defense. In some species, there is also a small pocket inside the mouth to hold food for passing to others.

The thorax of the ant is where the six legs are attached. At the end of each leg is a hooked claw that helps ants climb and hang onto things. Most queens and male ants have wings, which they drop after the nuptial flight. The wing scars are then visible, a distinguishing feature of queens.
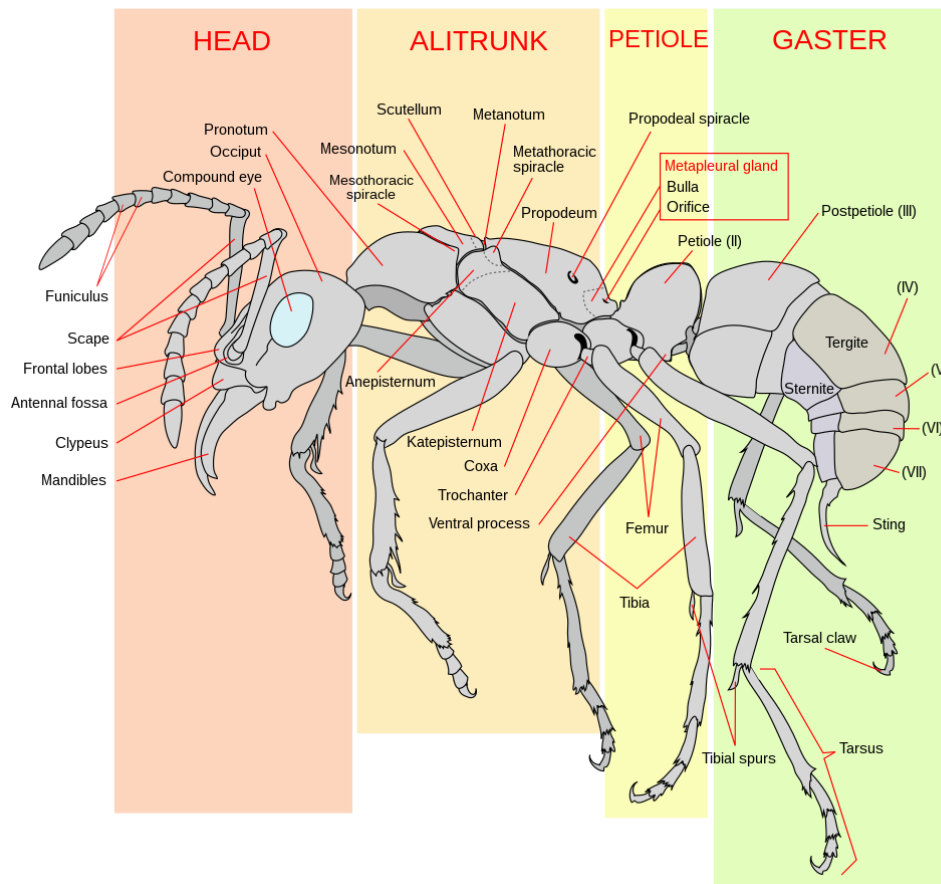
(Fig 3: Different body parts of An Ant)

Wingless queens (ergatoids) and males can also occur.

The metasoma (the "abdomen") of the ant houses many of the important internal organs. These include the crop, where food is stored for the ant's own use or to bring back to the colony; the stomach, where food is digested for the ant's own use; and the reproductive organs. Many species of ants have poison glands and stingers used for subduing prey and defending their nests.

1.2.   Life Cycle of an Ant:

All reproductive adult ants bear wings and swarm to find a mate. The adults mate and the female leaves the colony looking for a nesting spot. Once the female ant locates a suitable site for the nest, she breaks off her wings. She then starts digging the nest. Once it is large enough she starts laying eggs which take a few weeks to hatch. She cares for her first-generation, rarely leaving if at all. Once the first generation is reared, they take care of the queen and she never leaves the nest again.

The queen ant can continue to produce young without mating with a male or she can generate

young through asexual parthenogenesis. The offspring will be exact replicas of their mother but will remain, infertile females unless they are selected to become reproductive.

The Typical Sugar Ant Life Span Encompasses Four Stages.

The order goes from egg, larva, pupa and to adult.

Egg: The queen can produce two types of eggs. One egg-type can be a female ant, and the other can be a male ant. The queen ant can lay up to 200-1,000 eggs in 24 hours. The unusually large egg that is produced is a queen egg. The eggs hatch in 7-14 days and the workers take the eggs to the hatching chambers.

Larvae: After hatching the larvae come out of the egg. They look like tiny worms that must get larger and they do not have eyes or legs yet. The larvae are fed by the workers. This is where having two stomachs in their anatomy plays a major role in the ants. The worker regurgitates food from its stomach to nourish the young. The larvae ant moults several times over this stage and depends on adult worker ants for food. The ant
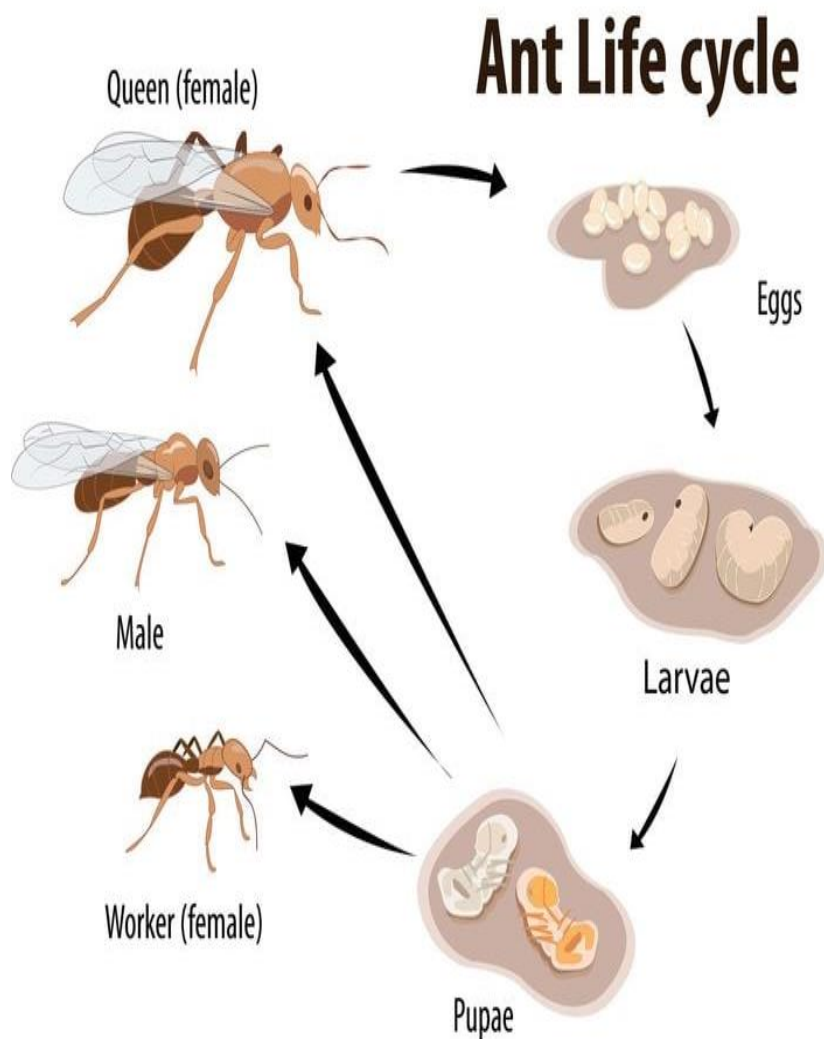

(Fig 4: Life Cycle of An Ant)

larvae then transform into a pupa stage. The pupae have physical features like eyes, legs and wings start to appear. In the pupa stage, the ant has antennae and legs that are folded against their body.

Pupa: Once the ant larvae have reached the desired size, they become pupae. The larvae spin a cocoon around itself where it pupates. A major development of the ant takes place during this phase.

