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Diversity, distribution and secrets of ant transportation networks

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Abstract
One of the most striking examples of transport networks are the trail systems formed and used by several species of ants. Ants forage to find food from a central nest, building a network of trails radiating out to nearby food sources and bring it back to the colony. During the entire tenure of survey 11 ant species trails are encountered in the various locations of study sites. All along, there is a physical contact between the trails of the outgoing and incoming traffics. The way to get back home, after grasping a food load (eggs, larvae, dead carcass of colony members, other invertebrates & vertebrates, sugar cube, plant leaf & seed, piece of bread, etc.) is to follow the up route. In many species such trails are chemically marked by pheromones providing orientation cues for the ants to find their way. Other species count on their faculty of sight and markers as signals. Few opportunistic species like *Diacamma scalpratum* (Smith), *Diacamma vagans* (Smith), *Tetraponera rufonigra* (Jerdon), *Tetramorium christiei* Forel often abscond themselves in the trail due to search of food. Often only male morphs of few spider species namely *Myrmarachne melanocephala* MacLeay and *Myrmarachne plataleoides* O.P.Cambridge are encountered within the ants' populations in the trail throughout the period of survey. Such a Batesian mimicry exhibited only by the male spiders is possibly an intrinsic escape behaviour from their female mates so as to avoid cannibalism.

Keywords: Ant trail, opportunistic species, Batesian mimicry

Introduction
Transport operation is a mandatory event at all steps of biological organization. One of the most striking examples of these transport networks are the trail systems formed and used by several species of ants. Ants form an up traffic for foraging from a central nest, typically dendritic in nature (Hölldobler and Möglich 1980) [17]. Each trail starts from the nest as a single thick pathway out of the nest. This "trunk" splits first into thinner branches and then peters out as the distance from the nest increases into twigs, often barely distinguishable in the undergrowth.While sharing this dendritic form, there are often between-species differences in the time for which trails persist and the mechanisms used in their construction (Buhl *et al*., 2009) [3]. Ants may seem like automatons, surprisingly sophisticated in their navigational strategies.

Ants communication through body language
Like most social insects, ants need to communicate with each other by use of body languages (Czaczkes *et al*., 2015) [8]. If one watches ants on a trail, he will notice that they often touch each other with their antennae (long feelers on the head) when they meet (Hölldobler, 1999) [16] or by touching or pressing different body parts to other members (Fig. 4). Physical contact of antennae and head between two communicating ants produce jaw reflex, thus sharing the taste of the diet. Myrmecologists have mapped out twelve different categories of ants communication. 1) Alert/Warn, 2) Entice, 3) Recruit (to food sources or new nest locations), 4) Grooming (the cleaning and tending to other ants), 5) Trophallaxis (the exchange of liquids, orally/anally), 6) Exchange of solid food, 7) Peer pressure, 8) Recognition (members of the colony, determine caste, telling apart dead or living ants), 9) Influencing castes (stimulating or preventing the development of different castes), 10) Controlling rivals (other fertile females of the same nest), 11) Marking territories (distance to the colony, marking of territorial borders and 12) Sexual communication (determining species and genders as well as synchronising the nuptial flight.

What is an ant trail? How does ant trail works?

Trails those are made by ants through the help of any particular pheromone to guide the other ants of the colony, to reach the food source or to return back to the nest, are known as ants trail. Ants rely on a scent left by their scouts to use for communication and to make trails and guide the workers from their colony to specific food sources. The trail is made of pheromones, natural volatile chemicals the ant's deposit along their route, thus guiding the workers to reach to the food source. Each worker then reinforces the trail on the way back ants use their sting to lay down a product of the poison glands (in some myrmecine and ponerine ants) as a trail pheromone, while nonvenomous ants synthesize their pheromone in Dufour's gland, tibial gland, tarsal gland, abdominal gland or in the hindgut (Athula & Attygalle, 1984; Resh, & Carde, 2003) [1, 21] (Fig. 1). Trail pheromone is supposed to indicate the amount of food available at distant location. This is effected by the returning workers that add to the trail intensity (Nicholson *et al*., 1999) [19]. Once the food is exhausted, returning workers no longer lay down a trail, and it soon dissipates. Trail pheromones tend to be more stable than alarm pheromones, but they are still relatively volatile; if trails that are no longer informative need to be avoided (Gruter *et al*., 2011) [15]. One ant species can also react to the trail pheromone of other allopatric species. This phenomenon has been found in *Camponotus modoc* & *Myrmica rubra*. Eavesdropping ants may accrue benefits by learning about the location of profitable food sources (Chalissery *et al*., 2019) [5]. Life of pheromone trails may vary from few minutes to some days. The best example for this are the carpenter ants, their pheromone trail must be dealt with because it can last for a few days (Green *et al*., 2008) [14]. Trail pheromones appear to have arisen as metabolic by-products that are eventually adapted as signals and may be exceptions to the rule that pheromones exist as specific component blends.

Fig 1: Fire ants deposit trail pheromones by discharging the contents of the Dufour's gland through the extruded sting. The continuity of the trail is made visible when a worker walks over a treated glass slide, removing soot where her body contacts the substrate. Marks made by the tarsi and hairs on the tip of the gaster are visible. Increase in the continuity of the sting trail can be seen.

Role of Pheromones in trail

Ants uses many types of pheromones according to need and time but in ant trails there are some specific pheromones used as such –

1) Trail pheromones
2) Information pheromones
3) Signal pheromones
4) Alarm pheromones.

1. Trail pheromones

Ants mark their paths with these trail pheromones. These are volatile hydrocarbons. Many ants lay down an initial trail of pheromones as they return to the nest with food. This trail attracts other ants and serves as a guide. As long as the food source remains, the pheromone trail will be continually renewed. In at least one species of ant, trails that no longer lead to food are also marked with a repellent pheromone.

2. Information pheromones

It can be said that these types of pheromones are indicator of a particular territory of that species so that individuals of same species return back to their own nests.

