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ROLES OF ANT PHEROMONE TRAIL IN COOPERATIVE FORAGING OF FOOD

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ABSTRACT

Ants are very active in foraging to find food source and competitive in retrieving for safe storage in nests through pheromone trail laying (PTL). In the present review, the characteristics of trail pheromone that has a prominent role in foraging activities are discussed. While PTL results in paving direct pheromone route between food source and nest and recruitment of mass workers which learn the route for successful retrieval, behavioural plasticity in foraging was reported because of many factors like temperature, food quality, quantity, competitors influencing on PTL. Among several glands found in ants, poison gland is the prominent one secreting chemical compounds associated with PTL, while studies about association of other glands (Dufour's gland, Pavan's gland, rectal/pygidial gland) with PTL and functional utilities are very meager.

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INTRODUCTION

Ant colonies are famous for using trail pheromones to recruit in mass nest mates, which follow to the target site, or they walk with other ants to the target site. Though female workers lay pheromone trail on different occasions, at the time of foraging and after locating heavy food, they lay pheromone trail between place of food located and nest with a characteristic pheromone trail run to inform others, so that the informed workers rush to the site of food which is retrieved. In the figure 1 is shown a weaver ant, *Oecophylla smaragdina* laying pheromone trail. The Madagascar ant, *Eutetramorium mocquerysi* (Myrmicinae) during foraging lay recruitment trails with secretions from the poison gland (Tentschert *et al.* 2000). Gordon (2017) reported that an arboreal ant colony maintains, extends, and repairs its pheromone network of foraging on vegetation and that ruptured trails are rapidly repaired with a new path. Hence, foraging success depends on how efficiently ants communicate the presence of food and thus recruit workers through pheromone trail to exploit the food resource. Figure 2 shows the weaver ant, *O. smaragdina* dragging food (given chicken food) towards the nest during food retrieval, after mass recruitment through pheromone trail laying. In the present paper, the important characters of pheromone trail laid by female workers are discussed for implication and connection of complex behavioural pattern of ant foraging.

Pattern of Pheromone trails

Species specific

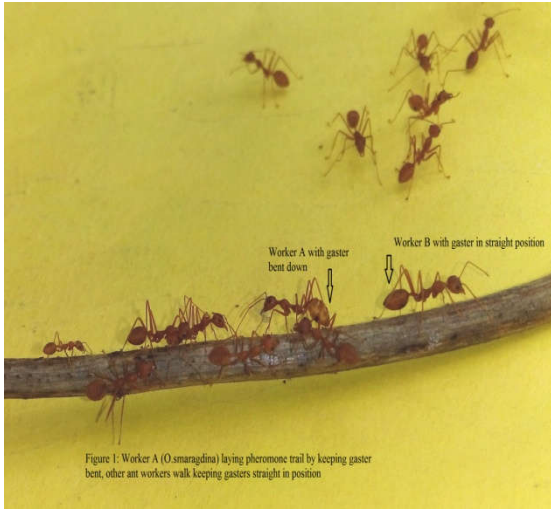
Campos Rda *et al.* (2016) used three nitrogen-containing compounds identified in the pheromone of *A. opaciceps* venom gland secretion to find their effects on pheromone trail laying (PTL). Four different bioassays performed with workers from different castes of *A. opaciceps* suggested that the trail pheromone elicits the trail-following behaviour in conspecifics of all castes, but the foragers respond more strongly to their own pheromone than to that of other castes (gardeners, generalists and soldiers).

Trail pheromones, produced by different exocrine glands, are a key part of ant foraging strategies. Mashaly *et al.* (2011) reported that ant species use branching networks of pheromone trails for orientation between nest and resources. Their study demonstrated that workers of the venomous samsum ant, *Pachycondyla sennaarensis* (Mayr) (Formicidae: Ponerinae), employ recruitment trail pheromones discharged from the Dufour's gland. Secretions of other abdomen complex glands, as well as hindgut gland secretions, did not evoke trail following. The optimum concentration of trail pheromone was found to be 0.1 gland equivalent/40 cm trail. This concentration demonstrated effective longevity for about one hour. Besides they showed that *P. sennaarensis* and *Tapinoma simrothi* each

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respond to the trail pheromones of the other species as well as their own. Among three sizes of workers (small, medium and large), medium workers of *Solenopsis geminata* exhibited a high trail-following behavior as well as a high antennal response to Dufour's gland secretion thereby suggesting that medium-sized workers are specialized in foraging activities (Brindis *et al.* 2008).