Adult: The adult form is the finished result. The pupa shell or cocoon is then exited by the new fully grown adult ant. This life cycle can take anywhere from five to ten weeks. The average lifespan of an ant is around 1-3 years. However, the queen can live up to 25-28 -years.

1.3.   Role in Nature:

Ants play a tremendously important role in the earth's natural ecosystems. They remove dead plants and animals and recycle their materials back into the soil. By digging their nests they loosen

the soil and bring organic material underground, which enriches the soil and promotes the growth of plants. One study in the United States estimated that ants add one inch (1.5 cm) to the topsoil every 250 years [129]. Some ants pollinate flowers as they feed on their nectar, and uneaten seeds left underground by ants are in an ideal situation to spout and grow. Some plants have an even closer symbiotic relationship with ants. The bullhorn acacia of Central America, *Acacia cornigera,* has hollow thorns that serve to house colonies of Aztec ants, *Pseudomyrmex ferruginea,* which defend the tree against other insects, browsing mammals, and epiphytic vines. In return, the ants obtain food from protein-lipid Beltian bodies, which the tree produces. Many animals use ants as food. These include other insects, spiders, frogs, reptiles, birds, and mammals. Some species of mammals, such as anteaters, pangolins and several marsupial species in Australia, have special adaptations for living on a primary diet of ants. These adaptations include long sticky tongues to pick the ants and strong claws to break into the ant nests. The brown bear, *Ursus arctos,* one of the largest land mammals, often gets a significant portion of its nutrition by eating ants. Other animals take advantage of ants in other ways. In South and Central America, there are 28 species of ant birds, belonging to the family Formicariidae, that specialize in following army ant swarms and eating insects that are flushed out by the ants. They do not eat the ants themselves. Thousands of species of arthropods (insects, spiders, mites, etc.) are found in close symbiotic relationships with ants. In some cases they prey on the ants or steal their food, in some cases they live on waste produced by ant colonies and do not benefit or harm the ants, and in some cases the relationship is beneficial to both. One of the strangest is the mite *Macrochelesrettenmeyeri* which lives on the foot of the army ant *Euitondulcius.* It lives off of the blood of the ant and in return it serves as a extension of the ant's foot, using its legs in place of the ant's claws. Some beetles, as well as other insects, are social parasites, which in effect infiltrate ant society by tricking the ants into protecting them and giving them food. There are also ant species that are social parasites of other ants [129].

1.4. Benefits to Humans:

Humans benefit greatly from the ants' role in helping to maintain the balance of nature. In addition ants may help keep potentially harmful insects, such as termites and agricultural pests, under control. The Masai of Africa had an abiding respect for the siafu ants, voracious predators that consume a large amount of insects and are welcomed for the benefit they bring to farmers, as they will eliminate all pests from a crop and quickly move on. The use of weaver ants in citrus cultivation in southern China is one of the oldest known uses of biological control [59]. In some cultures, ants are used as food and ingredients in traditional medicine. In some parts of the world large ants, especially army ants, are used as sutures by pressing the wound together and applying ants along it. The ant in defensive attitude seizes the edges in its mandibles and locks in

place. The body is then cut off and the head and mandibles can remain in place, closing the wound.

2. What is Foraging?

Foraging behavior includes all the methods by which an organism acquires and utilizes sources of energy and nutrients. This includes the location and consumption of resources, as well as their retrieval and storage, within the context of the larger community. Foraging theory seeks to predict how an animal would choose to forage within its environment, based on the knowledge of resource availability, competition, and predation risk. The purpose of foraging is to create a positive energy budget for the organism. In order to survive, an organism must balance out its energy spent with energy gained. In order to also grow and reproduce, there must be a net gain in energy. The major theoretical statement of this concept is Optimal Foraging Theory [84,100], which assumes that an organism will optimize its energy budget by maximizing energy intake and minimizing energy expenditure. In other words, organisms with an ability to evaluate and selectively consume food will choose items with the greatest energy yield (E) per unit time (t); i.e., will maximize the ratio E/t. An alternative to Optimal Foraging Theory is an evolutionary stable strategy, or a strategy that is used by all members of a population and cannot be invaded or replaced by a newer strategy so that an individual's strategy is determined by that of its competitors and predators. Energy is spent searching for resources, moving to the resource, and exploiting the resource. Energy is only gained during the exploitation phase of foraging. Under these assumptions, organisms will evolve to accurately assess the location and value of resources, to select among alternative resource locations, and to minimize the distance travelled to reach them [84, 100].

3. Foraging System Evolution

the traits that are used to categorize ant foraging are highly variable in their distribution among the more primitive (e.g. ponerine) or advanced (e.g. forrnicine) subfamilies of ants. For example, "diffuse foraging", in which foragers leave the colony singly and retrieve food solitarily, occurs in the Ponerinae and Myrrneciinae. The *forrnicines Cataglyphis* spp. and *Ocymyrmex* spp. also collect randomly dispersed food largely through individual effort [87,83] , but the ponerines *Pachycondyla laevigata* and *Leptogenys* spp. have chemically mediated cooperative foraging [77]. Ecological influences on foraging systems, therefore, seem to override phylogenetic tendencies. Also, any one foraging mode must not be mistaken for a species-typical characteristic when in fact it may be a behaviorally flexible component of total foraging strategy. The use of such a foraging categorization to indicate the outcome of higher-level ecological processes may thus yield conclusions that are not entirely valid. For example, the gross categorization of ant species as being "individual," "recruit," and/or "group" foragers [7,8] may be "too weak and artificial to be useful" [56] when used to define foraging

systems in studies of community organization. Given the wide variety of feeding habits and levels of organization and complexity, I suggest that foraging systems be analyzed as a series of components that may each have individual and social influences and that have all evolved in response to resource distribution patterns, competition, and predation. The designation of systems or species as "individual foraging" should be dropped because the behavior of a forager is probably never completely independent of the activities of other foragers and the state of the colony as a whole. Therefore, the idea of individual foraging is erroneous or at least misleading, even in species lacking recruitment communication. Some components of foraging behavior, such as search or retrieval, may largely be individual activities. Search and retrieval tactics will depend on the size of resources, their temporal and spatial distribution patterns, and their resistance to retrieval, as well as on the loading capacities of foragers. Therefore, retrieval may be an individual or group process when viewed as a component of foraging, but this one feature should not be used to categorize the entire system. In summary, any single categorization of ant foraging systems is inadequate in that it does not consider the components of foraging behavior and their ecological influences, which are necessary to fully understand the total expression of a colony's foraging strategy.

4. Use of social & Personal Information in Regulating of Foraging:

4.1. Social Information:

The chemical trail, which usually contains multiple pheromones, transmits information about the food source to potential recruits. The number of ants laying trail pheromones as well as the intensity of pheromone deposition is related to the quality of food in several species such as the black garden ant *Lasiusniger*, the pavement ant *Tetramorium caespitum* and the Pharaoh's ant *Monomorium pharaonis*. However, it has recently been suggested that pheromone trails may actually provide rather inaccurate information about food quality. In addition to recruiting workers from the nest, the trail also stimulates scouts who are already outside to join the trail, as has been seen in the neotropical species *Pheidole oxyops*. Use of a combination of two pheromones – a long-lasting pheromone and a shorter lasting one – which allows colonies to track foraging resources more effectively while maintaining foraging cohesion has been documented in *M. pharaonis* [62], the army ant *Leptogenys distinguenda* [133] and the big headed ant *Pheidole megacephala* [133]. In order to down regulate recruitment to a food source, *L. niger* foragers reduce pheromone deposition on trails that have already been heavily marked by trail pheromones while a no-entry pheromone appears to repel foragers from unrewarding paths in *M. pharaonis* [91,93]. Much information can be exchanged through direct physical contact between nest mates. High collision rates between foragers on a trail cause them to reduce pheromone deposition[25]or drive some ants to choose an alternate path in *L. niger* [30]. Encounters between returning and outgoing foragers convey information about the partner's identity, the type of food