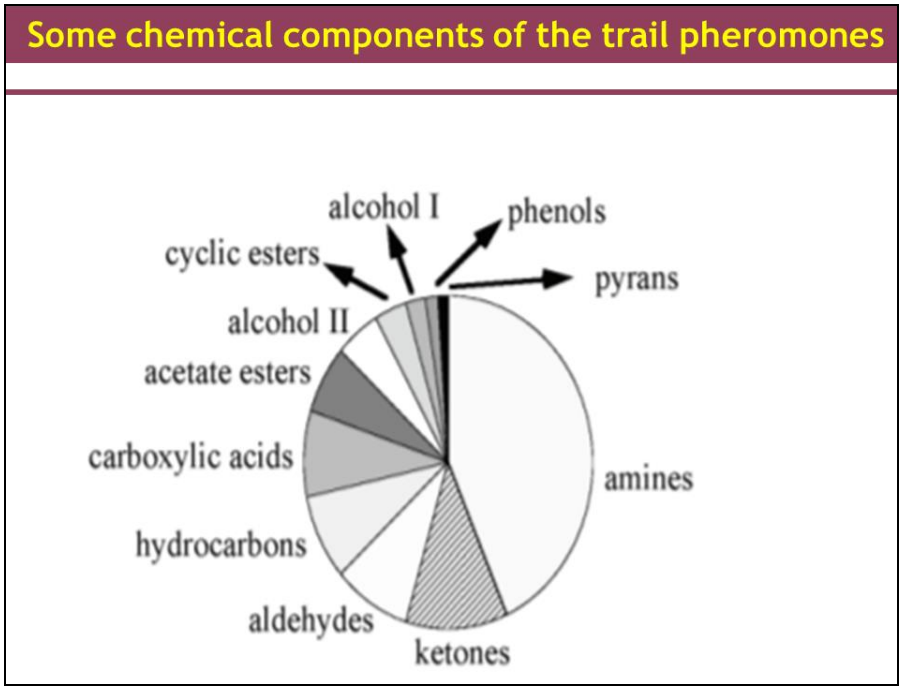
3. Signal pheromones

It can be used as providing signals about food or other things like path.

4. Alarm pheromones

When attacked by predators or in other dangers they secrete a volatile substances to create an alarm for safety, fight or aggression.

A single component, 3-ethyl-2,5-dimethylpyrazine, is present in the poison glands of several species of *Myrmica* and is able to induce trail-following in all those species, but there are some other species that do indeed use multiple components (Cerdá *et al*., 2014) [4] (Fig. 2). Ant trail pheromone biosynthesis can also be triggered by a neuropeptide hormone SolinPBAN (Choi and Vander Meer, 2012) [6].



(Cerda *et al*. 2014)

Fig 2: Chemical compounds used as trail pheromones by ants. Data obtained from literature (168 compounds from 75 ant species

The regulatory mechanism underlying foraging organization is called mass communication. Foraging is initiated when scouts locate new food, determine its quality, and deposit trail pheromone according to the food's energetic value and the colony's nutritional needs. This trail induces recruitment in nestmates, which repeat the cycle of food quality assessment and trail pheromone deposition until the food source has been depleted or the colony satiated. The entire process is regulated by the concentration and evaporation of the trail pheromone. If the recruitment trail is not reinforced, the trail substance evaporates and foraging rate decays over time until food collection ends (von Thienen *et al*., 2014) [24]. Different ant species show variations on the theme of mass communication that likely are associated with the foraging ecology of individual species (Fig. 3).

Fig 3: Ants trail & it's Signature

Fig 4: Ants communication through antennae

How Do Ants Find the Shortest Path?

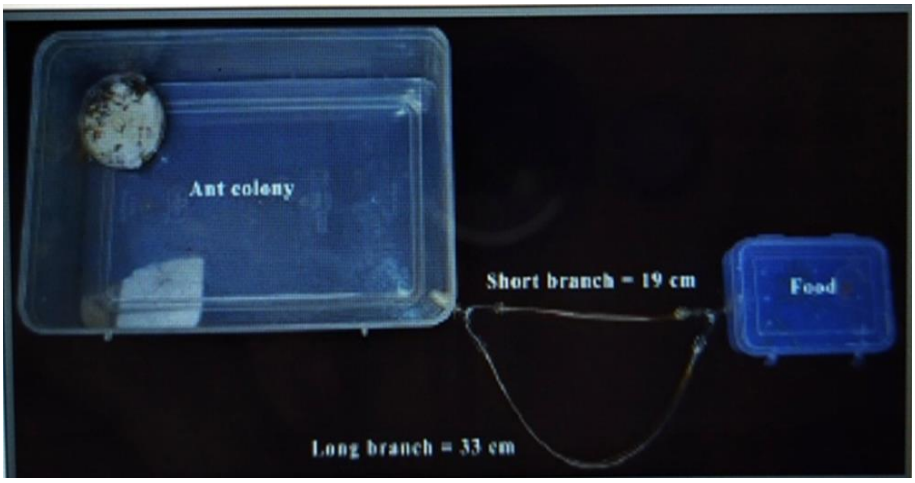


Fig 5: Experimental Setup used by my Undergraduate student Ankan and Jadeera to study if ants can choose the shorter of two paths provided between their nest and the food source

Experimental Setup: Deneubourg and his colleagues (1990) [10] put an ant colony in one box & some food in another box and connected the two boxes with a bridge with two branches – a long one and a short one – and let the ants forage (Fig 5).

Observation: Ants began by randomly using either branch but soon, nearly all the traffic was on the shorter branch. Ants measure and compare distances & natural selection would have selected for ants that choose the shortest path.

Inference: It has been proved both experimentally and mathematically (Shah *et al*., 2013) [23] that there will, of course, be more traffic per unit time on the shorter branch because ants choosing the shorter branch will reach the food sooner Here there will be more pheromone build up on the shorter branch and through a similar positive feedback, the shorter branch will win over the longer branch.

On this backdrop, the present work deals with the observation of the foraging and food gathering behaviour of different ant species in the trail, Identification of different ant species making trail& detection of ant mimicking species in the trail, if any.

Study sites (Fig. 6)

The study was carried out in various locations of Shyamnagar & Barasat State University Campus, North 24 Parganas, West Bengal, India.