Up regulating pheromone trail

Latty *et al.* (2017) found that Argentine ant colonies maximised access to high concentration of feeders by building additional pheromone trails and routes connecting the nest to the feeder. At the same time, it is observed in several instances where new trails appear to have been built to accommodate a surge in demand. In majority of cases, there exists combination of trail building when traffic demand is high and trail pruning when traffic demand is low. Consequently, this happens in a demand-driven network formation system that allows ants to monopolise multiple dynamic resources.

Shorter path selection

Bles *et al.* (2018) found that ants, *Lasius niger* laid a stronger pheromone trail on the straight path for efficient foraging.



Argentine ants (*Linepithema humile*) selected the shorter of two alternative paths from their nest to a food source (von Thienen *et al.* 2015) serving as an important example for

making foraging fast since quicker the food retrieved, safer the food stored in the nest.

Route learning

Route learning is essential for survival of ant foragers which lay pheromone trails, since the presence of a trail may act as an important source of information about whether an error has been made (Czaczkes *et al.* 2016). As previously reported, ants, which make errors on their outward journey, up regulate pheromone deposition on their return. Surprisingly, ants that would go on to make an error down-regulate pheromone deposition on their outward journey, hinting at a capacity for ants to gauge the quality of their own memories.

Czaczke *et al.* (2013) studied *Lasius niger* workers foraging on a doubly bifurcating trail with four end points. Route learning was slower and errors were greater on alternating (e.g. left-right) versus repeating routes (e.g. left-left), with error rates of 32 and 3%, respectively. However, errors on alternating routes decreased by 30% when trail pheromone was present. Trail pheromones also help route learning, leading to lowered errors in following journeys without pheromone. If an experienced worker makes an error when returning to a food source, it reacts by enhancing pheromone deposition on the return journey. As a whole, it is obvious that the role of trail pheromones is associated with sophistication of foraging system of ant colonies, especially in their relationship of route learning and memory within a complex environment.

Synergistic use of pheromone trail and route memories

Ants integrate numerous sources of information to coordinate collective activities of foraging, e.g. use of trail pheromones to guide foragers to food sources, and route memories to locate sources of food. Often, route memories are more precise than trail pheromones in guiding and are frequently followed as first choice when the two conflict. In the ant *Lasius niger*, trail pheromones and route memory act synergistically during foraging; increasing walking speed and straightness by 25% and 30% respectively, and maintaining trail pheromone deposition, but only when used together (Czaczkes *et al.* 2011).

Ant *Lasius niger*, may use trail pheromones (social information) or route memories (private information) or both to make foraging decisions. The combined use of both the information by individuals' results in greater efficiency at the group level than when either information source was used alone (Czaczkes *et al.* 2015). Such a composite collective decision-making system reaps the benefits of both its constituent parts. Thus, ants share information to make adaptive group-level decisions.

Pheromone level and activity speed

Perna *et al.* (2012) found that Argentine ants turned in response to local pheromone concentrations, while their speed was largely unaffected by these concentrations. The ants did not integrate pheromone concentrations over time, with the concentration of pheromone in a 1 cm radius in front of the ant determining the turning angle. The response to pheromone was found to follow a Weber's Law, such that the difference between quantities of pheromone on the two sides of the ant divided by their sum determines the magnitude of the turning angle.

Back and forth travel

Collett and Waxman (2005) showed that while Pharaoh's ants travel along complex pheromone trail systems between their nest and foraging areas, they can work out from the geometry of individual branch points on the trail whether they are heading towards or away from the nest.

Trail polarity

When pheromone trails are used by many ants to guide foragers between nest and food, a laden forager, for example, should walk towards the nest. Polarized trails would enable ants to choose the appropriate direction, thereby saving time and reducing predation risk (Jackson *et al.* 2004). When Pharaoh's ants (*Monomorium pharaonis*) produce elaborate trail networks throughout their foraging environment, by using information from the geometry of trail bifurcations within this network, foragers joining a trail can adaptively reorient themselves if they initially walk in the wrong direction. The frequency of correct reorientations is maximized when the trail bifurcation angle is approximately 60 degrees, as found in natural networks. Thus, ant trails can provide polarity information.