being exploited and the richness of the food source. Leaf-cutter ants, *Atta cephalotes*, which collect leaves for the symbiotic fungus gardens inside their nests, use encounters on the trail to exchange information about the type of leaves being collected . Contact with food residues on a recruiter's body informs the recruits about the food type that is being exploited and this increases the success of finding the food patch in *L. niger* [70]. In tandem running species, continuous antennal contact between the recruiter and the recruit is essential for progression of the tandem run[88]. During each tandem run, the recruits get the opportunity to learn the path to the food source and they, in turn, recruit other nest mates [36]. Scouts of *Formica polyctena* appear to convey quantitative information about the location of food sources to recruits through antennal contact [87]. Cuticular hydrocarbons (CHCs) comprising of a blend of different hydrocarbons are present in a wax layer on the insect body [10]. The CHC profile of individuals is related to their task repertoire and can inform the task decisions of nest mates. For example, it has been shown in the red harvester ant *Pogonomyrmex barbatus* that foragers have a higher ratio of saturated, linear hydrocarbons to linear alkenes and branched alkanes on the cuticle as compared to workers performing tasks inside the nest [116]. This forager-specific CHC profile not only helps in preventing water loss, which is critical as these ants forage in hot and dry conditions, but has also a communicative function by affecting task decisions of others [43]. Brief antennal contacts with a returning forager at the nest entrance allows inactive foragers to assess its CHC profile and whether it is carrying food. The combination of both odors is required to stimulate foraging in this species [44].

4.2. Personal Information:

Personal information may be related to an individual's physiology with leaner individuals making extra foraging trips in response to an increased demand for foraging, as has been observed in *Temnothorax albipennis* [92]. A forager's decision to initiate recruitment may be based on an internal response threshold such as ingestion of a desired volume of liquid food at a food source as shown in *L. niger* [75] and this threshold increases under conditions of starvation [76]. Enhanced response to recruitment signals after a period of starvation has been observed in species such as *L. niger* [74], *Linepithema humile* and *Euprenolepis procera* [114]. Personal information may also be based on prior experience. In *Ooceraeabiroi*, foraging tendency among individuals of the same age is strongly correlated to successful foraging experiences in the past [85]. In two *Formica* species, individual foragers tend to return to sites where they have had positive experiences in the past [107]. Tandem running recruiters use visual landmarks to improve upon previously learnt routes [83] and likelihood of becoming a recruiter increases with experience [37].

4.3.   Interplay Between Social & Personal Information:

Individual ants extensively use both social and personalinformation to make foraging decisions but reliance on a particular source of information depends on its content relative to other sources. *L. nigeruses* a combination of route memory and trail pheromones to maximize foraging efficiency [24]. In species that use visual cues to form route memory, low light conditions may lead to reliance on social signals rather than reliance on personal memories as has been reported in *L. niger* [68]. and *Formica pratensis* [9]. In *T. albipennis*, contact with returning foragers at the nest entrance causes bouts of activity. In the absence of this social information, physiology of individual foragers predicts which ants will leave the nest as mentioned earlier [90]. When there is a conflict between social and private information, individuals depend on personal information to make foraging decisions in many species such as *Acromyrmex subterraneus* [1], *Formica lugubris* [35], *L. Niger* [4,46]   and *Paraponera clavata* [50]. The reverse, i.e., preference for social informationover private information, has been observed in *L. humile* [4], *Atta cephalotes*, *Atta laevigata*, and *Acromyrmex octospinosus* [113] while no clear preference for either is shown in *Iridomyrmex purpureus* [79]. It has been suggested that ants prioritize social or personal information based on the information content of each source and choose the source that provides more detailed, accurate and reliable information about the food source. Thus, a change in the accuracy and reliability of information from one of the sources may cause individuals to switch their choice of information source as has been demonstrated in *L. niger*.

5.   Caste Evolution & Foraging Strategy:

Because foragers are sterile they do not have conflicting demands on their time and energy budgets that involve trade-offs between searching for food and searching for mates. As a result, they are often viewed as the products of selection for traits that maximize energy return to the colony. Several social traits have consequences that affect a colony's economy; among these are temporal polyethism and senescence, caste polymorphism, and foraging tempo [71]. Selection at the colony level can not only affect the behavioral repertories of foragers to enhance their food harvesting ability,   but can also shape patterns of age demography and mortality. In *Pogonomyrmex owyheei*. the life expectancy of a forager averages 14 days under natural conditions; survivorship is similar in the laboratory under conditions of starvation . However, in *Cataglyphis bicolor*, foragers have a life expectancy of 6.1 days in the field but live for months or longer in the laboratory [97]. Colony fitness may be correlated with the morphology and size frequency distribution of foragers. Their structural morphology per se may reflect feeding habit. Although it is clear in the case of some specialist predators such as Amblyopone, Odontomaehus, and Strumigenysspecies that mandibular shape and head structure reflect feeding habits, the relationship between morphology and foraging ecology is often unclear. Recent studies using digitization analysis to detect the ecological correlates of variation in head

morphology have shown that head shape, as differentiated from size, is related to diet (B. Cole, personal communication). Other studies have ascribed a role to vertebrate predation as a selective agent of form [61]. Among monomorphic species, body size may shift owing to interspecific competition and may facilitate coexistence. It is assumed that there is a correlation between forager size and food-item size, so that morphological divergence produces resource partitioning. Body size of *C. bieolor* foragers is considerably smaller in populations in Greece than in Tunisia, apparently owing to the sympatry of the smaller-bodied *Cataglyphis albieans* in the latter environment . In Greece, where *C. albieans* is absent, the body size of *C. bicolor* foragers is intermediate in size between that of *C. albicans* and *C. bicolor* in Tunisia, which suggests that a morphological shift has occurred because of local competition. Several studies have indicated a correlation between body size and food-item size for desert seed-eating ant communities and communities of generalist ant species[16,17,26,47,109,122]. However, given the limitations of the use of body size as an indicator of food choice and niche [53,59,128] and the fact that the food recruitment systems of ants make them less constrained by their morphology than other animals [14,23,109], size-based partitioning of resources among sympatric species may be the exception rather than the rule in ants [26]. The species diversity of granivorous ants of the southwest desert in North America is related to productivity, and coexistence is based upon body size differences or foraging strategies that are correlated with seed size selection or seed density distributions [26,27,28,31]. In the Australian arid zone, species density is similar to that of North American deserts, but there is less separation by size among sympatric species. Also, differences in productivity among sites do not appear to have a strong influence on associated harvester ant communities in Australia as in North America, seemingly because population density is not limited by food availability [11,12]. Vegetation structure, and perhaps productivity, appears to be related to community organization [2,11,12,27]. Worker size/seed size correlates can be found among some species, but other factors such as seed morphology and biochemistry affect seed choice as well [27] . In the Negev Desert one of three sympatric Messor species shows a small but significant correlation between forager size and seed size harvested (S. Rissing, personal communication). In North-Temperate open field ants and other communities of ants with similar generalist feeding habits, prey size is correlated with body size but mechanisms of cooperative foraging and interference also seem to be important determinants of prey selection and community-level interactions.