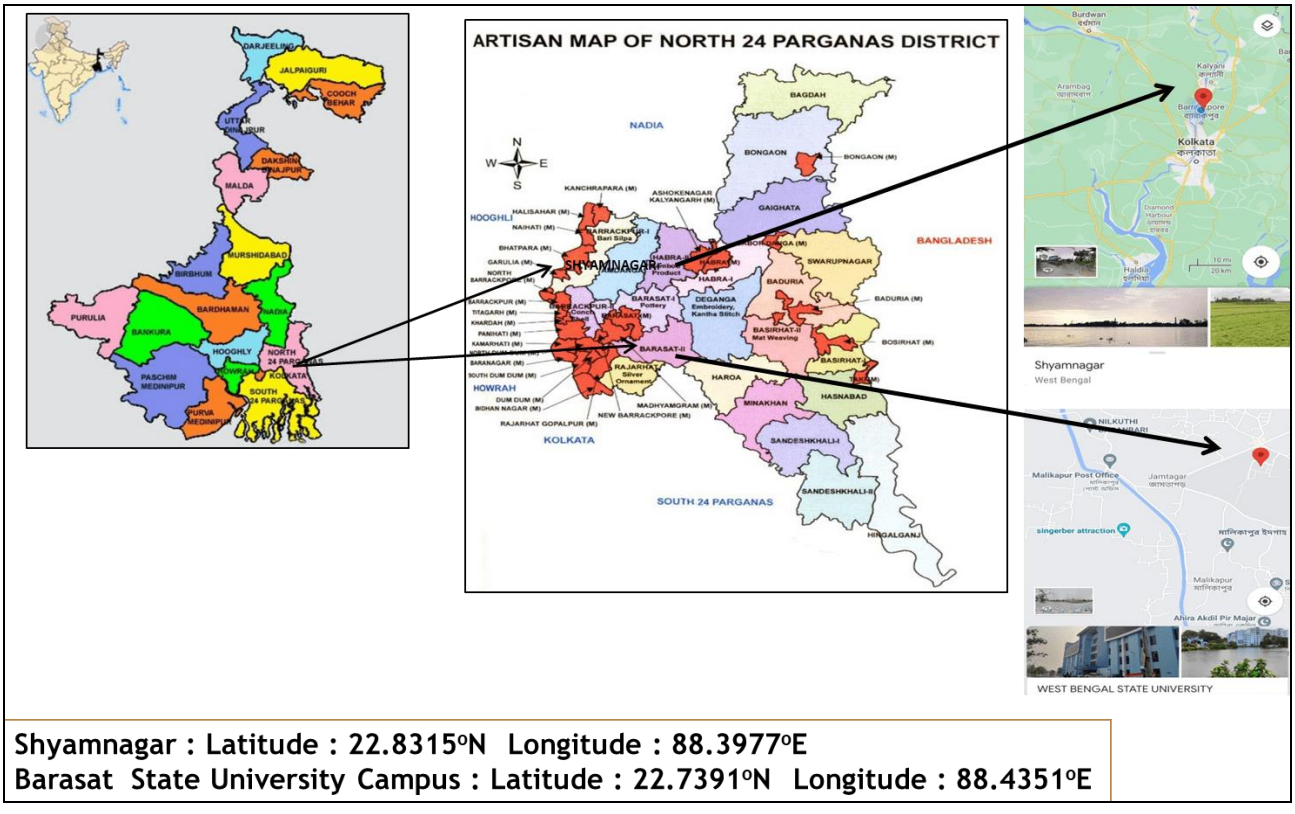


Fig 6: Study sites

Materials & methods

Survey was conducted once a week since September 2021 - till June 2022 within various locations of North 24 Parganas, West Bengal. Ant trails were observed in various habitats within 10 am to 3 pm & took photographs & videos. Ant activities within trail were keenly and carefully observed. Ant sampling were done by hand picking. Samples were killed and preserved in 70% alcohol as per recommendation of Raychaudhuri and Saha (2014) [20] Experimental protocol for "observing ants follow shortest route" at home were designed following Gadagkar (2018) [12] (Fig.7). The materials were studied using Stereo Zoom Binocular Microscope, model Olympus SZX-16. The measurements are in millimeters, made with an eye piece graticule. Specimens were identified following Datta (1988) [9] and Bhattacharjee (2009) [2]. Materials are in the deposition of Post Graduate Department of Zoology, Barasat Government College, Barasat, Kolkata.

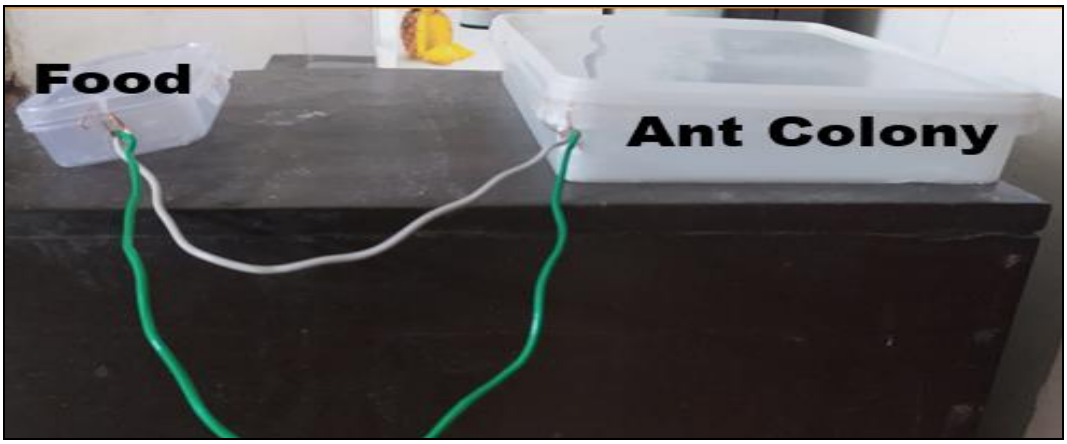
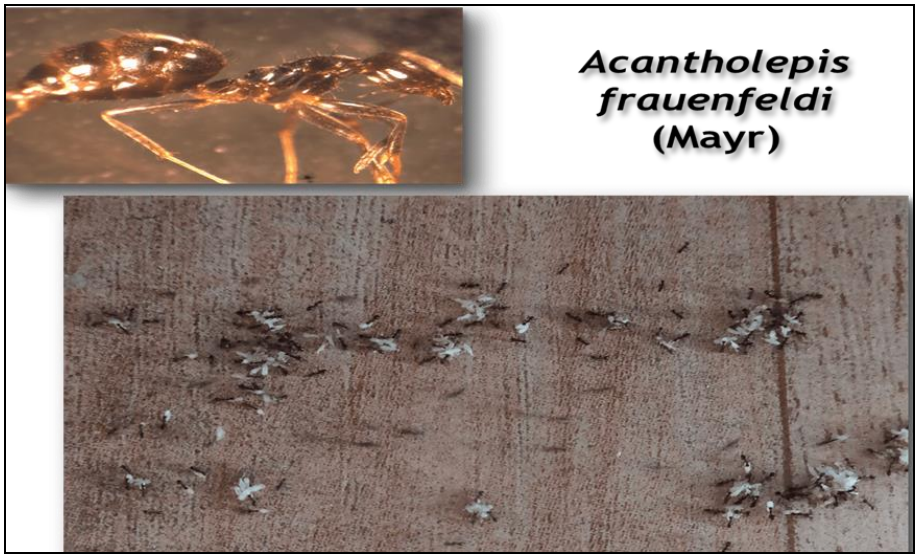