Preferable substrate choice

Bernadou and Fourcassié (2008) reported that in ants *L. niger*, locomotory behaviour differed due to substrate coarseness: ants moved considerably faster and had more sinuous trajectories on a fine than on a coarse substrate. Ants trained on fine sand made significantly more correct choice than those trained on coarse sand. Substrate coarseness may be more important at the collective level, by interacting with the chemical properties of the pheromone trail used in mass recruitment to food source than at the individual level.

Patrollers' direction

In the harvester ant *Pogonomyrmex barbatus*, the patrollers regulate the direction taken by foragers each day by depositing secretions of Dufour's gland onto a sector of the nest mound about 20 cm long and leading to the beginning of a foraging trail. So, the colony's 30-50 patrollers act as gatekeepers for thousands of foragers and choose a foraging direction, but they do not recruit and lead foragers all the way to a food source (Greene and Gordon 2007). It is also found that in the absence of patrollers, most foragers used the direction they had followed on the previous day.

Pheromone for no entry path

Robinson *et al.* (2005) reported that when foragers (Pharaoh's ants, *Monomorium pharaonis*) lay attractive trail pheromones to guide nest mates to food, they lay a 'no entry' signal to mark an unrewarding foraging to repel foragers from unrewarding routes path for effective foraging networks of pheromones.

Complexity of pheromone trail

Vittori *et al.* (2006) reported that ants lay a trail pheromone while moving in the network and simple behavioral rules can lead ants to find the shortest paths in the network; however, pheromone trail was better for nest bound than for outbound ants. Price *et al.* (2016) found that when food quantity is high or low, Pharaoh ant, *Monomorium pharaonis*, laid accordingly either high or low pheromone trail for mass recruitment of foragers.

Mailleux *et al.* (2005) found that among *L. niger* foragers, 14% never participate in the formation of the chemical pathway and never lay a trail over successive trips. Among the others foragers, interindividual differences in the persistence of trail-laying behaviour over successive trips are observed, but do not rely on an individual specialisation, in which some ants would lay a trail more frequently and persistently than other scouts.

Effective period

Hölldobler *et al.* (1990) identified two anatomical sources and duration of trail pheromone effects on ants, *Daceton armigerum*; trails drawn with poison gland contents can last for more than seven days, whereas trails drawn with the newly discovered sterna glands (in the VIth and VIIth abdominal sternites) are effective but relatively short-lived.

Levels of effect

The recruitment pheromone originates in the Dufour's gland and the number of ants responding to a trail varies with pheromone concentration (Adams and Traniello 1981). Attygalle and Morgan (1984) reported that the trail pheromone of the ant *Tetramorium caespitum* L. is a 70:30 mixture of 2,5-dimethylpyrazine and 3-ethyl-2, 5-dimethylpyrazine. The average total amount of the two pyrazines present in the poison vesicle was found to be 3.9 ng per ant, of which 2.7 ± 0.4 ng is 2,5-dimethylpyrazine and 1.15 ± 0.25 ng is 3-ethyl-2,5-dimethylpyrazine. The pyrazines constitute only 0.03% of the volume of the poison vesicle but account for the whole of the trail-following activity. A 70:30 mixture of the respective pyrazines evoked the highest activity in artificial trail-following tests.

Maschwitz and Schonegge (1983) investigated the communication in relation to foraging and nest-moving in North Central Sri Lankan ant, *Leptogenys chinensis*. While foraging, single workers lay a trail. Successful scouts return to the nest and perform recruiting runs. By this means, groups of workers are recruited and led to a feeding place by a scout. The secretion of the Janet gland has a recruiting effect, whereas the venom consists of two compounds: a compound of low volatility responsible for orientation, and a highly volatile compound, which interpret as being a way of estimating the age of the trail.

Attractive and repellent pheromone trails

In Pharaoh's ant colony, both attractive (positive) and repellent (negative) trail pheromones are used (Robinson *et al.* 2008) for foraging. Both the repellent and attractive pheromones have a role in trail choice and that the repellent pheromone prevents random fluctuations with a positive feedback loop causing the colony to concentrate foraging on the unrewarding trail; hence, the repellent pheromone is adaptive, as it increases the robustness and flexibility of the colony's overall foraging response.

Influencing factors

Ants are responsive and reactive to an environmental change. When ants were trained to one feeder location, and the feeder was then moved to a different location and found that ants responded to different situations by strongly upregulating pheromone deposition immediately after experiencing the change (Czaczkes and Heinze 2015). This may help maintain

the colony's foraging flexibility, and allow multiple food locations to be exploited simultaneously.

