

CHAPTER 4

INTERSPECIFIC COMPETITION

Interspecific competition through resource exploitation or interference has been thought to affect the population of competing species and to influence community structure (Begon et al. 1990, Tanseley 1917, Gause 1934). Much work has been done to look at the effects of interspecific competition but its role in shaping communities is still not definite (Begon et al. 1990). Community organization in ants has often been considered to be governed by interspecific competition. A number of studies have demonstrated the evidence for intense exploitative competition among coexisting species of ants and partitioning of resource between competing species has often been documented. Similarly, interference competition has also been demonstrated to be intense among ants. Presence of linear competition hierarchy has also been demonstrated often. This undeniable importance of interspecific competition in structuring communities of ants is noteworthy in the current climate of doubts that has been raised in the recent times regarding the importance of interspecific competition in animal communities (Andersen 1990 b).

The present study attempted to answer the following questions directed at assessing the importance and process of interspecific competition in organizing the ground foraging ant community in a tropical evergreen forest habitat :

1. Whether the community is structured into a competition hierarchy?
2. How does interference by the top species in the hierarchy regulate the activities of other species at momentary food source.
3. How do the different species that compete at bait overlap in utilizing food resources?

4. How are the nests of different species located with respect to each other and whether it is possible to infer interspecific competition from the nest dispersion patterns?

I have first identified the competition hierarchy following Schoener (1983)' scheme and then attempted to answer the above mentioned questions by looking into the interspecific interactions among the species which are representative of the different levels in the competition hierarchy. The hierarchy includes 1) territorial species 2) encounterer species and 3) submissive species. Evidences were sought from the observations on the behaviours of different species at baits, utilization of foods by these species and the nest dispersion of different species in the study area. Nine species that occurred regularly at the bait were subjected to analysis.

Background Information:

a) The Role of Interspecific Competition in Organizing the Community.

The role of interspecific competition in shaping the community has recently come under intensive criticism. Many of the patterns described and explained as result of interspecific competition has been argued as due to random effects (Strong et al. 1979, Connor and Simberloff 1979) and often more importance has been attached to non-equilibrium and stochastic factors (Gee and Giller 1987, Kikkawa and Anderson 1986, Begon et al. 1990). The role of interspecific competition in community organization has been downplayed compared with factors like predation, parasitism and physical factors (Connell 1980, Lawton and Strong 1981, Strong et al. 1984). The basic premise of interspecific competition is resource limitation, and there are many situations where predation, parasitism or frequent natural disturbances

hold down the population densities, so that resources are not limited and interspecific competition may not play any role in organizing the community.

The conventional approach of assessing the role of competition has been to test the basic predictions made from the competition theory. The major predictions of the competition theory as summarised in Begon et al. (1990) are as follows:

1. Potential competitors that coexist in a community should, at the very least exhibit niche differentiation.
2. The niche differentiation will often manifest itself as morphological differentiation.
3. Within any community, potential competitors occupying similar niche should be unlikely to coexist.

Over decades, these predictions have been tested intensively through field experiments in various habitats; sometimes between pairs of species or sometimes taking more than one species into consideration. Schoener (1983), Connell (1983) have extensively reviewed these field experiments. Schoener started his review by arguing that the " results of some of the field experiments are in fact responsible for the competition's present beleaguered state." Analysis of studies known till 1982 showed that in 90% of the studies interspecific competition was detected. Underwood (1986), on the other hand analysing 95 articles on the field experiments on interspecific competition concluded that while interspecific competition is undoubtedly important as an organizing factor in structuring the community, the "prevalence of interspecific competition is not as well understood as suggested by the large number of experimental papers currently available in literature."

Comparison of null models with the real patterns in the natural communities has often been used to assess the importance of interspecific competition. While in an important study on resource partitioning in 10 North American lizard communities, use of null model has conclusively proved the

presence of interspecific competition (Lawlor 1980); Connor and Simberloff (1979)'s reanalysis of Diamond (1975)'s data on complementary distribution of morphologically similar species in an archipelago showed that the patterns in the island bird communities are not significantly different from the random distribution that may be predicted from the null model. Although at a later stage the extent to which null models were really stochastic was questioned, the attempts to study the role of interspecific competition using null models and the intense arguments that it triggered has cast a cloud of confusion over the whole topic.

b) Mechanism of competition.

Interspecific competition operates both directly and indirectly. *Exploitative* competition has been described as indirect interaction whereas *interference* competition is seen as a direct competitive mechanism. (Schoener 1983, Strauss 1991). Which is the mechanism through which competition operates? Strauss (1991)'s review on the indirect effects in community ecology suggest that resource exploitation rather than direct interference is the mechanism behind competition. There has been conflicting views regarding the relative roles of these two competitive mechanisms. Ambiguities were detected with regards to the nature of the resource being competed for as in some cases both exploitative and interference competition seem to be the likely mechanism eg. competition for space (Schoener 1983). Schoener's further classification of the competitive mechanism into six categories was an attempt to remove these ambiguities. These mechanisms are 1) consumptive, 2) pre-emptive, 3) overgrowth, 4) chemical, 5) territorial and 6) encounter competition. He describes consumptive competition to be the clear case of exploitative competition and pre-emptive competition as a mechanism closer to exploitation. He described chemical, territorial and encounter competition to be interference mechanism. He classified overgrowth competition also as a form of interference competition. As apparent from his review of existing literature on the mechanism of competition, the mechanism differ from taxon to taxon and from habitat to habitat. Fellers (1987) also opines that the

effective mechanism is taxon specific. However, there are not enough studies assessing the relative roles of exploitation and interference mechanism as apparent from the review by Schoener (1983). Fellers (1987) also opines the same.

c) *Niche overlap measures and its use to detect competition.*

Correlating the degree of overlap in resource use with the intensity of competition has been a common practice in studies on interspecific competition. With a number of niche overlap measures presently available, the first attempt to measure niche overlap and equate that with the intensity of competition was made by Levins (1968). This measure represented by $a_{12} = \sum p_{1j} p_{2j} / \sum p_{1j}^2$ eqn.(1), p_{1j} = fraction of total resource use by species 1 from resource j and p_{2j} = fraction of total resource use by species 2 from resource j, reflects the degree of overlap of one species' resource utilization curve with that of another species and is one of the most popular measure. The reason for its popularity is because of its close relation with the competition co-efficients as formulated by Lotka-Volterra equation of interspecific competition (Schoener 1974, Lawlor 1980). But arguments have been raised on the ground that great ecological overlap need not indicate great intensity of competition (Colwell and Futuyama 1971, Vandermeer 1972). Lawlor (1980) however points out that the measure of niche overlap may be the first approximation for competition coefficient, as measurement of competition co-efficient in nature is extremely difficult and rarely done. One of the main argument against this measure was that it does not take the effect of resource abundance into consideration while availability of resource definitely affects the utilization by the consumers (Schoener 1974 a, Hurlbert 1978, Hanski 1978). Lawlor (1980) explains how the overlap measure between two species might vary depending on the difference in resource abundance in two different environments.

A more complicated derivation of equation (1) by McArthur (1968) and elaborated by Schoener (1974b) and Abrams (1980) is represented by ,

$$a_{12} = \sum (K_j/r_j) w_j a_{1j} a_{2j} / \sum (K_j/r_j) w_j a_{1j} \dots \text{eqn.(2)},$$

K_j = carrying capacity of resource,

r_j = intrinsic growth rate of resource,

a_{1j} = electivity of consumer i on resource j,

w_j = Relative value of resource j.

This equation assumes that, consumers encounter resource types according to their proportion in the system. Schoener (1983) cautioned that regardless of the popularity of eqn.(1) the use of this measure may be too simplistic and researchers need to ensure that adequate formula is being tested and commented that although, this assumption may be violated with regards to macrohabitat overlap, it will stand valid for microhabitat or food type overlap and this derivation can successfully extrapolate strength of competition from overlap measures. Overlap measures can be broadly categorised as asymmetric and symmetric measures. A symmetric measure calculates the overlap of species 1 on species 2 to be equivalent of the overlap of species 2 on species 1. An asymmetric measure can assess the differential overlap of one species on the other. Slobodchikoff and Schulz (1980) reviewing various measures of niche overlap concluded that, a better measure of niche overlap is an asymmetric measure eg. Levins' equation.