Fig 7: Experimental Set up

Results

During the entire tenure of survey 11 ant species trails are encountered in the various locations of study sites (Fig. 8). All along, there is a physical contact between the trails of the outgoing and incoming traffics. The way to get back home, after grasping a food load (eggs, larvae, dead carcass of colony members, other invertebrates & vertebrates, sugar cube, plant leaf & seed, piece of bread, etc.) (Figs.9-11) is to follow the up route. In many species such trails are chemically marked by pheromones providing orientation cues for the ants to find their way. Other species count on their faculty of sight and markers as signals. Few opportunistic species like *Diacamma scalpratum* (Smith), *Diacamma vagans* (Smith), *Tetraponera rufonigra* (Jerdon), *Tetramorium christiei* Forel (Fig.12) often abscond themselves in the trail due to search of food. Often only male morphs of few spider species namely *Myrmarachne melanocephala* MacLeay and *Myrmarachne plataleoides* O.P.Cambridge (Fig. 13) are encountered within the ants' populations in the trail throughout the period of survey. Laboratory experiment proves that ants measure and compare distances & natural selection would have selected ants that choose the shortest path for reaching the food.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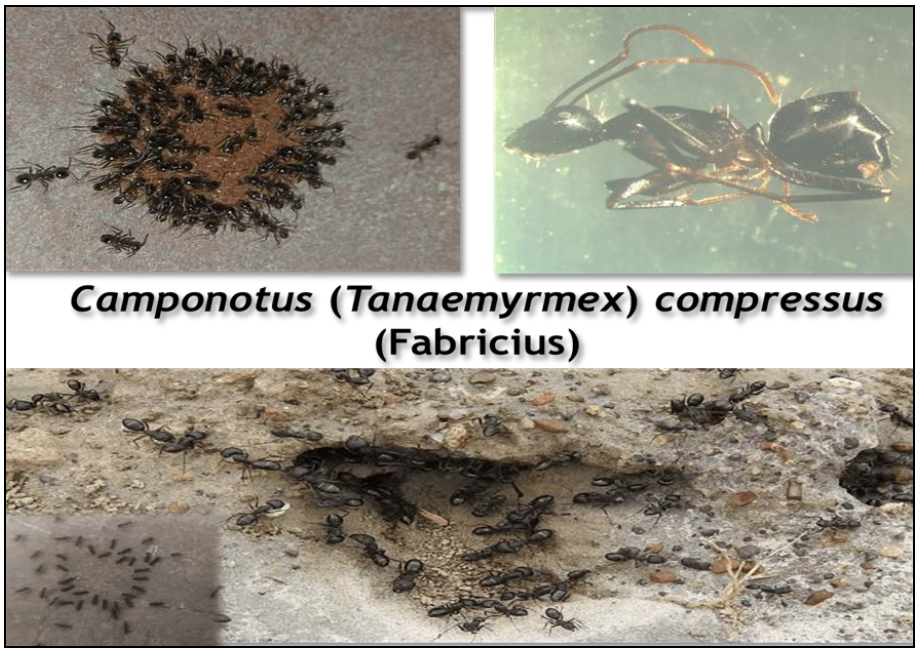
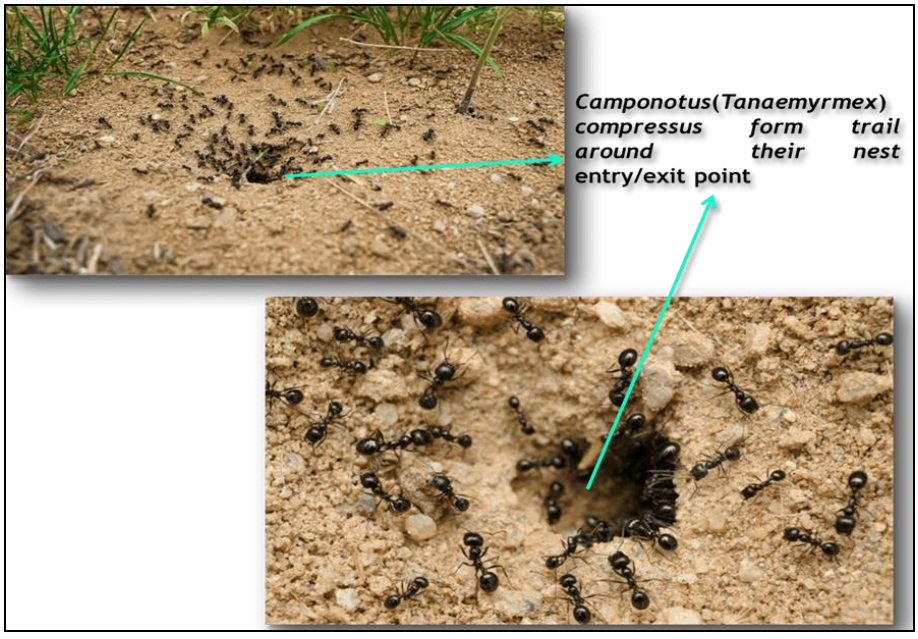
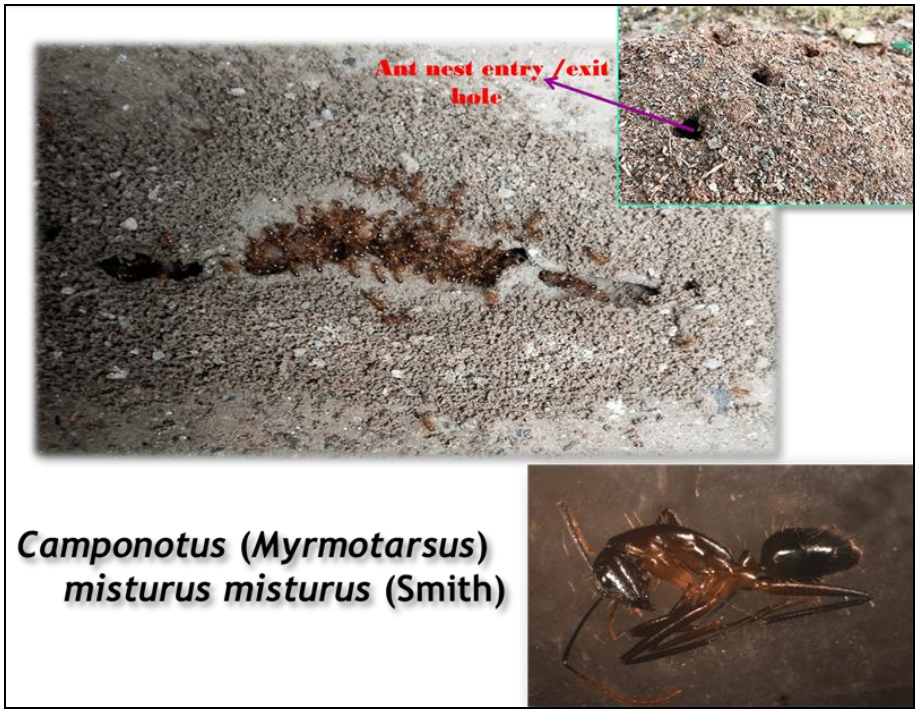
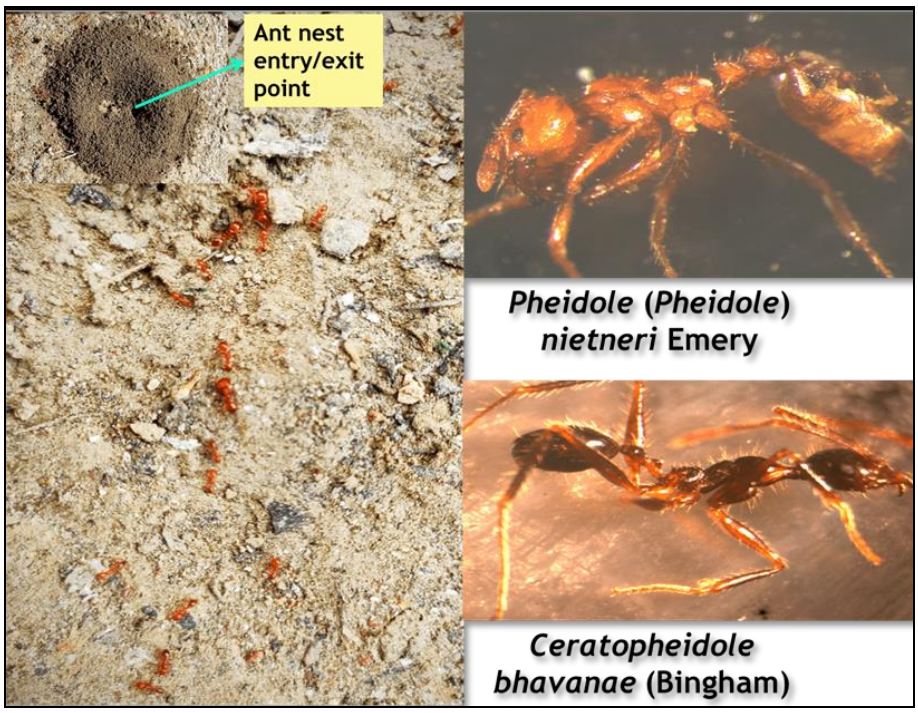
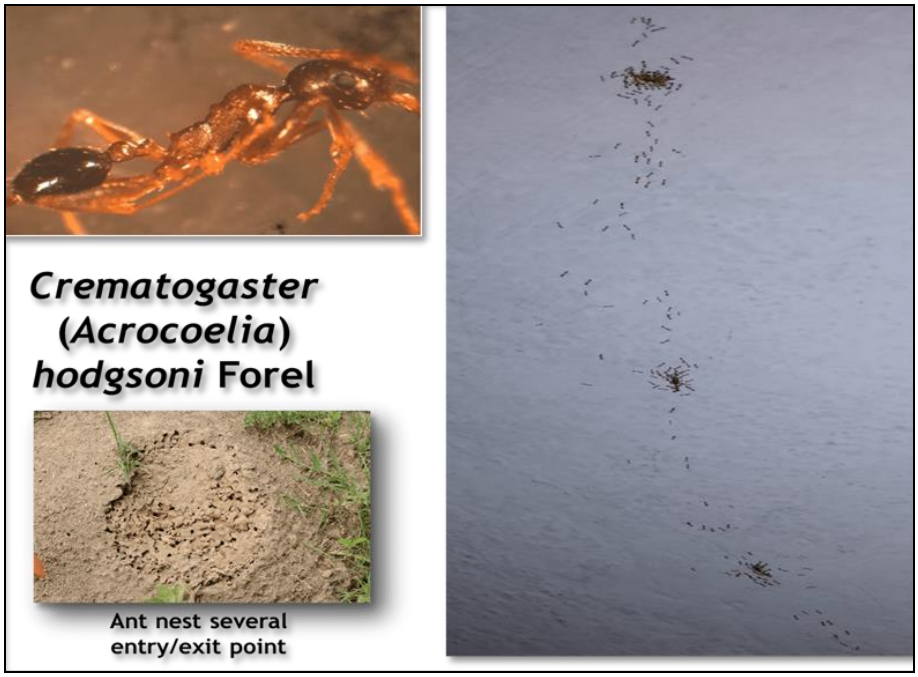
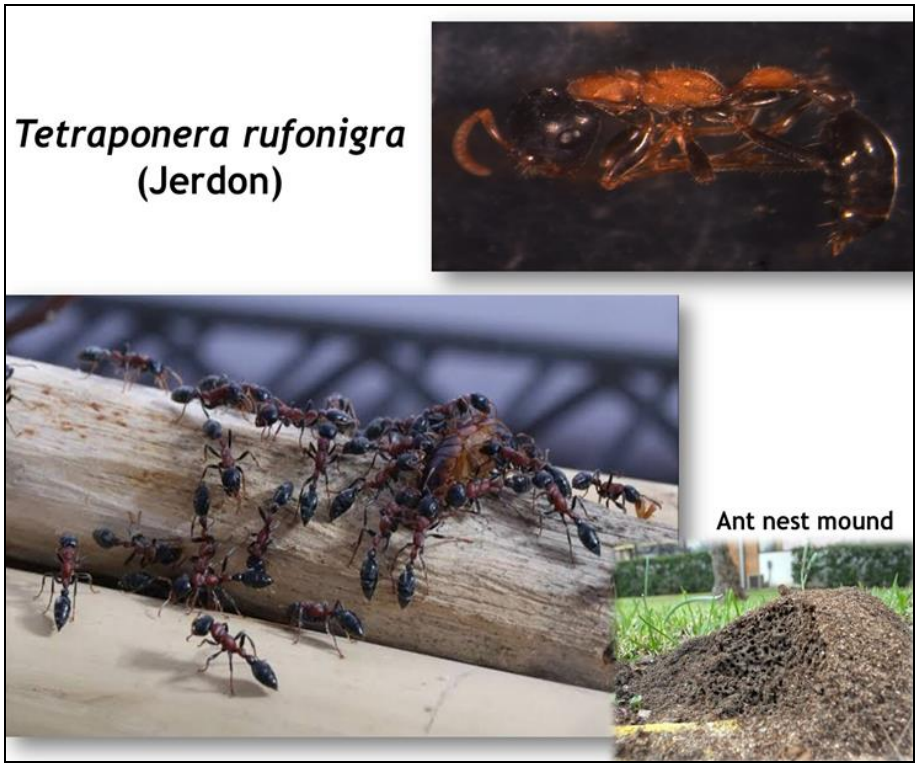