Czaczkas *et al.* (2012) found that ant, *Lasius niger* uses both trail pheromones and memory of past visits to navigate to and from food sources and a synergistic effect between route memory and trail pheromones: during PTL experienced ants leave less pheromones and uses it for walking straighter and faster in comparison to novice. The ants show multifaceted regulatory mechanisms during foraging and recruitment behaviour that are influenced by multiple interacting factors such as presence of trail pheromone, travel direction, route memory and home-range markings.

Temperature effect

Temperature affects both ant foraging and community structure in Mediterranean habitats and that dominant species often forage at lower temperature than subordinates (van Oudenhove *et al.* 2011). High temperatures (> 30°C) reduce the foraging activity of *T. nigerrimum* independently of every day and seasonal rhythms of the ants and to accelerate pheromone degradation. They highlighted that high temperature effects on recruitment intensity were partly due to pheromone evaporation. In the ant communities, this may influence dominant ants relying on chemical recruitment, more than subordinate ant, to avoid pheromone use and high temperatures and to depend on other means of route memories.

Chemical composition pheromones

In the table 1 are shown the chemical compounds identified in Dufour's gland or poison gland of ant species with use of solid-phase microextraction and gas chromatography with mass spectrometry. When three nitrogen-containing compounds were identified in the poison glands of ant species, predominantly only one specific compound was found to be the most abundant

and the most behaviourally active component namely, methyl 4-methylpyrrole-2-carboxylate in *A. opaciceps* (Campos Rda *et al.* 2016), 3-ethyl-2,5-dimethylpyrazine in *P. barbatus* (Hölldobler *et al.* 2001), methyl 4-methylpyrrole-2-carboxylate in the leafcutting ant, *Acromyrmex octospinosus* (Cross *et al.* 1982) and 2,3-dimethyl-5-(2-methylpropyl) pyrazine in the Madagascar ants (Tentschert *et al.* 2000). But in the Dufour's gland of ant, Blatrix *et al.* (2002) reported that a mixture of the 4-methylgeranyl esters are highly active trail pheromones, while the bishomogeranyl esters are either marginally active or not active at all. Kohl *et al.* (2000) reported that among ten components identified, only methyl 6-methylsalicylate 1 elicited trail following behavior in ant, *Mayriella overbecki* during foraging and nest emigrations.

Cerda *et al.* (2014) revealed that ants use many different chemical compounds to communicate with their nestmates. Of the 168 compounds identified, more than 40% are amines. In the subfamily Myrmicinae, trail pheromones are mostly produced in the venom gland, while in the subfamily Formicinae, they come from the rectal gland. Torres-Contreras *et al.* (2007) proposed that the major compounds in the poison gland were the alkylpyrazines, 2,5-dimethylpyrazine, 2,3,5-trimethylpyrazine, and 3-ethyl-2,5-dimethylpyrazine and the Dufour's gland contained five alkanes, from tridecane to heptadecane, with pentadecane being most abundant. Tullio *et al.* (2003) detected farnesol as a minor component of Dufour's gland of workers of *Messor capitatus*. The trail pheromone of *Acromyrmex subterraneus subterraneus* consists simply of the heterocyclic ester methyl 4-methylpyrrole-2-carboxylate in the venom reservoir of workers at about 1.2 ng/ant (Do Nascimento *et al.* 1994). In behavioral bioassays, poison gland extracts and the mixture of pyrazines produced a trail pheromone effect, whereas the Dufour's gland extracts and the alkanes had no effect on ant locomotion.

Table 1 Showing chemical compounds identified in both poison and Dufour's glands of various ant species