A number of field experiments have shown that the strength of competition increases with increase in microhabitat or food overlap (Schoener 1983). Schoener (1983) comments that these findings are consistent with eqn.(2) and that the applicability of the overlap measure as indicator for the strength of competition will depend much on the 1) nature of the resource for which overlap is being measured and 2) assumption made for a particular derivation for overlap.

Hurlbert (1978) derived an equation to measure niche overlap weighing it by the availability of resource. Petriatis (1979) criticizing that the measures in use cannot be tested directly, derived a likelihood measure of specific overlap which is equivalent to Levins' measure. This equation assumes that

specific overlap by species 1 onto species 2 is the probability that species 1's utilization curve could have been drawn from species 2's utilization curve and the amount of specific overlap by species 1 onto species 2 is the probability that species 1's utilization curve could have been drawn from species 2's utilization curve. This equation is represented as,

$$E_{12} = \sum(p_{1j} \ln p_{2j}) - \sum(p_{1j} \ln p_{1j}) \dots(3) \text{ and,}$$

$$E_{21} = \sum(p_{2j} \ln p_{1j}) - \sum(p_{2j} \ln p_{2j}) \dots(4).$$

Petriatis (1979) suggested a chi square test to measure the significance of these overlaps.

Evidences of Interspecific Interaction in Ants

Holldobler and Wilson (1990) opined that ants have all the traits expected to generate interspecific competition. They concluded interspecific competition to be the most ubiquitous phenomenon in ant community based on the following four major lines of evidences :

1. Local communities of ant species often show divergence with reference to body size, food type, or weight of food item.
2. Nest sites and foraging columns of the same or closely related species are overdispersed.
3. Experimental removal of the colonies of one species causes increased growth in the colonies of other species in the locality.
4. Displacement of individual foragers or colonies by other foragers or colonies is commonly observed (Holldobler and Wilson 1990).

As suggested by Holldobler and Wilson (1990) resource partitioning in ants has been demonstrated in a number of studies. Not surprisingly hence, ants have often been taken as model organisms for the documentation of interspecific competition (Torres 1984a, b, Culver 1974, Levins et al. 1973, Davidson 1977 a, b)

Exploitative competition :

Morphological divergence : Coexisting competing species are expected to show divergence in their mode of utilizing limiting resource eg. food and nesting sites. These may be reflected in their morphological traits. There are ample evidences for these in the communities of ants. Chew and Chew (1980) demonstrated it in a woodland ant community. Ants belonging to the same guild had maximum difference in body size, while ants of different guilds had the minimum. This was supported by Whitford (1978) in Southern Mexican granivore and omnivorous ant guilds and Chew and De Vita (1980) in Arizona desert granivore and insectivore ant guild. Wilson (1955) showed that whenever *Lasius flavus* is found in sympatry with *L. nearcticus* another closely related congeneric, the two species can be distinguished by at least five different morphological characters.

Divergence in foraging activity : Resource partitioning through divergence in foraging activity has been demonstrated in several cases. Bernstein (1974) showed that two dominant seed eating ants in Mojave desert forage at two different surface temperatures i.e. at two different times of the day. Delage - Darchen (1971) showed two coexisting species of *Crematogaster* in Ivory-Coast to partition their nesting space by one of the species nesting in the canopy and the other near ground. Plowman (1981) in a study involving two New Guinea rain forest ant species showed spatial separation in activity and divergence in food resource utilization. Torres (1984b) showed that different species of ants were active at different layers of the litter in the Puerto Rican upland tropical forest. Through field studies and laboratory experiments, he also demonstrated that ant activities were greatly influenced by temperature in all the habitats he studied i.e. grass land, forest, and agricultural land. Species that tolerated high temperature did not tolerate low temperature as well. However he cautioned that activity separation with regards to temperature should not be taken seriously into consideration as most forest species were predominantly nocturnal and high temperatures are rarely experienced in forest. He also suggested that some species in the community possibly have coexisted quite by random chance. Cerda and Retana (1990)

found partitioning of foraging time among three species of *Camponotus* in savanna like grass land of Spain.

Divergence in foraging schedule has also been observed. Bernstein (1979) in her study on the Mojave desert ants showed that foraging temperature range of species utilizing similar food are not similar for coexisting species. Holldobler (1986) reported diel activity separation between *Iridomyrmex purpureus* and *Camponotus consobrinus* who feed on the same homopteran aggregation but at different times of the day. Swain (1977) observed the same between Costa Rican Dolichoderine ant *Monacis bispinosa* and a Formicine species of the genus *Camponotus*. Levins et al. (1973) observed that shaded food baits are dominated by *Pheidole megacephala* while when the same baits are flooded with sunlight they are taken over by *Brachymyrmex heeri*. Hunt (1974) observed coexistence through diel activity separation between two species of ants in Chile.

Divergence in food choice: Torres (1984a) studying coexistence in Puerto Rican ant communities in upland tropical forest, grass land, and agricultural lands found separation of niche in terms of food size, foraging space and diel activity pattern. He was able to characterise the communities into four functional groups based on their food type choices. Resource partitioning through utilization of food resources of different sizes has been demonstrated by Davidson (1985). Davidson (1977b) found specialization of different species in exploiting foods of different densities. In south western Arizona desert, trail foragers specialize on high densities of food while individual foragers specialize on low densities of food. Hansen (1978) found the body size and size of seeds collected by different species to be closely correlated.

Field experiments showing competitive release : As apparent from the excellent review by Holldobler and Wilson (1990) experimental manipulations have provided ample evidences for interspecific competition in ants. In an important experiment Cole (1983) introduced colonies of two species of ants in separate empty islets (approximately 12 sq. m area) in

Florida Key and found them to persist. But when the same two species were introduced in islets having any of the two species already existing, the population of the introduced species declined. Davidson (1985) experimentally showed competition among three coexisting desert ants species with overlapping food size range. Food ranges overlap between *Pogonomyrmex rugosus* and *P. desertorum* and between *P. desertorum* and *Pheidole xerophila* where *P. rugosus* has competitive impact on *P. desertorum*. *Pheidole xerophila* population declined when she removed the colonies of *P. rugosus*. Lynch et al. (1980) showed that removal of one of the two competing species from the baits increased the abundance of the other species. Kuglar (1984) showed that removal of one species (*Ectatomma ruidum*) increased the foraging area of the competing species *Pogonomyrmex mayri*. In another experimental studies by Rosengren (1986) competition was demonstrated among three species of ants in Finland. *Formica truncorum* competes with *Lasius niger* while *L. niger* competes with *L. flavus*. When *F. truncorum* was introduced in an island off Finland coast already occupied by *L. niger* and *L. flavus*, the population of *L. niger* declined but *L. flavus* population increased (Holldobler and Wilson 1990).

However, not many workers have investigated the mode of resource partitioning in tropical rain forest ant community as apparent from the above review and this remains almost an open area of research.

Interference competition:

Interference competition has been shown conclusively many times in ants. Such interactions could be through use of chemical repellants (Adams and Traniello 1981; Holldobler 1982), agnostic interactions at territorial boundaries (Holldobler and Lumsden 1980; Levings and Traniello 1981) and food robbing (Holldobler 1986). As put by Holldobler and Wilson (1990) 'Ant wars' are a common place among species with large colonies.

Fellers (1987) evaluated the effects of interference and exploitative competition on the foraging behaviour of nine species of ants in a woodlot.

These species overlapped significantly in the size and type of prey. He classified four species as dominant species by looking at their aggressive interactions at the bait. He found an inverse correlation between the exploitative and interference ability as the submissive species maximized their resource utilization efficiency by faster recruitment at the food item but their feeding time was reduced in the presence of a dominant species.

De Vita (1979) showed interference competition among different colonies of desert seed harvester ant *Pogonomyrmex* sp. He also measured the amount of aggression in the Mojave desert ants and calculated the cost of interference competition to be 0.06 death per ant foraging hour in this community (De vita 1979).

In another study on the ant communities of some Finnish Baltic islands Vepsalainen and Savolainen (1990) showed that the submissive species *Myrmica* sp. partition their foraging time from the other territorial and encounterer species in the community. This study showed that despite interference and reduced foraging success on the bait *Myrmica* sp. were able to coexist with most aggressive ant species. The foraging activity of *Myrmica* sp. was affected by the territorial species but not by the other non-territorial but aggressive species.