Camponotus (Tanaemyrmex) compressus
(Fabricius)


Camponotus(Tanaemyrmex)
compressus form trail
around their nest
entry/exit point


Ant nest entry /exit hole
Camponotus (Myrmotarsus) misturus misturus (Smith)


Ant nest entry/exit point
Pheidole (Pheidole) nietneri Emery
Ceratopheidole bhavanae (Bingham)


Crematogaster
(Acrocoelia)
hodgsoni Forel
Ant nest several
entry/exit point


Tetraponera rufonigra
(Jerdon)
Ant nest mound

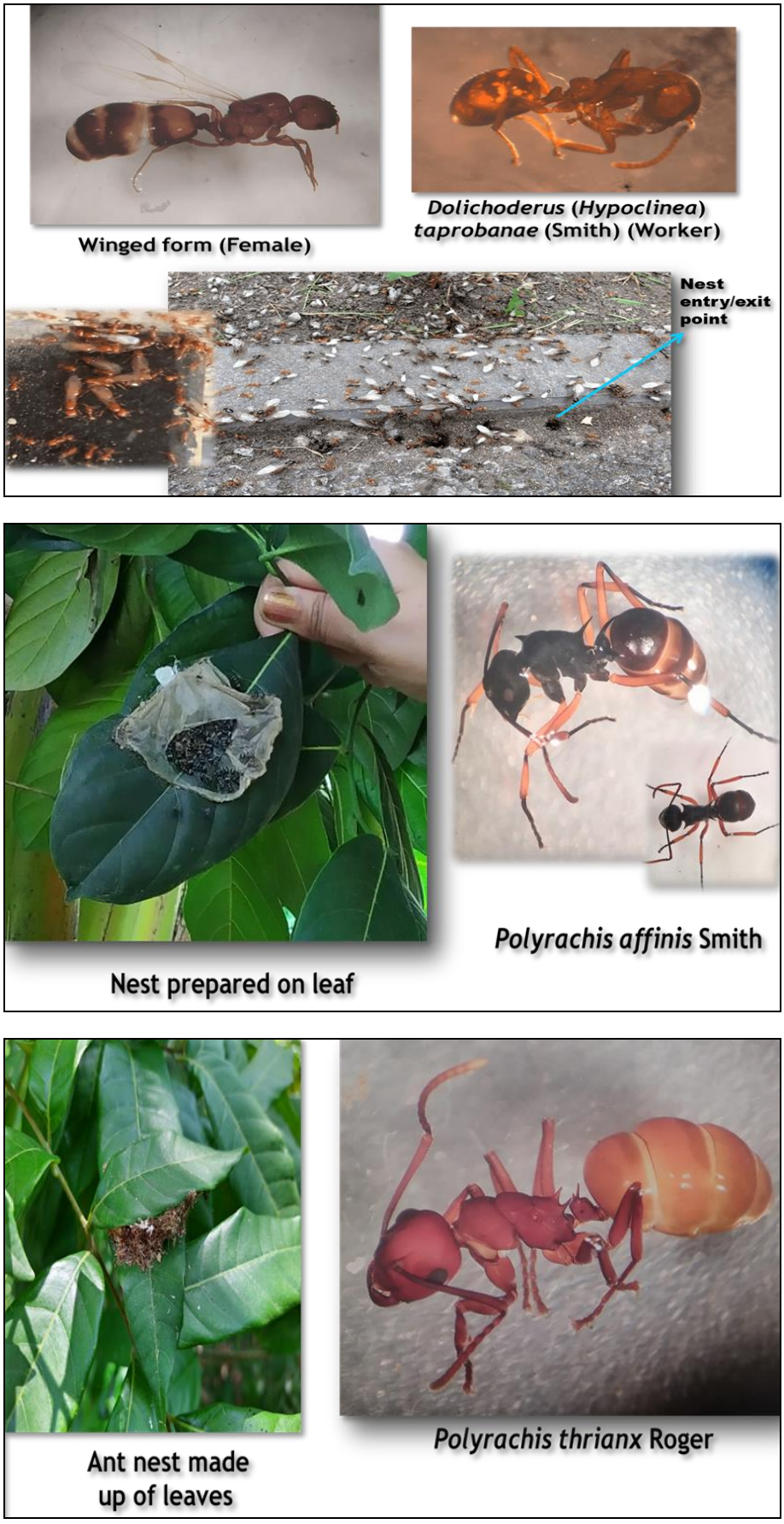


Fig 8: Species found in ant trail

Fig 9: Ant carrying self eggs/larvae in trail

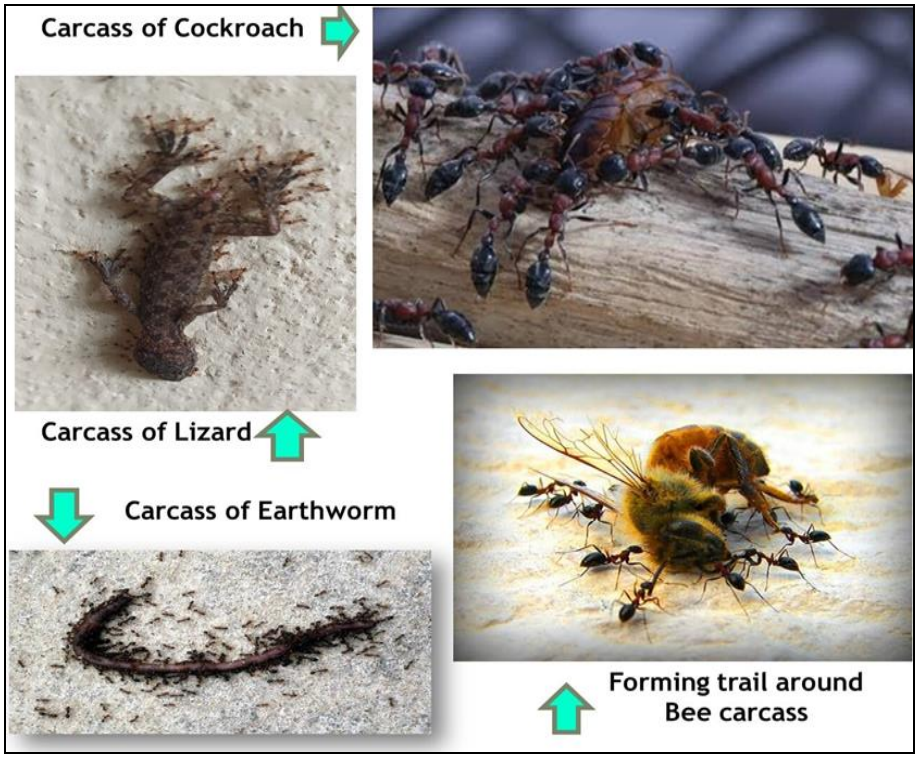
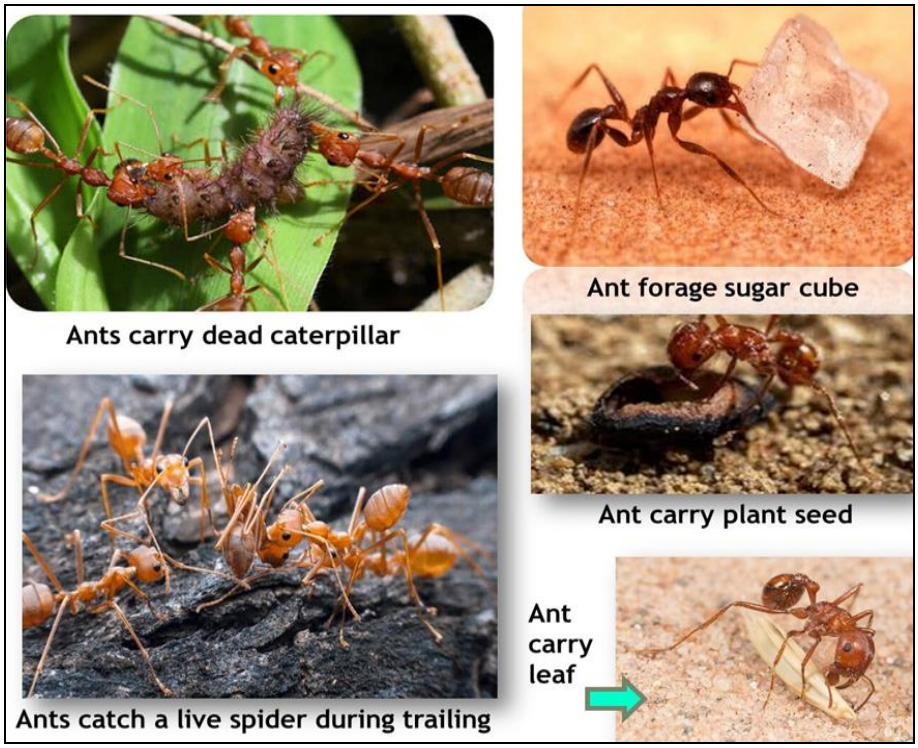