6. Communication:

6.1. Foraging communication

Natural selection will favour communication if it helps nest mates to forage more efficiently. In social insects, workers collect the food for the colony. So if worker A helps worker B to collect more food, this is as good to worker A as if she collected it herself, because the food is brought back to the same nest to feed the same larvae. Nevertheless, many species of social insects do not share foraging information. In some cases this may be because foragers have no useful information to share. For example, desert ants (*Cataglyphis* spp.) collect dead insects, but there would be little point in directing nest-mates to the site of a

discovery if no food remains.
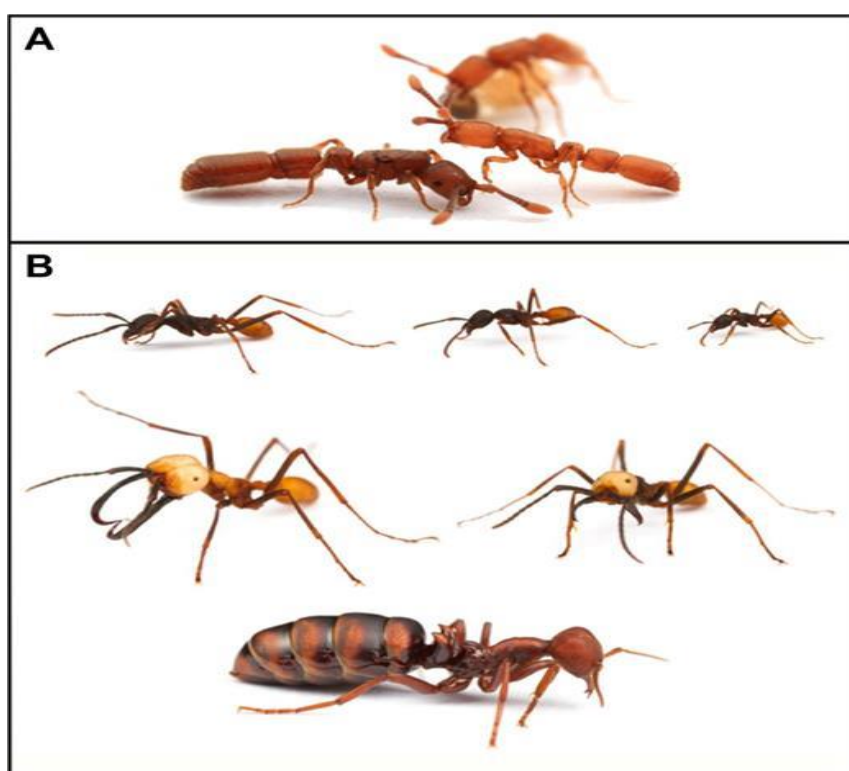
(**Fig 5**: Caste polymorphism in two army ants. (A) *Sysciaaugustae* has a caste system similar to the ancestral condition in ants, displaying workers (right) and queens (left) with modest differences in size and morphology. (B) *Eciton burchellii* has a derived caste system, displaying workers (top), subsoldiers (middle right), soldiers (middle left) and wingless ergatoid queens (bottom). *Eciton burchellii* exhibits extreme variation in size and morphology. Massive ergatoid queens in *E. burchellii* and some other army ants likely represent a secondary increase in size relative to recently evolved

Communication is most useful when food resources are found

that are larger than can be exploited by a single forager, or that need defending. Large or renewable feeding sites would be well worth communicating to nest-mates, such as the location of a group of aphids secreting honeydew or a patch of flowers. In a general sense, social insect colonies live in a dynamic, competitive environment in which food sources of variable quality are constantly changing in location. Most ant species are dependent upon ephemeral food finds. In such an environment, there is an advantage to sharing information if it can help the colony direct its workers quickly to the best food sources. Persistent or recurring food sources may also be available, such as the aphids or scale insects 'farmed' by many ant species. The best strategy is

often to remember rewarding foraging sites but also to be flexible enough to exploit newly discovered food and to select the better sources from those available. To this end, information directing nest mates to food also enables them to select the highest quality food find when multiple resources are available. Different ant species employ a range of communication methods for directing nest mates to foraging sites. The simplest is 'tandem running', where a successful forager leads a recruit. Recruitment is faster when the successful forager leads a group of recruits. The recruit or recruits follow the leader by physical contact or pheromone from the leader. The most spectacular use of trail pheromones is in mass foraging. Here the recruitment and guiding aspects of foraging communication are usually decoupled. The pheromone trail provides only the route to food, whilst recruitment of additional foragers is caused by other behaviours, such as dances or direct physical contact in the nest. In honeybees, the waggle dance recruits additional foragers but also directs them to the food. However honeybees have another dance, the vibratory signal, which helps recruit more foragers but does not guide them to food. Decoupling means that mass foraging ants broadcast guidance information widely, potentially to all foragers, in the form of a trail network marked with varying amounts and types of pheromone. In contrast, the broadcast range of the honeybee waggle dance is limited to workers in contact with the dancer.

6.2. Multi-pheromone trails

Ant pheromone trails contain many chemicals that differ greatly in their persistence. Trail pheromones are also secreted from a diverse range of glandular sources, such as the Dufour's gland, poison gland, anal glands, glands on the feet, and glands on the thorax or abdomen. The use of multiple trail pheromones by a single ant species means that foraging communication can be more complex than is possible with a single pheromone. Many foraging insects, for example a worker honeybee, can individually remember where they have foraged and can return to rewarding sites. However, for trail-following ants this memory need not be an individual memory encoded in the brain. Instead, it can be a group memory encoded externally in the pheromone trail system. The use of several trail pheromones that differ in their persistence provides memory over differing time scales. In particular, a non-volatile pheromone can provide a longer-term memory while a volatile pheromone can allow rapid choice among potential feeding locations by quickly 'forgetting' depleted locations. The traditional view of ant pheromone trails as short-lived signals designed for rapid effect is often illustrated by the swarm raids of army ants. Raiding army ants certainly use short-lived trails to coordinate their lightning raids. But recent research has detected a more complex array of pheromone signals. For example, in the Malaysian ponerine army ant, *Leptogenys distinguenda* (Figure 3, distinct roles have been assigned to trail pheromones from two glands (poison and pygidial). Temporal and spatial variation in the use of three trail pheromones communicates context-specific information in directing and organizing raids. The poison gland of *L. distinguenda* contains two pheromone components. One elicits a strong short-term attraction to

prey items. The other guides workers from foraging sites to the colony, but only weakly. The prey-attraction component directs more ants to prey encountered during raiding to ensure that the prey is swiftly overwhelmed. The number of foragers attracted is a non-linear function of pheromone concentration, such that a trail laid by just a few ants leads to a rapid increase in workers attacking the prey. In this way a small number of workers encountering prey can rapidly attract enough nest mates to capture the prey. This prey-attraction pheromone is highly volatile and lasts only 5 minutes, ensuring that ants are not attracted long after the prey item has been captured. In contrast, the pygidial gland of *L. distinguenda* produces a longer-lasting trail pheromone (approximately 25 minutes). When attacking prey, workers often become detached from the trail network and this pheromone guides them back to the trail, or the colony. The pygidial gland is responsible for maintaining the spatial organisation of raiding ants, helping them explore the environment for prey in a systematic manner. Raiding parties advance in a single direction on the trail, only departing when locating prey or when signalled to do so by the poison gland pheromone. Thus, the longer-lived trail pheromone forms a well-connected network from which all raiding excursions are made. The trail network ensures rapid and reliable communication between foragers and enables the rapid transport of prey items back to the colony [3,28,31].

6.3. Caste-specific communication

Division of labour, in which different workers do different tasks, is universal in insect societies. For example, some workers forage and others nurse the brood. Within the foragers there is also specialization. In the honeybee, most foragers collect nectar but some specialize in collecting pollen, water or tree resin. Most are guided by waggle dances to known food sources but some scout out new sources. Recent research shows that individual specializations also exist in relation to ant pheromone trails. In Pharaoh's ants, only workers that walk with their antennae in contact

(Fig 6: Leafcutter ants, *Attacephalotes*, form dense foraging columns when trans-porting leaves back to the nest along pheromone trails.)

with the substrate can detect the long-lived trail pheromone. Although it is not possible to individually mark Pharaoh's ant workers because they are so small (body length approximately 2 mm), ants that are individually confined for several hours show consistent behaviour with

approximately 17% being able to detect a previously established trail that has been unused for 24 hours. These 'pathfinder' ants are probably a behaviourally specialized sub-caste of foragers that help re-establish existing trails. That is, they convert a long-term memory into a more easily detected signal. In addition, approximately 40% of the Pharaoh's ant foragers on an active trail make repeated U-turns. They walk with their sting extended indicating that they are maintaining the trail by laying additional pheromone. Thus, in Pharaoh's ant trail networks there is specialization for both laying and detecting trail pheromones. Pharaoh's ant workers are all of the same size. But some cases of individual differences in relation to trail pheromones involve different size castes. In the physically dimorphic *Pheidole embolopyx* the minor workers specialize in laying trail pheromone (from their poison gland), but both major and minor workers follow trails in foraging. Major workers do not lay trails but do most of the food transporting. Both castes actively cooperate in defending food finds. The two castes also have different defensive roles. Minors bite the legs of competitors whilst majors attack the heads. During foraging minor workers also guard food finds whilst majors transport food back to the nest. Specialization in pheromone communication among different worker castes also extends beyond foraging trails. For example, Atta leafcutter ants (Figure 6) use alarm pheromones to signal predators or other dangers. The different size castes in Atta possess different blends of the same overall alarm pheromone components, but worker castes respond differently to the blends produced by other worker castes.