Cole (1983) showed from a study on the mangrove ant community that two primary (first invaders on the island) and dominant species when present in an island of less than 5 cubic meter, precluded the invasion by any other species. Workers of the two dominant species were always aggressive towards other submissive species. After removal of the dominants the submissives could invade the islands.

The submissive ant *Zacryptoceros maculaus* can not only coexist with the dominant species, they use the pheromone trails laid by *Azteca trigona* a territorial species for discovering new source of food. Their 'stealthy' nature and heavy body armour protect them from the territorials (Adams 1990). The

'meat ant' *Iridomyrmex* sp. was shown to be the topmost species in Australian ant community dominance hierarchy (Greenslade 1979, Greenslade and Halliday 1983).

Many species of ants are known to maintain exclusive territories. Territorial fights leading to mosaic distribution of coexisting territorial species have been demonstrated by a number of authors (Majer 1976a, Jackson 1984).

Vepsalainen and Pisarski (1982) reported *Formica polyctena* to directly destroy colonies of *Lasius*, *Myrmica* and *F. fusca* of food.

There are a number of instances where native species have given way to another invading species, sometimes to introduced species as well, where the invading species have been observed to take over through direct interference with the native species. Holldobler and Wilson (1990) has given several accounts of this phenomenon. *Pheidole megacephala* an introduced species in Hawaii totally destroyed the native species. Similar phenomenon has been observed in Southern part of North America with introduced fire ant *Solenopsis invicta* and *Iridomyrmex humilis*. *I. humilis* has been seen to eliminate all the workers from an *S. geminata* nest. Higashi and Yamauchi (1979) showed a 'supercolonial ant' *F. yessensis* virtually eliminating other species of ants through a combination of warfare and local population saturation. Another unique example is *Wasmannia auropunctata*, an introduced ant in the Santa Cruz island in the Galapagos drastically reducing or even extinguishing the populations of other ant species through interference including two endemics of Galapagos from almost half of the island (Clark et al., 1982). The list of such takeover by dominant or invader species is nonetheless short (see Holldobler and Wilson 1990).

Interference through stealing the brood of another species is observed with European thief ant *Solenopsis fugan* which leaves close to colonies of other species and steal the brood of the other species by burrowing into it's

colony. They also release a chemical repellent while invading the colony (Holldobler and Wilson 1990).

Interference by nest plugging has been reported in a number of cases. One of the most striking example is probably *Choanomyrma bicolor* who picks up pebbles or some other material and drops them down the nest entrances of the competing species *Myrmecocystus* sp. (Moglich and Alpert 1979). *Myrmecocystus clepilis* are known to block the nest entrances of the colonies of *Forelius pruniosus*. *M. clepilis* has also been seen to exclude *F. pruniosus* from bait (Holldobler and Wilson 1990). Gordon (1988) reported *Aphenogaster cockrelli* to block the nests of *Pogonomyrmex barbatus* and thereby reducing the later's foraging period by 1 to 3 hours. Samways (1983) reported interference on other species by a south African ant *Myrmicaria natalensis* through soil dumping over the nests of other species during nest construction.

Spatial dispersion of colonies.

Ryti and Case (1992) addressed the following two questions on spatial distribution with regards to the strength of competition and population densities of coexisting species:

1. How does the relative strength of interspecific competition affect the inter-specific nest spacing and,
2. Whether nest spacing is dependent on the population density.

They arrived at the following conclusions from a simulation study :

1. Colonies are spaced closer to conspecifics when interspecific competition is strong and interspecific nest spacing need not be random in the case of weak interspecific competition.
2. Density dependent spacing is observed where established colonies interfere with the establishment of young colonies; as at low population density established nests will have marginal effect on nest establishment. Random spacing of nests is predicted for low density sites or for any community

where interactions between established colonies are stronger than the effects of colonies on nest establishment.

Overdispersion has been commonly seen as an indirect effect of competition. This measure has been of use among the plant ecologists since long. Levings and Franks (1982) used this measure to examine the presence of interspecific competition among ant colonies. What could be the reason for overdispersion? Most plausible reason is the mutual aversion of colonies from their nearest neighbour colony, either conspecific or of different species. Territoriality from a dominant species in the community can cause overdispersion. It can also arise through '*pre-emption*', where the first established colony would annihilate the foundress of other colony (Hollidobler and Wilson 1990).

Attempts to assess the occurrence and extent of interspecific competition through studying the spatial distribution of different species with respect to each other has been a common place for sessile organisms like plants and some marine invertebrates. Ant communities have also been subjected to such spatial distribution analysis because of the sessile nature of their colonies and evidence for interspecific competition has often been sought from such analysis (Levings and Traniello 1981).

Three types of dispersion patterns has been categorised to occur in nature, 1) random, 2) overdispersion or regular and 3) clumped or aggregated. Regular dispersion is generally viewed as evidence for interspecific competition as it is argued that regular dispersion can occur as a result of mutual avoidance of neighbours from each other. Analysis of *intraspecific* nest spacing is common literature. Levings and Traniello (1981) in an excellent review summarized the dispersion patterns among the conspecifics of 136 species of ants from 160 published studies. They found regular nest arrangement to be prevalent among most of the species and concluded this to be a natural outcome of high overlap in food utilization in many species. The focus of Levings and Traniello's review was more on the

intraspecific nest arrangement and as Ryti and Case (1992) pointed out, the role of interspecific competition on nest dispersion pattern has not been reviewed extensively enough although evidence for interspecific overdispersion of ant nests appeared in the literature (Majer 1972, Levings and Franks 1982). Bernstein and Gobbel (1979) found conspecific nest overdispersion in 2 desert habitats. When they considered species pairwise colony positions, only 10 species pairs out of 557 species pairs showed evidence for interspecific nest overdispersion. Doncaster (1981) reported that in an island off South Wales nests of 5 common species of ants are aggregated. Nests were aggregated at favourable nesting sites and he concluded that the density and dispersion of nests are broadly determined by the pattern of habitats and distribution of resources. Herbers (1989) found evidence for interspecific aggregation of colonies in two temperate ant communities and concluded that nests are aggregated at suitable microsites. Gallé (1990) found random nest dispersion in a community of sand dune ants in Hungary and concluded weak interference competition in this community.

Levings and Franks (1982) showed that 15 ground ant species in a central American forest showed significant overdispersion with respect to each other. They concluded that this was because of killing of the foundress queen by workers of another species.

Interspecific competition and community organization.

A number of studies are available showing linear or almost linear competition hierarchies in the ant communities. Detailed studies on the presence of dominance hierarchy are common in literature (Kaczmarek 1953, Marikovski 1962, Yasuno 1963, 1965, Brian 1965, 1983, Dlusski 1965, Wilson 1971, Levings and Traniello 1981, Vepsäläinen and Pisarski 1982, Savolainen and Vepsäläinen 1988).

In an important study with regards to the precise role of interspecific competition in organizing the community, Savolainen and Vepsäläinen (1988) showed through a series of bait experiments that following the dominance

hierarchy based on interference competition, it is possible to predict the structure of the species assemblage. According to them a dominant species takes the role of organizing the community. They showed that the territorials and the encounterers could not coexist. Submissives behave recessively and may coexist with stronger species but their (submissive species) forager numbers and nest densities should decrease. They also predicted the nesting pattern of different species based on the dominance hierarchy. Nests of the territorials were far apart from the encounterers. They found that pressure from stronger species (territorials and encounterers) caused the submissive species to shift to less nutritious food. Gallé (1990) demonstrated linear competition hierarchies in two communities of sand dune ants in Hungary.