Fig 10: Ant foraging & carrying insect/animal carcasses in trail



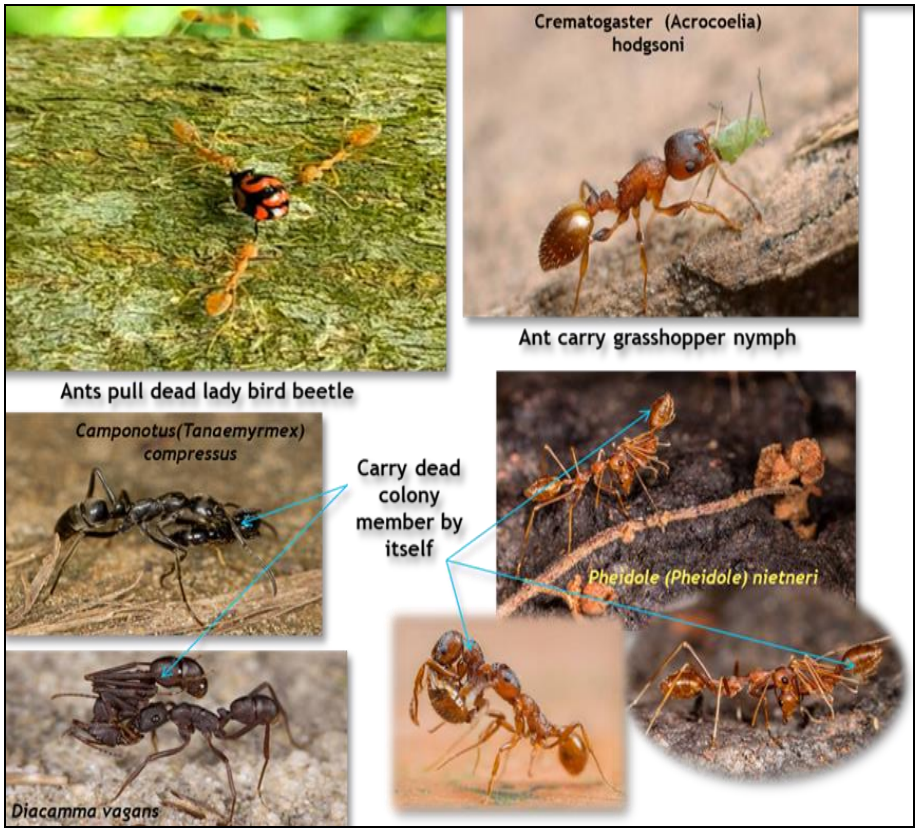


Fig 11: Ant foraging & carrying food in trail

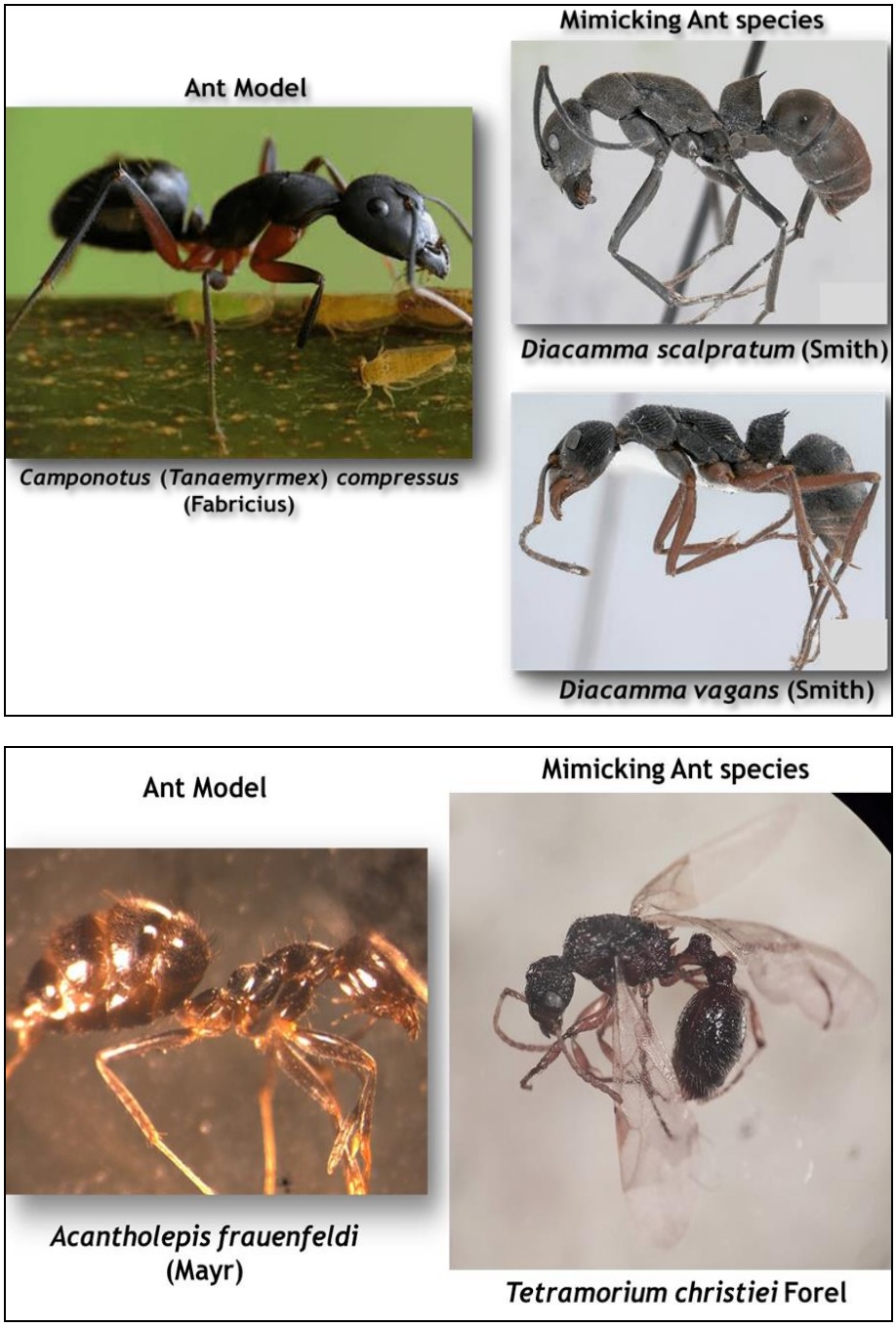


Fig 12: Mimicking ant species encountered in the trail

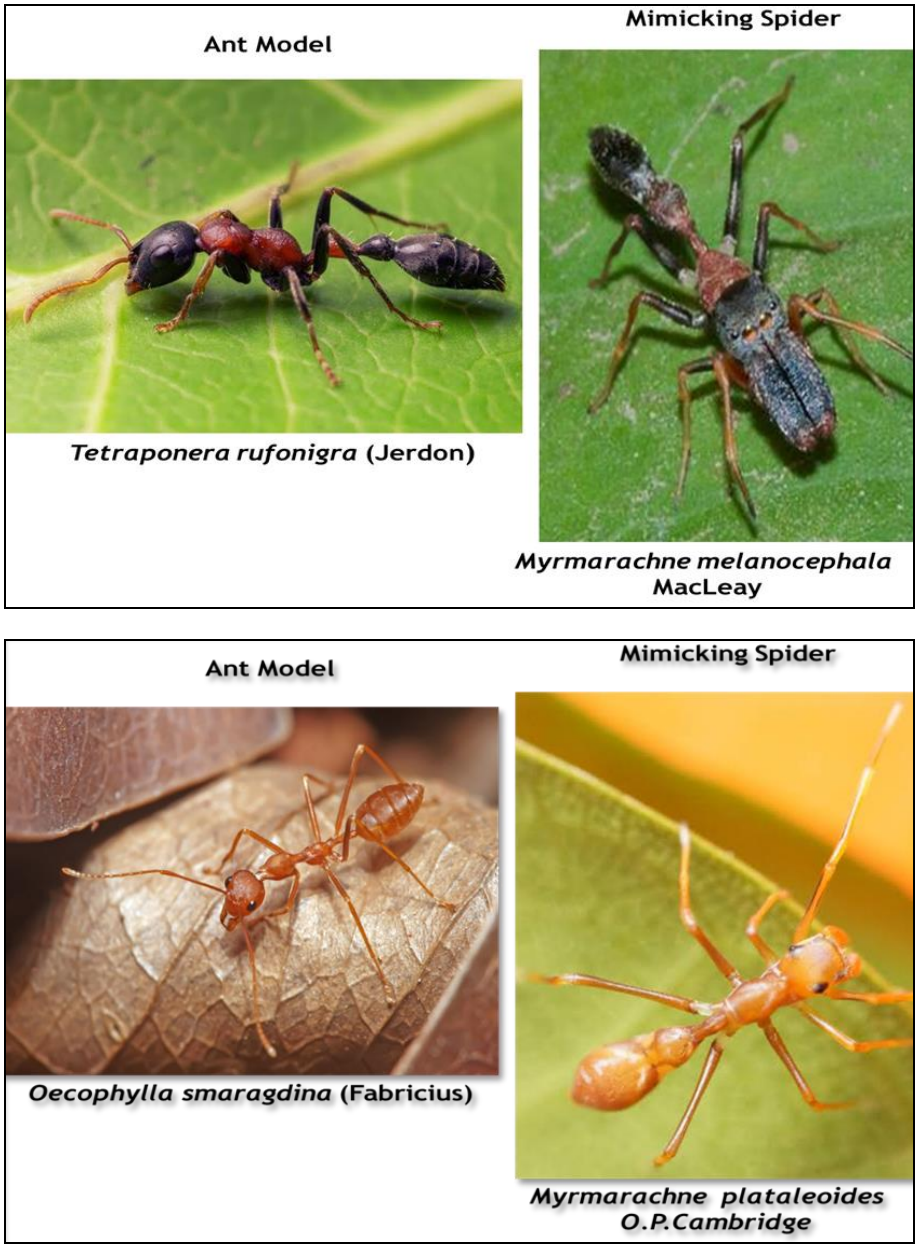


Fig 13: Ant Mimicking Spider species encountered in the trail

Discussion

Ant foraging and food gathering provides an excellent opportunity for us to directly observe a form of animal communication. Ants secrete the trail pheromone from an exocrine gland located in the posterior abdomen and the trail is established as the pheromone flows down the sting. Antennal receptors guide other ants to receive and analyse the chemical signals. Evaporation of pheromones cause upward movement from the trail to the receiving ant's antennae. One worker, upon finding food, leaves a fairly uniform trail, but the volatile nature of the pheromone causes the trail to dissipate within a short time. Trail gets prominent and reinforced with the contribution of the subsequent ants. However, in case of loss of the trail, worker travels in small circles until it finds the main trunk. Ants forage to find food and bring it back to the colony. Collaborative transport is opted only when an object is too heavy for any single ant. (McCreery and Breed, 2014; Czaczkes and Ratnieks, 2013; Gelblum *et al*., 2015) [18, 7, 13]. If they come across food items that are too large or heavy for a single individual to carry, some species are able to form teams to cooperatively carry these items to the nest. This collective shipping is largely dependent on the abilities of the individuals. When cooperating to move large objects, the ants use scent marks to form a new type of trail that is highly dynamic. In such situation, new trail is formed at every step of movement. Furthermore, the team of ants carrying the item only follows these local directions in a loose manner and often ignores them (Fonio *et al*. 2016) [11]. Fonio and his team members (2016) [11] used a mathematical model and experiments to show that this new type of trail effectively solves the problems of collective navigation during cooperative transport. The trail locality and unsteady way tune the degree to which collective motion depends. This allows the group to benefit from the useful information available to individuals while avoiding local traps that may occur when these individuals wrongly direct them towards dead ends. We feel it relevant to highlight the fact that often other ant species and only male morphs of few spider species could be encountered within the ants' populations in the trail throughout the period of survey. Such a Batesian mimicry exhibited only by the male spiders is possibly an intrinsic escape behaviour from

their female mates so as to avoid cannibalism. This is over and above the usual defensive strategy adopted by spiders. On the other hand ant mimicking species only share food from the trail (Saha and Raychaudhuri, 2019) [22].

Conclusion

Trail-following behaviour is a key to ecological success of ants allowing them to orient themselves between the nesting and foraging sites. This behaviour is controlled by specific trail-following pheromones, metabolic by products that are eventually adapted as signals, exist as specific component blends, used for recruitment, for marking pathways to resources and for indicating resource richness. Different ant species show variations on the theme of mass communication that likely are associated with the foraging ecology of individual species.

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