6.4.   Multimodal communication

Chemical communication is of great importance in ant foraging organization. But foraging ants also use other modalities to communicate, and signals of different modalities may combine in promoting the organization of a colony's foraging system, and in other areas of colony life such as defense. Close behind chemical communication in overall importance is the use of tactile communication, either through substrate-borne vibration or direct contact. Direct contacts may take the form of ritualised movements in communication, such as displays, dances, waggling and jerking. Physical displays by returning foragers of many ant species often serve a similar excitatory/recruitment role to that observed in honeybee waggle dances. The commonest form of physical contact is mutual antennation. This is seen very frequently when ants pass in opposite directions on a trail but has yet to be assigned a purpose. It probably does not comprise a 'language', as suggested by Wassmann, but it is hard to believe that no information is transmitted. In contrast to the widely broadcast information of pheromone trails, the use of sounds, physical contacts and displays are primarily mechanisms whereby information can be communicated to near neighbours. In some situations, however, the message is passed from ant to ant and so travels further.

(Fig 7: Foragers of *Aphaenogaster albisetosus* use stridulation and a poison gland pheromone to attract additional foragers when they locate prey they cannot capture alone. Transport of the prey back to the nest is via highly volatile trails.)

(Source: Alex Wild)

Camponotus senex live in large arboreal nests built from larval silk. If a small area of the nest is disturbed physically, or by carbon dioxide, then the ants affected produce an alarm response by drumming their abdomens on the nest substrate. This stimulates other ants to follow suit, resulting in the communication of alarm throughout the entire nest, which can be up to 1m in length. The volume of a medium-sized colony drumming is greater than human speech. Multiple pheromones, displays, contacts and sounds are often used in combination. This is probably not to provide backup mechanisms (redundancy) but to communicate a wider repertoire of messages. For example, *Aphaenogaster albisetosus* (Figure 7) modulate the recruitment pheromone by rubbing their abdominal tergites together to make sound. When individual *A. albisetosus* workers locate large prey items, such as dead insects, they release a poison gland pheromone and audibly stridulate to attract workers in the locale. The stridulation encourages other workers to release further pheromone and this feedback leads to rapid trail recruitment to the prey site. *A. albisetosus* retrieves prey items significantly faster when stridulation is present.

7. Ecology of Foraging by Ants:

7.1.   Hunting

7.1.1. Hunting Mobile Insects:

Mobile insects are protein- and calorie-rich resources that are energetically costly to harvest and of uncertain location in time and space. Even in the tropics there is a strong seasonal component to insect prey availability [40,65,66,67]. Many edible prey can escape easily from substrate-bound ants owing to their limited vision, small size, and reliance on direct capture by mandibles and sting alone. Almost all truly predaceous ants supplement their carnivore diet by scavenging and/or collecting secretions from Homoptera. Very few ant species are exclusively hunters of mobile insects, and these species tend to be far from the representative ant in hunting technology.

Dacetine ants (Myrmicinae) are highly predaceous [130], with most species preying on Collembola and other soft-bodied litter organisms [13]; *Strumigenys*, *Smithistruma*, and other genera have greatly elongated mandibles with specialized cocking mechanisms and "trigger" hairs lining the inner mandible edge [13]. By preying on abundant soil arthropods [45,101,102,103], dacetines appear to be specialized for short prey handling and location times. The pantropical *Odontomachus* (Ponerinae) has mandibles highly convergent with dacetine mandibles. However, *Odontomachus* is 7 to 12 mm in length and it is likely that the abundant soil and litter micro fauna is unavailable to them. *O. haematodis*, a pantropical species, preys on large and live insects. Even this specialist predator, which we have frequently seen in Costa Rica with large insects as prey, tends coccids (Homoptera) for their sugar-rich exudates and may even construct shelters over them [34]. Even the neotropical *Ectatomma* (Ponerinae), which are able but generalized predators on single large insects such as Trigona bees visiting sugar baits, also tend Homoptera [14]. For a colony of their biomass, the ants mentioned above have a small number of large workers, have nests that are scarcely more than cavities in the ground, litter, or fallen stems, and may be viewed as effective predators only at a prey density that is far above that for diminishing returns by more generalized foragers. Army ants (Ecitoninae, Dorylinae) are generalized predators that greatly extend the size and behavioral range of live arthropod prey by foraging in large groups [129]. They may lose as much as half the colony through foraging mortality over a two-month period, but take in an immense amount of prey in exchange. To various degrees, they lack permanent nests [86,98], and it is very unlikely that an army ant colony could sustain itself from a fixed nest site. As with the solitary foraging predators mentioned in the previous paragraph, army ants harvest so exclusively from the "cream" of the arthropod biomass that they appear not to be food limited. This is, of course, not true if efficiency is taken into account in harvest economics. Most species also raid other social insect nests [86], an exceptionally concentrated food source.

7.1.2. Raids on Nests of Social Insects:

Social insect nests are rich sources of food for ants. They are relatively sessile, often perennial at the individual and population level, chemically conspicuous, and well protected from other types of predators. They may even be directly (Termitopone continually raiding the same termite nest) or indirectly (Eciton catching only the larvae from a vespid wasp nest) renewable resources. That portion of the ant colony's resource budget that could have been expended on searching may be diverted evolutionarily to overcoming the nest defence. It is somewhat surprising that other social insects can survive at all in ant-rich habitats. Stingless bees (Trigona, Melipona) and army ants seem to be the only conspicuous social insects that are free of nest predation by ants. Stingless bees are notorious for very well- developed chemical defense [129], which should be the only truly effective defence against a numerically superior attacker. Tropical wasps with open-faced nests (comb) are under constant threat of attack [33]and *Mischocyttarus drewseni* coats the nest

pedicel with an ant-repellent chemical [14]. That most tropical social wasps have arboreal and closed nests may well be in major part a defence against foraging ants. Neotropical army ants (Ecitoninae) frequently prey on other ant nests. Rettenmeyer [86] found that "all species of army ants studied captured more [broods of] ants than any other kind of prey." However, they catch few adult ants. Some ants show an explosive escape behaviour that is triggered by army ant pheromones. Trails of the army ant *Neivamyrmex nigrescens* cause a "startle reaction by workers of *Camponotus* and other ants preyed on by army ants" [98]. In the dry forests of Guanacaste, Costa Rica, the nests of a common stem-dwelling ant, *Camponotus planatus*, are often raided by army ants when the stem is large and near the ground; when a worker army ant enters the nest, each worker *C planatus* picks up a larva or cocoon and rushes out of the nest; these workers escape. If air from an aspirator containing army ants (*Labidus* sp.) is blown over a *C. planatus* colony in the laboratory, the same reaction occurs (R. Carroll, unpublished). On the other hand, Old World tropical army ants (Dorylini) avoid trees occupied by the very aggressive formicine *Oecophylla longinoda* [112,119]. *O. longinoda* is very abundant in African lowland forest [112,119] and thus a major part of the ant biomass in the forest is not harvested by army ants. Some much less conspicuous ponerine ants, such as *Simopelta*, and cerapachyine ants, such as *Cerapachys*, *Phyracaces*, and *Sphinctomyrmex*, make group raids on ant nests and sometimes catch adults as well as larvae [41,42,131,132]. Wilson [132] notes that the raided colony often survives the raid with a substantial part of the brood and worker force unharmed; this might well be a place where there is true selection for a "prudent predator." Both specialized and generalized ants prey on termites in the nest. *Leptogenys*, *Termitopone*, and *Megaponera* mount small raids against termite colonies all times of the year, but only harvest a small amount from each nest visited [127,132]. *Pheidolemega cephala* is an important predator on West African savanna termites, especially following heavy rains when the walls of the termite nests are soft and exits have been made for the sexual forms [132]. It is perplexing that ants in general (and especially army ants) do not prey more heavily on termite colonies, as a very large number of species harvest individual workers if caught by themselves. The major deterrents to the ants probably lie in the defensive ability of the termite soldier castes (in Costa Rica, one Nasutiternes soldier placed by itself on an ant-acacia is able to repel 10 to 40 worker ants before it exhausts its supply of defensive secretions; Janzen, unpublished) and in the improbability of the evolution of foraging behaviour that encompasses both complex group raiding from termite nests and more generalized foraging when termites are absent. The temperate zone "slave-making" ants (e.g. *Polyergus rufescens* and *Formica sanguinea*) obtain a major part of their worker force from colonies of other Formica [104,105], which is a behavior we might expect to evolve where the growing season is short and success in resource harvest is directly related to the number of workers foraging for the colony. There is the possibility for an interesting feedback between the density of slave-making