Greenslade developed a classification of the Australian ants into six functional groups based solely on the habitat requirement and competitive interactions through studies in the southern Australian arid zone (Greenslade 1978, Greenslade and Halliday 1983). Lately, this has provided a fundamental framework for the studies on Australian ant communities and has been applied extensively (Andersen 1986 a, b, Andersen and McKaige 1987, Greenslade and Thompson 1981). The functional groups are , 1) dominant species (one that is both abundant and capable of exerting strong influence on other species (Greenslade 1976); 2) subordinate species (species that successfully co-occur with dominant species but are inferior competitors and never attain the dominant status); 3) climate specialist (species that are restricted to hot and cold climates respectively; 4) cryptic species (species that forage predominantly within litter and soil rather than on the open ground); 5) opportunist (species having generalized habits, omnivorous diet, flexible foraging time, poor competitive ability and abundant in disturbed habitats); 6) generalized myrmicinae (ubiquitous species abundant all over Australia). Andersen (1992) experimentally showed the role of the 'dominant species' (according to Greenslade's functional group classification) of *Iridomyrmex* and *Oecophylla* in regulating the momentary diversity in Australian ants. He observed that interference competition from the dominant species regulates

the total number of nondominant ants, species richness and species diversity of ants foraging at rich food resource in a manner following the 'humped diversity model' applicable to plants and sessile organisms which according to him indicates suppression of the foraging abundances and diversity of other species under climatically favourable conditions.

METHODOLOGY

Resource Utilization : Food items were collected during 1990 and 1991, from the representative species belonging to different levels of the competition hierarchy according to Schoener (1983)'s scheme, whose interference interactions were also monitored at the bait (*vide* next section). These species are: *Oecophylla smaragdina* (territorial), *Pheidole* sp.1, *Tetramorium tortuosum* (encounterer), *Crematogaster* sp., *Tetramorium* sp. 2, *Camponotus compressus*, *Aphenogaster beccarii*, *Monomorium* sp.1 and *Phedologiton* sp. (submissive). All the collections were made during three dry seasons (January through early May). Food items were collected from five nests per species and twenty foragers per nests, i.e. from 100 individuals for each species. Size of each food item was measured and identified. Doubtful food items were measured and preserved in 70% alcohol for later identification. Petriatis (1979)'s asymmetric equation for calculating resource overlap was used to calculate overlap in utilization of foods among different species.

Interspecific Interactions at Baits : Activities of different species were measured by placing baits within 0.5 X 0.5m square frames (bait quadrats) 1) placed randomly at 8 points during 1990 and 1991, 2) placed at 15 points along four transects 100 m apart during 1993. Minimum distance between any two bait stations was atleast 100 m. The study was conducted during the dry seasons of 1990 (February through April), 1991 (February through early May) and 1993 (March). Honey solution and dried fish were used as baits.

Quantity of the bait items were kept constant and were replenished as and when necessary. Activities of different species at a bait were monitored at hourly intervals. Duration of each experiment was five minutes and this was conducted through the day. Behavioural interactions among the species present on the bait were recorded within each five minute observation session. Frequencies of the various aggressive behaviours were then calculated. 'Attack' and 'Chase' were considered active aggression. 'Indirect threat' in the form of 'Avoidance' is described as when one species changes its path when faced with an aggressive species. An individual would 'Attack' another by biting the later's antennae or mandible. Often an individual 'Chased' another from the bait eliciting escape by the later.

Nest Dispersion : Nests of the ground foraging ant species were located and mapped in fifteen plots of equal size (10 m x 10 m). Five plots were laid randomly during 1990. During 1993, 10 plots were laid in four transects 100 m apart. Minimum distance between two plots along a transect was atleast 250 m. Each plot was subdivided and the corners of each square meter were marked by a flag. Prior to searching for nests, the litter in the plot was removed superficially. At least 5 days were spent searching for nests. The search was terminated when no new nest was discovered. Searches were made during the day by following the foragers to their nests and hence nests of nocturnal species were poorly represented in the sample. Litter was placed back on the forest floor after the search was finished. under estimation of the nests of some species (especially the ones which are occasional or obligatory twig nesters) is also possible because of superficial litter removal. After a nest was discovered, it was located on a map by the distance from the nearest flag of the one meter quadrat. Dispersion of nests were studied using randomness index (R) by Clark and Evans (1954). 'R' can range from 0 (perfect aggregation) to 2.1491 (perfect over dispersion). A value of 1 indicates a random dispersion pattern. Statistical significance of 'R' was tested following a z transformation, as suggested by Clark and Evans (1954).

RESULTS

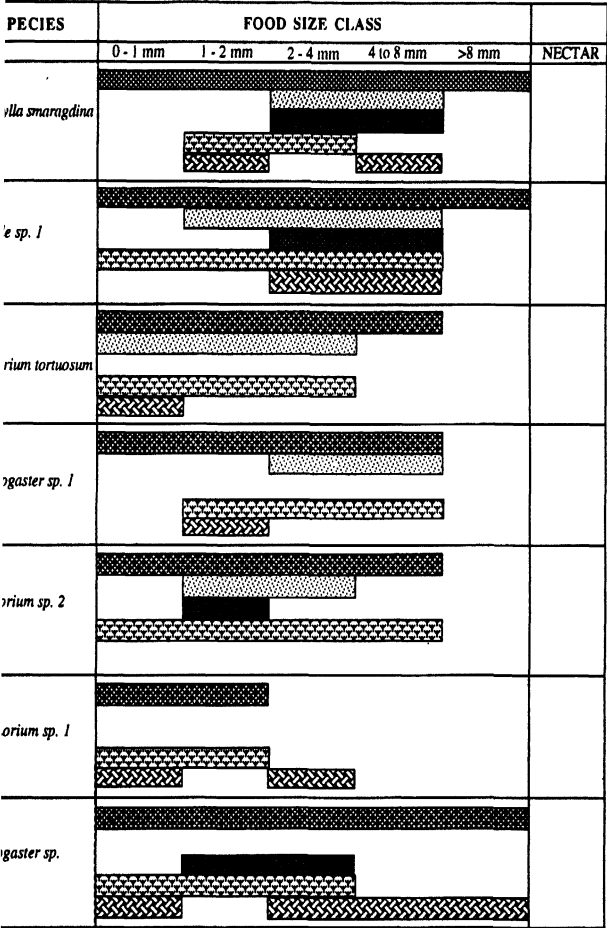
Resource Utilization Frequency and Niche Overlap :




Food items collected by the nine species considered for analysis ranged from approximately 0.5 mm to 32 mm. There were marked differences among the nine species in utilizing foods items of various sizes and types (Figure 4.1).

Oecophylla smaragdina and *Pheidole* sp.1 utilized the widest size range of food items. *Aphenogaster beccarii* also collected food items of wide size range. *Monomorium* sp. 1 and *Phedologiton* sp. had the narrowest utilization range with regards to food size (Figure 4.2 a to i). Modes of utilization frequencies differed from species to species. Maximum utilization frequency was for the 4 to 8 mm size class for both *O. smaragdina* and *Pheidole* sp.1. For *Tetramorium tortuosum*, *Tetramorium* sp. 2 and *Phedologiton* sp. 1, maximum utilization frequency was for the 0 to 1 mm size class. For *Crematogaster wroughtoni* and *Camponotus compressus* maximum utilization frequency was for the size class 1 to 2 mm. *Aphenogaster beccarii* almost evenly utilized the food items of 0 to 1, 1 to 2 and 4 to 8 mm size classes. Only *O. smaragdina*, *Pheidole* sp. 1 and *Tetramorium tortuosum* utilized food item of more than 8 mm size.

Species differed also in utilizing different types of food. *O. smaragdina* and *Pheidole* sp. 1 utilized the widest type of food items. *Monomorium* sp.1, *Phedologiton* sp. and *Camponotus compressus* had the narrowest food type utilization range (Figure 4.3 a to i). For most of the species, except *Monomorium* sp. 1 and *Camponotus compressus*, highest frequency of utilization was for the food type 'Insects'. *Monomorium* sp. 1 showed affinity for 'Seed and other vegetative matter' while *Camponotus compressus* showed a distinct affinity for collecting 'Nectaries'.

4.1. Diagram showing the utilization of different types and sizes of food by different species.



SPECIES	FOOD SIZE CLASS					
	0 - 1 mm	1 - 2 mm	2 - 4 mm	4 to 8 mm	>8 mm	
<i>gilton sp.</i>						NECTAR
						
<i>otus sp. 2</i>						Consume



Insects



Seed & other plant parts



Dead ant



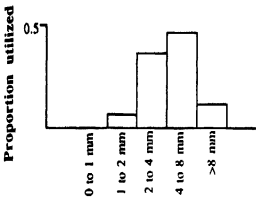
Grub



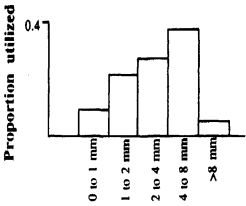
Termite

Figure 4.2. Utilization frequency of foods of different size classes, collected by different species.