SN	Ant species	Chemical composition	Gland	Use	References
1	<i>A. opaciceps</i>	2,5-dimethylpyrazine, 3-ethyl-2,5-dimethylpyrazine & methyl 4-methylpyrrole-2-carboxylate (M4MPC)	Poison gland	PTL	Campos Rda <i>et al.</i> (2016)
2	<i>Acromyrmex subterraneus subterraneus</i>	ester methyl 4-methylpyrrole-2-carboxylate	Poison gland	PTL	Do Nascimento <i>et al.</i> (1994)
3	<i>Mayriella overbecki</i>	methyl 6-methylsalicylate 1		PTL	Kohl <i>et al.</i> (2000)
4	<i>Eutetramorium mocquerysi</i>	2,3-dimethyl-5-(2-methylpropyl)pyrazine(DMPP)	Poison gland	PTL by only DMPP	Tentschert <i>et al.</i> (2000)
5	<i>P. barbatus</i> , <i>P. maricopa</i> , <i>P. occidentalis</i> & <i>P. Rugosus</i>	1, 2,3-dimethyl-5-(3-methyl-butyl) pyrazine 3, 2,3-dimethyl-5-(2-methylbutyl) pyrazine 4 3 pyrazines [trimethylpyrazine (TDMP), 2,5-dimethyl pyrazine (DMP), & 3-ethyl-2,5-dimethylpyrazine (EDMP)]	Poison gland	PTL by only EDMP	Hölldobler <i>et al.</i> (2001)
6	<i>Gnamptogenys striatula</i>	esters of (2E)-3,4,7-trimethyl-2,6-octadien-1-ol (4-methylgeraniol), and (2E)-3,4,7-trimethyl-2,6-nonadien-1-ol	Dufour's gland	PTL	Blatrix <i>et al.</i> (2002)
7	<i>Messor capitatus</i>	<i>Farnesol</i>	Dufour's Gland		Tullio <i>et al.</i> (2003)
8	<i>Pogonomyrmex vermiculatus</i>	alkylpyrazines, 2,5-dimethylpyrazine, 2,3,5-trimethylpyrazine, and 3-ethyl-2,5-dimethylpyrazine	Poison gland	PTL by extracts & pyrazines mixture	Torres-Contreras <i>et al.</i> (2007)
9	<i>Myrmica</i> sp.	alkanes, from tridecane to heptadecane, with pentadecane being most abundant.	Dufour's gland	extracts and the alkanes had no effect	
10	<i>Tetramorium caespitum</i> L.	3-ethyl-2,5-dimethylpyrazine	Poison gland	Not reported	Jackson <i>et al.</i> (1991)
11	<i>Solenopsis fugax</i> & <i>M. pharaonis</i>	a 70:30 mixture of 2,5-dimethylpyrazine and 3-ethyl-2, 5-dimethylpyrazine.	Poison gland	PTL	Attygalle and Morgan (1984)
12	<i>Acromyrmex octospinosus</i>	Not reported	Dufour's gland	PTL	Hölldobler (1973)
		methyl 4-methylpyrrole-2-carboxylate (I)	Not reported	PTL	Cross <i>et al.</i> 1982

Note: PTL-pheromone trail laying,

Structure of pheromone gland

Workers of the ant *Cylindromyrmex whymeri* exhibit mass recruitment through trail pheromone originating from a unique gland between abdominal sternites 6 and 7 (Gobin *et al.* 2001). Gland has secretory cells, duct cell widening to form a sclerotized pear-shaped reservoir chamber, lined with multiple duct cells. Each duct thus forms a miniature reservoir for secretions of each cell.

Structure-function relationship of olfaction

Zube *et al.* (2008) studied the relationship of structure-function for processing pheromonal and general odours within an ant's central olfactory system in the carpenter ant, *Camponotus floridanus* and reported that the antennal lobe (AL) contains up to approximately 460 olfactory glomeruli organized in seven distinct clusters innervated via seven antennal sensory tracts. The AL is divided into two hemispheres regarding innervation of glomeruli by either projection neurons (PNs) with axons leaving via the medial (M) or lateral (L) antenna-cerebral tract (ACT). M- and L-ACT PNs differ in their target areas in the mushroom-body calyx and lateral horn. Three additional ACTs project to the lateral protocerebrum only. They added that odour processing in AL glomeruli by retrograde loading of PNs with Fura-2 dextran and fluorimetric calcium imaging. Odour responses are reproducible and comparable across individuals. Calcium responses to pheromonal and nonpheromonal odours were very sensitive and patterns were partly overlapping, indicating that processing of both odour classes is not spatially segregated within the AL. The structure-function analyses contribute new insights into important aspects of odour processing in a highly advanced insect olfactory system.