colonies and slave colonies at a site. As the frequency of raids on slave colonies increases, the slave colonies should be weakened not only by the loss of workers but by the increasing foraging competition from their workers that are working for the other colony. Slaving activities will therefore have to be adjusted downward so as to maintain an optimal density of host colonies. In short, the slaver is explicitly leaving part of its prey population unharmed, just as we would expect of a long-established parasite. We may also expect strong selection for slave-making species which have small colonies of very aggressive and organizationally competent workers, as with *Harpagoxenus* [124]; the end result of such a chain might be a parasitic queen who simply enters the host nest and takes over the extant foraging system, e.g. *Teleutomyrmex* queens in Tetramorium nests [129]. Strangely, inter colony aggression among ants only occasionally involves predation, and then usually when alternate foods are unavailable and territorial boundaries are not yet established for e.g. during a temperate zone spring [32]. In summary, ant predation on social insects appears to be divided into two adaptive peaks. Huge colonies (Dorylinae, Ecitoninae) attempt to capture the entire prey colony and are continually on the move. Very small colonies (in comparison to their prey colonies) take small fractions of the colony, probably forage within the same small area for a long time, and otherwise behave in a manner we would expect of a parasite.

7.1.3. Seed Collection:

Seeds with an oily covering may be fed on by almost any kind of ant (including some army ants) [86,126]; whether the seed itself is eaten depends on its hardness and chemistry. When the seed bears an external oil body (elaiosome), a wide variety of ants are customarily the dispersal agents and do not eat the seed [6]; from a foraging standpoint, the elaiosome is simply a dead insect analogue. In this section we consider only those cases where the ant harvests seeds to eat.

Seed predation occurs in many genera of ants, most prominently in the Myrmicinae in dry habitats (Pheidole) [20,21,22,78,]; Pogonomyrmex [19]; Veromessor [108]; Messor. Seeds have high nutrient values (high lipid and nitrogen content) [5,52,57,65,] and should be almost as valuable as are insect prey. However, they can also be stored in quantities adequate to lower the need for continual foraging and may be metabolized for free water [123]. We know that many seeds contain large amounts of toxic compounds and the question then becomes how do seed-harvesting ants deal with them. Ants prey on many species of seeds [78,81,106,108]; Cole [18,19] recorded 29 species of seeds in the diet of *Pogonomyrmex* occidentalis at one site. There are several strategies available. (a) They may select from the nontoxic end of the spectrum. Such seeds are likely to be small and very seasonal in abundance, as they are likely involved with predator satiation as a plant reproductive syndrome. Grass seeds are low in toxins and sometimes constitute a major part of the diet of ant seed predators. However, ants are unlikely to be able to survive solely on grass seeds as many harvester ants live in grass-poor sites where they subsist on the very large store of dicot

annual seeds in the soil or blown into the depressions between sand dunes. (b) They may eat only a nontoxic part of the seed and the embryo is a possible candidate. However, there are no records of such fine resource partitioning. In a certain sense, eating the elaiosome and ignoring the seed, as does a Californian *Pogonomyrmex* with Dendromecon seeds, is such an event. (c) Toxic seeds may be eaten in small quantities or only when other seeds are not available (presumably at some loss in fitness to the ant) as when *Veromessor* progressively take more Plantago seeds as the supply of others is depleted [108]. Seed mixtures may be very important in this context; it may well be that the colony can eat toxic seeds only at some low proportion of the total seed intake (stored), and this proportion becomes the colony growth rate-limiting process. Seed digestion by *Veromessor pergandei* has high potential for seed detoxification [123]. The ants apply a secretion from the gasterto the seeds, which results in softening and degradation of the seed. (d) Ants may have a generalized internal detoxification mechanism for seed toxins, but there is no evidence for this.

Seed harvesting strategies clearly require discriminatory behavior by the individual ant. *Pogonomyrmex* badius workers apparently form a chemical search image for certain seeds, as a single worker tends to collect one species of seed repeatedly [81]. *Veromessor pergandei* switch abruptly from Plantago seeds to the seeds of other desert annuals when they become available after a desert rain [108].

7.2.   Bring the Food to the Nest:

Once a food item has been located, it may be brought directly to the nest in the mandibles or the crop. If very small (fungal spores, insect fragments), it may be retained in the mouth cavity until a mixed bag has been prepared. These cases are straightforward and of little interest in foraging economics compared to the problem of encountering a food item too large for one worker to carry. Many ants are capable of communicating information about a new food source to other members of the colony. The result is that the food is harvested (and defended) far faster than would be the case were each worker to locate the food independently. The dynamics of such an interaction are particularly critical with animals like ants, owing to their generalized food needs and home ranges that often overlap with those of severe competitors. Recruitment to a large food item seems to be involved with one or more of the following three systems. Worker ants search for food as individuals or as groups; the former is by far the more common strategy and includes those species with highly developed mass- recruiting behavior (e.g. *Solenopsis saevissima*) [108]. We do not know what the search pattern of the workers of an individual looks like with respect to the pattern of food items. At best, we can offer a few bits of information on what foraging behavior looks like. It is not clear to what degree individual ants rely on chemical trails while searching. Workers of *Pogonomyrmex maricopa* and *P. californicus* occasionally touch the gaster to the substrate when searching for food in a new area [60], a behavior reminiscent of trail laying (followed by mass-recruitment) into new areas by *Solenopsis saevissima* workers. Such chemical marks as described

for *Pogonomyrmex* may be of importance in aiding the worker to return to the same area (as ants do even in the absence of recruitment trails [60,104] ,and in aiding the worker to avoid redundant searching. These marks may be of great importance in worker fidelity to parts of the colony's foraging range, and therefore to the worker's efficiency and colony foraging flexibility. There is no suggestion of use of pheromones for individual foraging by many species of worker ants. A diverse group of diurnal ants orient visually (e.g. *Messor barbatus*, *Cataglyphis bicolor*, 137, 138; Formica rufa group, *Lasiusniger*, *Myrmica rubra*) and we have observed many tropical arboreal species acting as though they are intimately familiar with a large foraging area and are clearly not restricted to chemical trails [15,63,64,94,96,115,117,118,120,]. The good discussions of the ethology of orientation [63,64,129] conspicuously omit an analysis of the relationship of foraging pattern to food pattern. For example, we should expect that the frequency of visual orientation should increase with permanency of food location (the epitome being represented by extra-floral nectaries and Homoptera), use of vision in predation, worker size (bigger eyes and brain), and exposure to predators (vision being used to find one's way after evasive action, as well as for avoiding predators). Since trail pheromones should be strongly selected for ephemerality , the exclusive use of chemical trails to guide the individual worker to her hunting area should be restricted to short distances and colonies with many small workers. The recruited foragers of *Pheidole crassinoda* may even use a pheromone trail for a short distance from the nest to fix their angular direction, but rely on visual orientation past the end of the trail. Examination of such combinations of visual orientation and pheromones[58] in foraging behavior are needed to reverse the current reductionism in ant ethology, but are extremely difficult. Group forager species are spectacular, but constitute a very minor portion of the ant species (Ecitoninae and Dorylinae, Ponerinae). Tropical species of swarm-raiding army ants are extreme generalists and take many more non-social insect prey (i.e. more mobile and unpredictable) than do column- raiding species. Seasonal maps of the movements of swarm-raiding army ants suggest strongly that the food is comparatively uniformly distributed within a tropical forest habitat with the ant colony optimizing intake by rarely, if ever, doubling back on itself when in the migratory phase, and foraging along a new radius each day during the statary phase. Either type of army ant foraging could evolve from the other, with, for example, swarm-raiding being selected for in more seasonal lowland tropical habitats where prey densities fluctuate greatly between seasons and habitats, and column-raiding being a form of competitive specialization on the more reliably present social insect nests in wetter lowland tropical habitats. While it is not clear if group-raiding ponerinaes forage as a group, or are merely recruited as a group, Wilson (105) strongly suggests that the former is the case. They may even include large arthropods other than termites in their diet and raid other ant nests (e.g. *Simopelta*) [41,42,49].