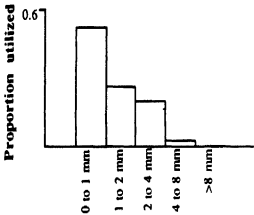
a) *Oecophylla smaragdina*



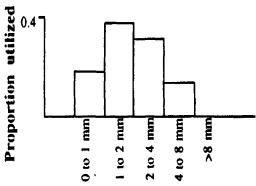
b) *Pheidole sp.1*



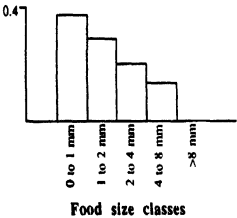
c) *Tetramorium tortuosum*



d) *Crenatogaster wroughtoni*



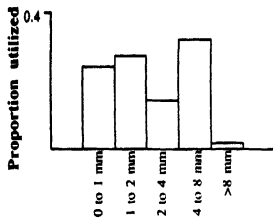
e) *Tetramorium sp. 2*



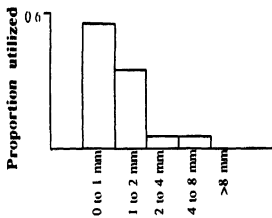
f) *Monomorium sp. 1*



g) *Aphenogaster beccarii*



h) *Phedogiton* sp.



i) *Camponotus compressus*

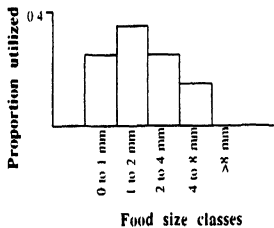
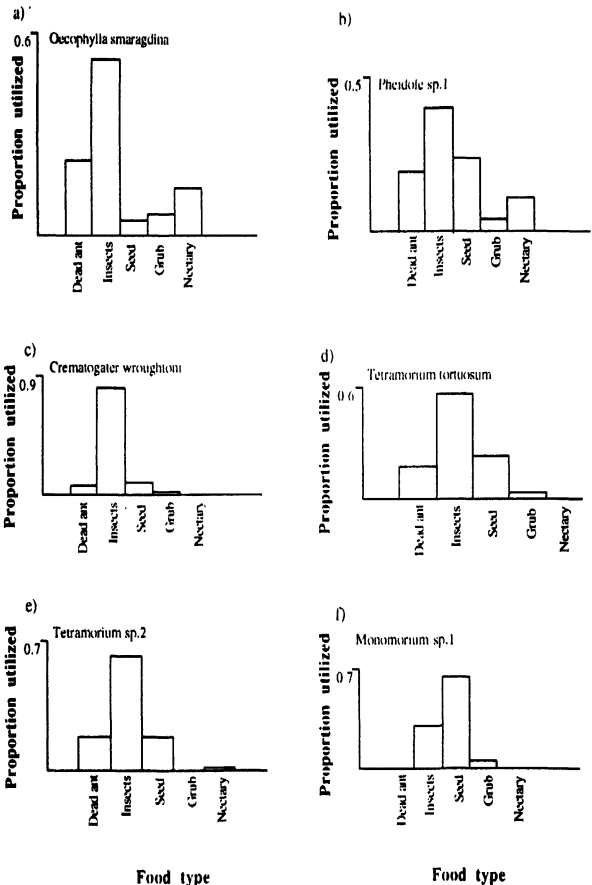
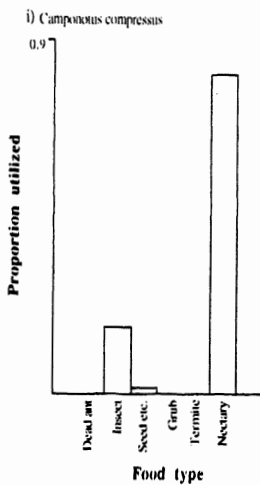
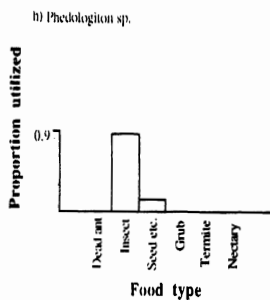
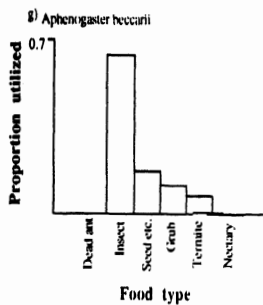


Figure 4.3. Utilization frequency of different types of food by different species.





General overlap index (Petriatis 1979) among different species in collecting different sizes and types of food was non significant, which indicates that the nine species considered for the analysis had a common utilization range with regards to food sizes and food type.

There were overlap among most of the species pairs in utilizing different types of food item (overlap between 66 species pairs out of 72). *Pheidole* sp. 1 partitioned their food type with *O. smaragdina*. *O. smaragdina* partitioned their food type with *Camponotus compressus*, *Monomorium* sp. 1 and *Phedologiton* sp., while *Tetramorium tortuosum* and *Monomorium* sp. 1 also partitioned their food type with *O. smaragdina* (Table 4.1).

When two species utilized the same type of food item, in most cases the food sizes overlapped. Sixty two species pairs out of 72 overlapped in food size for the food type 'Insect'. Fifty six out of 72 species pairs overlapped in food size while collecting 'Seeds and other vegetative matters'. Fifty eight out of 72 species pairs overlapped while collecting 'Dead ant.' Number of overlaps were however less for the food type 'Termite' (52 out of 72) and 'Grub' (40 out of 72).

Most of the species pairs also overlapped in collecting food items of different size classes (overlap between 69 species pairs out of 72 species pairs) (Table 4.2). *Tetramorium tortuosum* and *Monomorium* sp.1 partitioned their food sizes with *O. smaragdina*. *O. smaragdina* also partitioned their food item with *Monomorium* sp.1.

When different species pairs utilized the food items of the same size the number of overlaps in their food type varied from one size class to the other. Fifty eight species pairs overlapped in their food type while collecting foods of 0 to 1 mm size. Sixty one species pairs overlapped in their food type while collecting foods of 1 to 2 mm size class. Fifty two, 51 and 51 species pairs overlapped in their food type while collecting foods of 2 to 4 mm, 4 to 8 mm and >8mm size class respectively (Table 4.3a to 4.3e).

Abbreviations used in Table 4.1 to 4.3e.

PH :	<i>Pheidole</i> sp.1
CR :	<i>Crematogaster wroughtoni</i>
OSM :	<i>Oecophylla smaragdina</i>
T1 :	<i>Tetramorium tortuosum</i>
T2 :	<i>Tetramorium</i> sp.2
C2 :	<i>Camponotus compressus</i>
APH :	<i>Aphenogaster beccarii</i>
M1 :	<i>Monomorium</i> sp.1
PHG :	<i>Phedologiton</i> sp.

TABLE 4.1. Niche overlap among different ant species with regards to food types as resource classes. The values in the cells are Petriatis (1979)'s specific niche overlap indices. Food type categories for which overlaps have been measured are : Insects, dead ant, termite, grub & seed. * indicate non overlap at $p=0.05$ and ** indicate non overlap significant at $p=0.01$.

SPECIES	FH	CR	OSM	T1	T2	C2	APH	M1	FHG
FH		0,305	0,002	0,588	0,6	0,129	0,835	0,113	0,056
CR	0,601		0,503	0,646	0,766	0,223	0,809	0,104	0,079
OSM	0,473	0,192		0,099	0,116	0,006	0,649	0,002	0,002
T1	0,867	0,476	0,003		0,952	0,759	0,735	0,488	0,221
T2	0,858	0,648	0,014	0,95		0,655	0,83	0,464	0,267
C2	0,726	0,695	0,029	0,916	0,942		0,747	0,541	0,31
APH	0,855	0,621	0,089	0,505	0,612	0,036		0,026	0,018
M1	0,63	0,4	0,005	0,637	0,746	0,676	0,569		0,747
FHG	0,357	0,452	0,073	0,357	0,506	0,467	0,42	0,821	

Table 4.2. Niche overlap among different ant species with regards to food sizes as resource classes. The values in the cells are Petriatis (1979)'s specific niche overlap indices. Food size categories for which overlaps were measured are : 0-1mm, 1-2mm, 2-4mm, 4-8mm & >8mm. * indicate non overlap significant at $p=0.05$, ** indicate non overlap significant at $p=0.01$.