Macroglomerulus

Ants have a well-developed olfactory system needed for chemical pheromone communication. Primary olfactory centers (antennal lobes, ALs) in the brain of large workers contain a substantially enlarged glomerulus (macroglomerulus, MG) at the entrance of the antennal nerve (Kleineidam *et al.* 2004). The location of the MG is laterally reversed in the two species (*Atta vollenweideri*, *A. sexdens*), and workers of different size express a disproportional allometry of glomerular volumes. While ALs of large workers contain an MG, glomeruli in small workers are all similar in size. The species specific MG location in large workers provide correlative evidence that the MG may be involved in the detection of the trail pheromone.

Utilities

Foraging and nest migration

The natural habitats of ants are highly complex with heavy competition for food resources, hence fast and cooperative retrieval required for safe food storage, which could be achieved through effective pheromone communication among nest mates. Besides pheromone trail being used for foraging, it is also used by pheromone trail laying as a trail route between old nest to new nest to achieve collective participation of workers for shifting nest from one place to other. Since *G. striatula* generally preys on small arthropods rather than monopolizing large resources, it is assumed that trails are rarely used during foraging, but more often during nest migration for

new food source exploitation at different places (Blatrix *et al.* 2002).

Territorial defence

Adams (1994) reported that *Azteca trigona* maintains its territory and when the ant foragers detect workers of other species (*A. velox*, *A. instabilis*) in its territory, they organize an alarm recruitment using trail pheromone secreted by the Pavan's gland. Minor workers of the Myrmicine, *Pheidole dentata* also use odour trails to recruit major workers ("soldiers") to the vicinity of intruders (Wilson 1975). But further studies are required to find the association between pheromones used for foraging and territorial defence.

Workers of the African weaver ant, *Oecophylla longinoda* recruit nest mates to previously unoccupied space by means of odour trails laid from the rectal gland, a muscled organ located at the rear of the rectal sac (Hölldobler and Wilson 1977). When enemy ants and other intruders are encountered on the territory, the ants assemble nest mates into small resting clusters by dispensing an attractant-arrestant pheromone from the sternal gland, a second newly discovered organ located on the last abdominal sternite. Under prolonged stress, additional forces are recruited to the combat area with the aid of the rectal-gland trail substance.

Dufour's gland and venom gland of ants

Hölldobler (1973) reported that ant species, *Solenopsis fugax* a subterranean ant, lay odorous trails to the brood chambers of neighbouring ant species. The recruitment trail pheromone originates from the Dufour's gland. Similar chemical foraging pheromones discharged from Dufour's gland are used by another ant, *Monomorium pharaonis* for foragers' recruitment. In ants several glands are identified viz., poison gland, Dufour's gland, rectal gland, Pavan's gland etc. and are related to their use in pheromone trail laying required for direct route paving between two places (nest to work site or food site) and for travel of mass female workers. When the jobs with cooperative nature are many, like foraging, territorial defence, nest migration, a single common aspect is that pheromone trail is laid to make a direct route from nest to work site and to recruit the workers in mass. The studies explaining about association between different glands and their activities of pheromone trail laying are very meagre. Duncan and Crewe (1994) revealed that ants, (*Leptogenys nitida*) follow pygidial gland extracts with poison gland extract eliciting a limited response during cooperative retrieval.

Lack of trail pheromone

Although Cataglyphis species lack a trail pheromone system, *Cataglyphis fortis* employs olfactory cues for detecting nest and food sites (Stieb *et al.* 2011). Amorim (2015) showed that especially spontaneous pheromone trail laid, facilitated efficient removal of food sources resulting in foraging and that trail formation is correlated with efficient food removal, Choi *et al.* (2012) reported that trail pheromone biosynthesis in the Dufour's gland of the fire ant, *Solenopsis invicta*, is regulated by a neurohormone, pheromone biosynthesis activating neuropeptide. Thus, extensive behavioural activities of foraging associated with pheromone trail are reported in a few ant species, thereby implying well developed and advanced

behavioural and structural adaptation for competitive conditions of environment and evolutionary significance.

CONCLUSIONS

Ants of different species lay pheromone trail for mass recruitment of scouts during food retrieval that is to be achieved quickly in an intensively competitive habitat and the successful foragers are the opportunistic workers to exploit food resource of time and space in cooperative manner. The poison gland is the main gland for the secretion containing 3 nitrogen compounds of pheromone trail used by the forager for route learning which facilitates for easy and quick retrieval of heavy food. Pheromone trails used for foraging have positive features, like polarity and influenced by factors namely temperature, food quantity and competitors. Though pheromone trails are laid for nest migration, its utilities for other purpose of territorial defence is to be further substantiated.

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