7.3.   Interaction Among Founding Queens:

A queen that is founding a new colony may produce her first workers from food reserves in her body or she may forage for food. In the former (claustral) type of founding, the queen typically builds a small nest chamber and does not open the chamber until the first workers are produced. Claustral colony founding is found among some Myrmeciinae, Ponerinae, and many Myrmicinae, and is typical in Formicinae and Dolichoderinae. In general, the claustral queen is rather defenseless and her body is large relative to her workers. Non-claustral colony founding may involve groups of queens [51] but colony founding by multiple queens usually involves claustral queens [82,125,126,127]. When there is strong competition for food it is likely that each non-claustral queen will have greater fitness if she has her own foraging area, thereby reducing the average foraging distance and the time away from the brood [see Smith [99] for a similar argument as applied to squirrel territories]. Where there is an advantage to queen cooperation, as in building a worker force large enough to protect an acacia, then there may be a group of queens at the same site even if they have to forage . Claustral founding queens contain their food supply and do not compete for food at that stage. However, the energy expended to find a suitable mate and a nest site may reduce the number of workers critical for colony survival. Under these circumstances, there is selection for unrelated conspecific queens to pool their food reserves. Once the mixed colony begins growth, aggression is expected among the queens for colony ownership. We may expect group founding to occur frequently among claustral queens in food-poor environments or seasons. We also note that in the sense of traditional competition models, the sign of the competition coefficient will here depend on colony age in relation to food abundance in an odd sort of manner; with less food and more difficulty in locating a nest site, the more likely is cooperation.

8. Search Pattern:

Search pattern can be analysed at two levels. First, search concerns the use of foraging space by colonies within populations, and intra and interspecific territorial interactions may contribute to the partitioning of space between colonies [4,55,72,73,95,109,111]. Therefore, search pattern involves colony-level regulation of the spatial allocation of foragers. Second, each trip made by a forager has its own ecologically influenced spatial and temporal organization [51,97]. There is also a relationship between individual and colony-wide search patterns, since a forager may influence the search patterns of nest mates through communication. At both levels, resource distribution in space and time and competition should be major influences on the organization of search.

8.1.   Geometry of Search at the Colony Level:

In the desert harvester ant *V. pergandei* the direction of foraging columns is rotated in a clockwise or counterclockwise manner between consecutive foraging periods, and the size of a foraging column is adjusted to seed production and patch distance [89]. As food

density decreases, columns increase in length and rotate more frequently. Column rotation seems to represent a system of sectorial search with a radial shift following resource depletion. Consecutive raids of the army ant *E. burchelli* are systematically rotated an average of 1230 during the statary phase [38].Raiding also appears to be systematic in the nomadic phase, again seemingly for avoidance of redundant search. The geometry of search appears to be determined solely by prior raid direction, perhaps with modifications to avoid contact of foragers with other *E. burchelli* colonies [38]. Such systematic search during the statary and nomadic phases does not, however, appear to be the rule among army ants. In *Neivamyrmex nigrescens* the directions and distances of emigrations vary unpredictably during the nomadic phase [80]. The striking differences in the search and raiding pat- terns of E. burchelli and *N. nigrescens* may be related to the distribution and abundance of prey or to nest sites and climatic factors [80]. However, the density of prey species of ants in the southwest desert or grassland environment of *N. nigrescens* is approximately 3000 colonies/ha [80], and the density of ant species actually or potentially taken by *E. burchelli* is on average 6600 ± 2200 colonies/ha (range 4000-9000 colonies/ha) [72]. The highly organized raid pattern of *E. burchelli* may therefore reflect selection for efficient prey harvesting given the greater abundance of its prey, but the role of prey distribution is not clear. Limited study of the nomadic obligate termite predator *Pachycondyla* (Termitopone) laevigata has shown no predictable raiding pattern [29].

8.2. Search Patterns of Individual Foragers:

Forager decisions may include where to search, how long to search at a given site, and whether or not to return to a site where search was previously conducted. Some species, such as *Pachycondyla (=Neoponera) apicalis*, show strong route fidelity, each worker restricting its foraging activity to a given site [39]. In *C. bicolor* search effort is concentrated in sectors of approximately 50° and 30-m radius, and average search path length differs among populations according to food availability . The search pattern of a colony contains random components as evidenced in the exponential distribution of search times of foragers, increasing average distance of search in proportion to the square root of time, and selection of initial foraging direction. Thus the colony-level search pattern approximates a random diffusion process, which may be an efficient solution to harvesting food that is un- predictably distributed [48]. In *F. schaufussi*, search pattern is related to food distribution; collecting a single crop load of carbohydrate food produces a more spatially restricted and accurate search during a return trip than collecting a single load of insect prey .

9. Collecting Foraging Behaviour Model:

Ants perform a lot of complicated tasks ranging from nest building with various floors and compartments to waste management.Ants interact with one another through various chemicals,called 'phe

romones', and these chemicals may vary from one species to another.Especially in case of foraging they navigate on the basis of pheromone concentration in the arena. Once they found the food they leave a pheromone trail while bringing it back to the nest which is sensed by otherants and that in turn leads to the food source. The most popular models of collective foraging behaviour (which have been known since ~1989-90) can be briefly summarized as :

● While returning from the food source to the nest, ants deposit a trail of pheromoe leading back to it.

● The ants usually follow the trail of previously deposited pheromone when they leave their nest. If they reach a junction with two possible paths of equal length & different quantities of pheromone then the probability of taking the two paths is given by :

$$p_1 = \frac{(x_1 + \alpha)^\beta}{(x_1 + \alpha)^\beta + (x_2 + \alpha)^\beta}, \qquad p_2 = 1 - p_1$$

in which X_i is the amount of pheromone on branch 1, α and β are parameters depending on the species.

These rules in addition with the description of the evaporation of the pheromone and a random mo

(a)
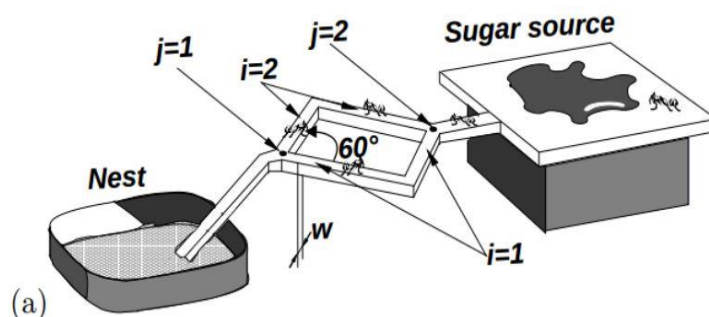
tion of the ants in addition to the above rules is sufficient to describe with a great deal of accuracy the observed complexity of ant foraging behaviour. As one can notice that the choice function is non-linear because of the parameter β. This binary choice model can be extended to an open arena by imagining it as a set of interconnected binary bridges.A typical binary bridge is shown below:

Here the nest is surrounded by walls which constraints the ants to follow the binary bridge which leads the ants to a food source.Then the patterns are observed wih respect to time.