SPECIES	FH	CR	OSM	T1	T2	C2	APH	M1	FHG
FH		0.486	0.268	0.266	0.415	0.462	0.834	0.021	0.278
CR	0.841		0.049	0.72	0.908	0.965	0.894	0.201	0.434
OSM	0.791	0.135		0.052	0.11	0.13	0.534	0.001**	0.13
T1	0.491	0.74	0**		0.92	0.797	0.734	0.753	0.269
T2	0.671	0.895	0.003*	0.86		0.954	0.907	0.254	0.364
C2	0.79	0.963	0.018	0.693	0.956		0.96	0.116	0.457
APH	0.832	0.754	0.024	0.464	0.763	0.817		0.03	0.416
M1	0.403	0.69	0.001**	0.833	0.791	0.741	0.652		0.504
FHG	0.395	0.434	0.069	0.282	0.35	0.418	0.489	0.26	

TABLE 4.3 a. Niche overlap among different ant species with regards to food types as resource classes within food size class 0 to 1mm. The values in the cells are Petriatis (1979)'s specific niche overlap indices. Food type categories for which overlap was measured were, Insects, dead ant, termite, grub, seed. * indicate non overlap significant at $p=0.05$ and ** indicate non overlap significant at $p=0.01$.

SPECIES	RH	CR	OSM	T1	T2	C2	APH	M1	PHG
RH		0**	0.201	0.526	0.377	0	0.377		
CR	0**		0.2	0.238	0.625	1	0.5		
OSM	0**	0**		0.056	0**	0	0.004		
T1	0.003*	0**	0.652		0.038	0	0.135		
T2	0.019	0.005	0.388	0.62		0.005	0.87		
C2	0.001	1	0.2	0.238	0.625		0.5		
APH	0.004	0.001	0.53	0.756	0.193	0.001			
M1									
PHG									

Note: M1, PHG did not collect any food of size class 0 to 1mm.

TABLE 4.3b. Niche overlap among different ant species with regards to food types as resource classes within food size class 1 to 2mm. The values in the cells are Petriatis (1979)'s specific niche overlap indices. Food type categories are: Insects, dead ant, termite, grub and seed.

* indicate non overlap significant at $p=0.05$ and ** indicate non overlap at significant $p=0.01$.

SPECIES	RH	CR	OSM	T1	T2	C2	APH	M1	PHG
RH		0.402		0.598	0.759	0.001	0.404	0.551	
CR	0.46			0.468	0.519	0.117	0.566	0.53	
OSM									
T1	0.654	0.04			0.873	0.015	0.039	0.036	
T2	0.469	0.158		0.52		0.024	0.295	0.152	
C2	0.523	0.833		0.692	0.714		0.8	0.636	
APH	0.339	0.417		0.337	0.902	0.075		0.387	
M1	0.938	0.805		0.599	0.766	0.005	0.802		
PHG	0.429	0.125		0.077	0.143	0.001	0.133	0.364	

Note : OSM & PHG did not collect any food of size class 1 to 2mm.

TABLE 4.3c. Niche overlap among different ant species with regards to food types as resource classes within food size class 2 to 4mm. The values in the cells are Petraitis (1979)'s specific niche overlap indices. '*' in a cell indicate no overlap. Food type categories are :Insects, dead ant, termite, grub and seed. * indicate non overlap significant at $p=0.05$ and ** indicate non overlap significant at $p=0.01$.

SPECIES	PH	CR	OSM	T1	T2	C2	APH	M1	PHG
PH		0,017	0,382	0,021	0,025	0**	0,002*	0,733	0,001**
CR	0,469		0,207	0,969	0,805	0,064	0,148	0,388	0,001**
OSM	0,841	0,015		0,016	0,017	0,001*	0,023	0,578	0,001**
T1	0,561	0,965	0,186		0,9	0,014	0,042	0,456	0,001**
T2	0,694	0,753	0,374	0,89		0,001*	0,002*	0,472	0,001**
C2	0,268	0,788	0,464	0,684	0,526		0,571	0,2	0,001**
APH	0,466	0,02	0,017	0,018	0,014	0,003*		0,634	0,001**
M1	0,631	0,003	0,004	0,003*	0,003*	0**	0,055		0,001**
PHG	0,049	0,091	0**	0,105	0,053	0**	0,143	0,2	

TABLE 4.3d. Niche overlap among different ant species with regards to food types as resource classes within food size class 4 to 8mm. The values in the cells are Petraitis (1979)'s specific niche overlap indices. '*' in a cell indicate no overlap. Food type categories are :Insects, dead ant, termite, grub and seed. * indicate non overlap significant at $p=0.05$ and ** indicate non overlap significant at $p=0$.

SPECIES	PH	CR	OSM	T1	T2	C2	APH	M1	PHG
PH		0,108	0,005	0,719	0,069	0**	0,003		0,719
CR	0,681		0,12	0,444	0,122	0**	0,018		0,444
OSM	0,616	0,043		0,585	0,004	0**	0,128		0,585
T1	0,678	0,003*	0,051		0**	0**	0,003*		1
T2	0,787	0,639	0**	0,4		0**	0,001*		0,4
C2	0,053	0**	0,077	0,2	0**		0,091*		0,2
APH	0,579	0,021	0,846	0,428	0,016	0**			0,428
M1									
PHG	0,678	0,003*	0,051	1	0**	0**	0,003		

Note: M1 did not collect any food of size class 4 to 8mm.

TABLE 4.3c. Niche overlap among different ant species with regards to food types as resource classes within food size class >8mm. The values in the cells are Petriatis (1979)'s specific niche overlap indices. '*' in a cell indicate no overlap. Food type categories are :Insects, dead ant, termite, grub and seed. * indicate non overlap significant at $p=0.05$ and ** indicate non overlap significant at $p=0.01$.

SPECIES	PH	CR	OSM	T1	T2	C2	APH	M1	PHG
PH			0,833	0,2			0**		
CR									
OSM	0,106			0,314			0**		
T1	0**		0**				0**		
T2									
C2									
APH	0**		0**	0,2					
M1									
PHG									

Note: CR, T2, C2, T1, M1 & PHG did not collect any food of size class >8mm.

Species at Baits :

A total of 778 observations were made at 24 bait stations during the dry seasons of 1990, 1991 and 1993. Observations were assumed to be independent of each other. Nineteen species occurred at baits, of which 15 were found more than 5 times in all the observations. This is about the half of the local species pool (Table 4.4). Of this 15 species, 9 species were present in $\geq 25\%$ of the baits and were possible to classify following Schoener (1983)'s scheme into territorial, encounterer and submissive species. based on qualitative observations. *Oecophylla smaragdina* was found to be the only territorial species. Species other than the territorial species having more than 10 % of the total number of aggressive behaviours shown by all species were considered as encounterers. By this criterion *Pheidole* sp.1 and *Tetramorium tortuosum* were the encounterers and rest others were the submissive opportunists.

Bait occupancy :

Pheidole sp.1 occupied maximum number of baits ($n=21$, 87.5%) followed by *Aphenogaster* sp. ($n=19$, 79.17%). *Oecophylla smaragdina* occupied 16 out of 24 baits (66.67%). *Pheidole* sp.1 was recorded in maximum number of observations ($n=420$, 55.78%) followed by *Oecophylla smaragdina* (297, 38.17%). Although 10 species showed higher abundance i.e. were dominant at some observation or the other on the bait, only 5 species were dominant at more than 5% of the total observations.

Domination and Monopolization :

If the abundance of a species was ≥ 20 individuals during any five minute observation session it was considered to be dominant and, if only the dominating species was present during any five minute observation the bait was considered to be monopolized. A total of 305 observations (39.13% of the total observations) were dominated by some species or the other. Number of observations monopolized by some species or the other was 104 (13.37%

Table 4.4. Summary of bait occupancy, domination and monopolization of 15 common species.

Species	% Baits Occupied	% 5 Minute Observation Occupied	% 5 minute Observation dominated	% 5 minute Observation monopolized
<i>Pheidole sp.1</i>	87.5	54.0	12.34	5.78
<i>Aphenogaster beccari</i>	79.2	16.4	0.00	0.00
<i>Monomorium sp.1</i>	66.7	10.7	2.83	0.26
<i>Oecophylla smaragdina</i>	66.7	38.2	3.86	3.47
<i>Phedologiton sp.</i>	29.2	14.6	4.37	0.00
<i>Tetramorium sp. 2</i>	29.2	11.95	0.90	0.00
<i>Crematogaster sp.</i>	29.2	24.81	12.98	1.03
<i>Camponotus sp. 2</i>	29.2	16.84	0.00	0.77
<i>Tetramorium tortuosum</i>	25.0	21.47	1.16	0.13
<i>Camponotus sp. 1</i>	16.7	4.24	1.16	0.77
<i>Crematogaster sp. 2</i>	12.5	4.5	1.16	0.00
<i>Amblyopone sp.</i>	12.5	6.3	1.16	0.00
<i>Leptothorax sp.</i>	12.5	1.93	0.13	0.00
<i>Monomorium sp. 2</i>	8.33	0.90	0.64	0.13
<i>Leptogenys sp. 1</i>	8.33	2.44	0.00	0.00

Total no. of observations = 778

of the total observations) (Table 4.4). *Oecophylla smaragdina* monopolized 90% of the baits that they dominated (3.47% of the total observations were dominated by them) and *Pheidole* sp.1 monopolized 46.88% of baits that they dominated (5.78% of the total observations were dominated by them). 34.97% observations were dominated (more than 20 individuals). Maximum number of observations were dominated by *Pheidole* sp.1 (12.34%) and *Crematogaster wroughtoni* (12.98%).

Aggressive Interactions at Bait. :

A total of 375 aggressive interactions were observed during the whole period of the experiment. *Oecophylla smaragdina* was engaged in the maximum number of direct aggressive interactions (47.77 % of the total aggressive behaviours shown by all species) while *Pheidole* sp.1 showed the maximum number of indirect threat (35.32 % of indirect threat shown by all species). However, totally, *O. smaragdina* showed the maximum number of aggressive interactions (32.27 %) compared to *Pheidole* sp.1 (31.73 %) (Table 4.5). Most of the aggressive behaviours of *O. smaragdina* was directed towards *Pheidole* sp. 1 while most of the aggressive behaviour of *Pheidole* sp.1 was directed towards *Tetramorium tortuosum*. All the species other than *O. smaragdina* and *Pheidole* sp.1 clustered together when a dendrogram was drawn based on the 'Euclidean distance' between species calculated from the frequency of different aggressive behaviours shown by different species (Figure 4.4). *O. smaragdina* and *Pheidole* sp.1, were the two most aggressive species, and did not cluster with any other species. Proportion of indirect threat shown by all species in the form of eliciting 'avoidance' were higher than direct interactions, i.e., 'attack' and 'chase'.

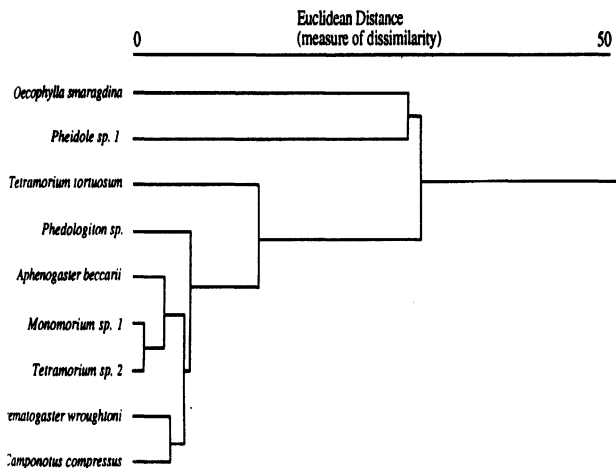
No significant correlation was found when total number of individuals of different species (pooled from all the baits) were correlated with the total number of aggressive behaviours shown by each of these species.

Table 4.5. Frequencies of different aggressive behaviours between different pairs of species. Osm = *O. smaragdina*, PH = *Pheidole* sp.1, CR = *Crematogaster* sp., PHG = *Phedologiton* sp., M1 = *Monomorium* sp.1, APH = *Aphenogaster beccari*, T1 = *Tetramorium* sp. 1, T2 = *Tetramorium* sp. 2. Indirect threat is described as avoidance of the aggressor by the submissive species. Species initiating aggression are in the extreme left column.

	OSM	PH	CR	C2	PHG	M1	APH	T1	T2	Total	% of behaviour shown by all spp.
OSM											
attack		18		13		17	3			51	73.91
chase		11		4		2	7			24	27.27
indirect threat		19		14		1	5	4	2	46	41.14
PH											
attack				1		6	2	4		0	0.00
chase	2		8	3			3	24	2	42	47.73
indirect threat	4		2	31		2	23	13	2	77	70.56
CR											
attack				2	4			1		7	10.14
chase		1						1		2	5.68
indirect threat				5						5	10.19
C2											
attack		3						3		6	8.70
chase		6						6		12	13.64
indirect threat		2		2			1	2		7	6.83
T2											
attack		3								3	4.35
chase		1								1	1.14
indirect threat		2					5			7	6.17
T1											
attack										0	0.00
chase										0	0.00
indirect threat	1	7	2	16			15		1	42	37.71
PHG											
attack										0	0.00
chase										0	0.00
indirect threat				2			2	13		18	15.13
M1											
attack		2								2	2.90
chase										0	0.00
indirect threat							7	1		8	8.19

Total number of aggressive interactions = 375; number of aggressive interactions initiated by the species mentioned in the table = 360. Fifteen times, aggressive behaviour was shown by the species that came irregularly at baits.

Figure 4.4. Dendrogram showing resemblances among different species in terms of aggressive behaviour at bait. Dendrogram was made based on the frequency of aggressive behaviour shown by each species at bait. Territorial, *Oecophylla smaragdina* and encounterer species *Pheidole* sp. 1 clustered separately from the submissive species.



Rate of Food Location and the Behaviour :

In the maximum number of experiments *Pheidole* sp.1 arrived at a bait during the first hour of the observation followed by *O. smaragdina* (Figure 4.5). An index of the ability of finding food items by different species was calculated in the following way: if a species found a food item during the first hour of observation it was assigned a rank of 6 and consecutively if a species found a food item during the sixth hour of observation it was assigned a rank of 1. All the scores for a particular species were then summed up to obtain the index of ability of a species in finding out a food item. *Pheidole* sp.1 was the fastest species in finding out food item followed by *Aphenogaster* sp. and *O. smaragdina* (Figure 4.6). Species which arrived at the bait during the first hour of the day were more aggressive ($r = 0.66$, $p = 0.05$) (Figure 4.7). Species faster in finding out a bait (higher score for the ability to find a food item) also showed more number of aggressive behaviours ($r = 0.635$, $p < 0.05$, Figure 4.8).

Relation Between Activity of the Territorial species and the Activities of Other Species :

Abundance of *O.smaragdina* significantly affected the total number of individuals of all other ants at the bait which included the number of both the encounterer and the submissive species ($Y = 46.6-8.46X$, $R^2 = 0.31$, $N = 17$, $p = 0.02$) as evident from the negative regression slope (Figure 4.9); although, it did not have any significant effect on the species diversity. It affected the abundances of *Pheidole* sp.1 and *Crematogaster wroughton* but, it did not affect the abundances of the other submissive species, except *Camponotus compressus* (Table 4.6).

Species Association at the Bait.:

Multiway contingency tables were used to analyse species interactions at the baits. The variables in the contingency tables were chosen keeping the territorial species- *O.smaragdina*, one of the encounterer species eg. *Pheidole* sp.1 and one of the submissive species eg. *Aphenogaster* sp. Abundances of different species were categorised into abundance classes to avoid zeros in the

Figure 4.5. Frequency of occurrence of different species during the first hour of observations. Total number of observations = 778.