Recently, In a paper titled "Individual Rules for Trail Pattern Formation in Argentine Ants (2012)"

$$\alpha = A \frac{(L-R)}{(L+R)}$$

Theraulaz et. al. have proposed a new model in which the function that describes the motion of ant s is linear.

The angle α is the change from previous direction.'A' is a constant dependent on species. L&R are the integrals of all pheromone in two circular sectors ahead of the ant on the left and right side, respectively.

10. Modelling Foraging Behaviour of Ant Colonies:

10.1. Kriman's Model:

Kirman [69] suggested the following simple stochastic process, dealing only with tandem recruitment. Consider an environment in which there are only two food sources, source A and   source B, which are identical. There are a total of n ants feeding a tone or the other of them.(Clearly this model doesn't allow for the discovery of further sources or foraging.) We define the state of n the system as the number of ants feeding at source A, and write Xt for the state of the system after t steps. At each step, two ants meet at random, i.e. two ants are randomly selected without replacement   from the$n$. The first is recruited to the second's food source with probability γ. We also introduce a small probability ε that an ant changes its food source in dependently', without interaction with another ant. It is this small probability of 'mutation' which prevents the process from being absorbed at either extreme $Xt=0$or$Xt=n$.

This simple process$\{Xt\}$ constitutes a Markov chain, and is fact is well-known from other contexts. The main point of interest is the proportion of the time the process spends in each state, i.e. the equilibrium distribution of the Markov chain. The equilibrium distribution depends on the values of γ and ε, and is uniform when $\varepsilon=\gamma/(n-1)$.

If$\varepsilon < \gamma/(n-1)$ the equilibrium distribution has a ' U' shape, which corresponds to the situation arising in the experiments (the state of the system spends most of its time in the extremes). Note that, to obtain such a distributional form, γ could take any value provided it is less than one, provided the probability ε of self conversion is sufficiently small. This implies that it doesn't really matter how persuasive the individual ants are. The probability that a majority at one of the two food sources will decrease, decreases with the size of the majority, indicating that large majorities will be stable for a length of time.

If $\varepsilon > \gamma/(n-1)$, i.e. the probability of self conversion is relatively high, then the equilibrium distribution will have a single mode: in this case the state of the system remains mostly around n/2.

Since large values of n are of interest, it is worth considering the asymptotic behavior of this process. As the number of individual sn becomes larger and e gets smaller, the equilibriumdistributionofXt/$n$approachesasymmetricbetadistribution(seee.g.Kirman1993).

Kirman's model is based on the view that ants are identical units, largely random and behaving in dependently of any past experience except the most recent. The model oversimplifies many aspects of ant behavior and the environment, but nevertheless it manages to simulate the co1lectivebehaviorobservedintheexperiments.

10.2.   A Detailed Model:

Our current work involves a more detailed study in which the movements of ants to and from the nest and two (or more) identical food sources are explicitly modeled. An ant travels to a pa.tc1i and feeds, and then returns from the patch to the nest. Thus, in the case of two patches, there are eight possible states for each ant at any given time: travelling to source A; feeding at source A; returning from source A; at the nest, having fed last at A; and similarly for source B. When the ant next sets out, it may go to the same patch, or it may change either completely at random (with some fixed probability e), or because of recruitment by an ant feeding at another patch. The ant used as the potential recruiter is the ant which has arrived at the nest most recently—the 'last ant'—when the potential recruit—the 'current ant'—1eaves the nest. The current ant will switch with probability γ to the patch used by the last ant.

Feeding Times

The model above was first studied with constant feeding times. This is a little unrealistic: in practice, it seems likely that feeding times of ants will vary depending on the number of other ants exploiting the same food source. So as a simple alternative, the feeding time of an individual ant was made proportional to the total number of ants feeding at that source. This is reasonable as the more ants feeding, the more difficult it is to obtain resources, and the longer the feeding time. (A more sophisticated model of feeding time will be described shortly.)

Growth Rate

An unrealistic feature of the simple models, albeit consistent with the somewhat artificial experimental set-up of Deneubourg and co-workers, is the interpretation of identical patches. The two patches are identical in that they are both constantly replenished to keep them at the same size. The more ants feed at a source, the more food has to be supplied to that source to maintain the equality of the sources. Therefore, the more ants feeding at a source, the greater the flow of food into and out of that source. This situation seems highly unlikely to occur in the ant world: more realistic would be food sources with constant or variable growth rate.

Constant Growth Rate: The simplest form of growth for the food sources is constant growth. Each source grows at the same constant rate r.

Logistic Growth: A more realistic model for the growth of many sorts of resources is that in which

$$ds(t) / dt = rs(t) (k – s(t))$$

giving the logistic equation

$$s(t) = k / 1+ (k/s(0) – 1) \exp \{-rt\}'$$

where s(t) is the amount of resources at time t, given amount s(0) at time 0 and assuming no removal by foraging, r is a parameter controlling growth rate, and k is the 'carrying capacity' i.e. the level the source would approach (asymptotically) if not exploited.

Feeding Time in Growing Patches

Given food sources which vary in size over time, according to their growth rate and the amount of resources removed by ants, a new function for the feeding time of an ant is required. This feeding time must now depend on the size of the food source as well as the number of ants exploiting it. The new function must satisfy certain obvious conditions. Firstly, the larger the source, the more easily the food can be removed and hence the smaller the feeding time, assuming the number of ants feeding remains constant. Secondly, for a source of a given size, food can be removed more quickly the smaller the number of ants exploiting it. The simple function implemented in the simulation will be

$$f(m, s) = m / s$$

where f (-, -) is the feeding time, m (≥ 1) is the number feeding at source, s (> 0) is the size of the source. This feeding time will only be calculated if s > m and to must be greater than 0, as there will always be at least the new arrival feeding at the source. If s < m, which means (since by definition each ant takes 1 unit of resources) that there is not enough food to satisfy the new ant, then that ant returns to the nest without feeding.

Communicating the Ease of Obtaining Food

In the simplest case, the only communication involved in recruitment is that one ant can communicate which patch it is currently using to another ant, which then switches Its attention to that patch with some fixed probability. It may be the case, however, that ants relay information to each other concerning the ease of obtaining food, such as their last feeding time. Taking the probability of conversion to the last ant's source as

$$\gamma(TC, TL) = TC / TL + TC$$

where TL is the (most recent) feeding time of the last ant, and TC is the (most recent) feeding time of the current ant, relays information about the ease of obtaining food.

2. CONCLUSION

The principal ecological determinants of ant foraging strategy are the distribution of food

resources in size, time, space, and quality; competition with sympatric ant species; and predation. Because a colony is generally sessile, the resource and competitive environment is in essence defined by its location. A colony must therefore spatially pattern foraging to harvest food efficiently and minimize competition. This is accomplished through in- dividual and colony-wide foraging. Elements of social organization are linked to virtually every aspect of foraging strategy. Although patterns of physical and temporal caste evolution have been shown to be integral components of some foraging systems, more sensitive empirical tests are required to provide detailed explanations of the origin and ecological significance of forager size and age-related behavior. Similarly, forager functional morphology and biomechanical characteristics associated with loading capacity should be examined to describe precisely the role of form as well as size and behavior in ant foraging ecology. The overall conceptualization of ant foraging strategy should therefore encompass theory and analyses on subjects ranging from the major elements of colony organization such as caste and division of labour to the time and energy budgets of foragers. Although in this review I have suggested a components approach, foraging systems must be analysed as whole entities. The pitfalls of extreme adaptationist reasoning that might develop from fragmenting the system should and can be avoided through an emphasis on social integration. A prudent application of foraging models, theories on caste evolution and ecology, and basic knowledge of natural history and social regulatory mechanisms can provide the necessary theoretical and empirical framework. Finally, it will be possible to evaluate ant foraging strategy fully when the energetics of foraging and the caloric and nutritional benefits of selected resources are quantitatively measured and used to estimate the conversion of food intake into alates. This analysis will remove the inaccuracies of assumptions of the energetic costs of foraging and will permit colony foraging economics to be quantified in terms of reproductive output.

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