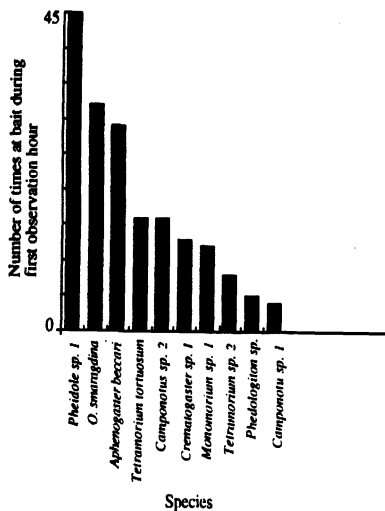


Figure 4.6. Score of food finding ability of different species. Calculated as follows: if a species found a food item during the first hour of observation it was assigned a rank of 6 and consecutively if a species found a food item during the sixth hour of observation it was assigned a rank of 1. All the scores for a particular species for all the experiments were then summed up to get a final score.

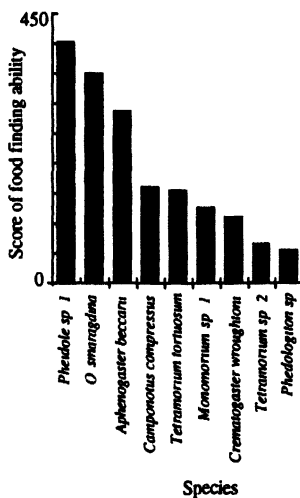


Figure 4.7. Relation between number of times each species discovered a bait during the first hour of observation and number of aggressive behaviour shown by it. Total number of observations = 778.

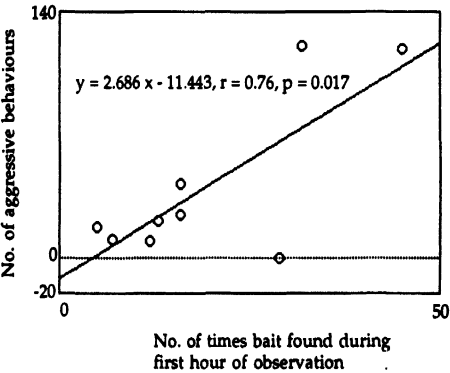


Figure 4.8. Relation between the ability score of each species for finding a bait at different hours and the total aggressive behaviour shown by the species ($r = 0.635$, $N = 778$, $p < 0.05$). If a species found the bait in the first hour after setting the bait it is given a score of 6 and if it found the bait in the sixth hour it is given a score of 1. Ability score of a species is the sum of all the scores of a species from all the experiments. Total number of aggressive behaviour is calculated summing the aggressive behaviours shown by respective species at all the experiments.

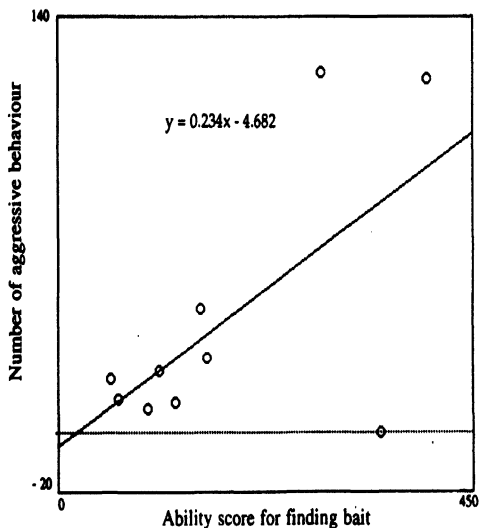


Figure 4.9. Relationship between the number of *Oecophylla smaragdina* and number of individuals of other ants at baits.

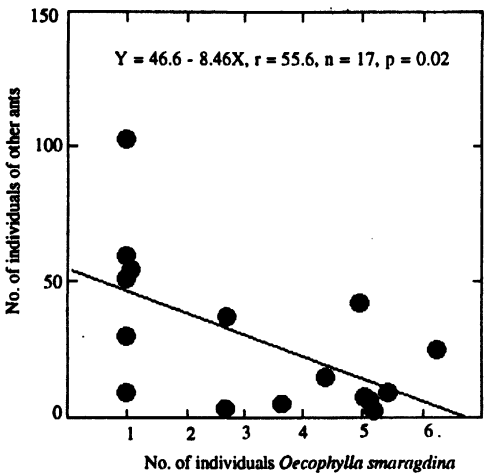


Table 4.6. Relation between the abundances of *Oecophylla smaragdina* and the encounterer and submissive species.
 n = 778. Only significant regression between *Oecophylla. smaragdina* and other species have been shown.

			Independent variable (Y= <i>O. smaragdina</i>)
Dependent variable (x)	Model	R ²	p
<i>Pheidole</i> sp. 1	13.613-0.64x	0.013	<0.01
<i>Crematogaster wroughtoni</i>	9.582-0.395x	0.011	<0.01
<i>Camponotus compressus</i>	0.323-0.013x	0.013	<0.01

Table 4.7. Effect of the territorial species on the interactions between the encounterer and submissive species.

G = Likelihood ratio chi-square statistic.

The first species in the model is territorial, the second one is the encounterer and the third species in the model is a submissive species. A significant three order interaction means the association between the encounterer and a particular submissive is dependent on the presence of the territorial.

O.sm = *Oecophylla smaragdina*, Pheid = *Pheidole* sp.1,

Phg = *Pheidogiton* sp., Cr = *Crematogaster wroughtoni*

T1 = *Tetramorium tortuosum*, T2 = *Tetramorium* sp.2,

M1 = *Monomorium* sp.1, C2 = *Camponotus compressus*

BEST MODEL	df	G	p
O.sm.-Pheid-Aph	6	45.02	<0.001
O.sm.-Pheid-M1	15	37.33	<0.001
O.sm.-Pheid-Phg	120	1739.57	<0.001
O.sm.-Pheid-T1	18	58.31	<0.001
O.sm.-Pheid-T2	16	29.87	0.019
O.sm.-Pheid-C2	6	23.67	<0.001

table. The following abundance scale was used: 0-1 individuals =1, 2-5 individuals =2, 6-20 individuals =3, 20-100 individuals =4, >100 individuals =5. If any three way association model was non significant, simpler models were tested (Sokal and Rohlf 1981). A significant three order association meant the association between an encounterer and a submissive species was dependent on *O. smaragdina*, the territorial species. Two way association models were also tested to see the interaction between the encounterer species and the submissives and also the interaction between different pairs of submissives.

Association between most of the submissive species and the encounterer species were dependent on *O. smaragdina*, the territorial species (Table 4.7). *Pheidole* sp.1 and *Crematogaster wroughtoni* affected the activities of most of the submissive species (Table 4.8). However interactions among the submissives in most of the cases were not significant.

Nest Dispersion :

When nests of all the species in a nest map plot were considered, in 9 plots out of a total of 15 , nests were randomly dispersed, while in 7 plots nests were overdispersed (Table 4.9). In one plot, nests were clumped. Nearest neighbour distance was less with the hetero-specifics than the conspecifics (Figure 4.10).

Table 4.8. Interactions between the i) encounterer species (*Pheidole* sp.1) and the other submissive species & ii) interactions between different submissive species.

A significant two way association signifies the activities of one species is affected by the presence of the other species at the bait.

G = Likelihood ratio Chi square test.

N = Total number of observations at those baits where particular species pair was found.

Pheid = *Pheidole* sp.1, Cremat. = *Crematogaster wroughtoni*, Aph = *Aphenogaster beccarii*

Mono1 = *Monomorium* sp.1, Camp1 = *Camponotus* sp.1, Phedg = *Phedogiton* sp.,

Camp2 = *Camponotus compressus*, Tetra1 = *Tetramorium tortuosum*,

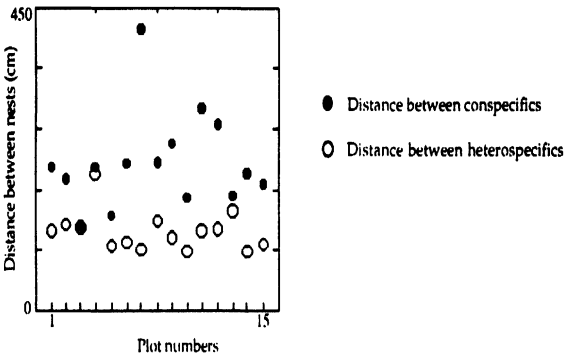
Tetra2 = *Tetramorium* sp.2

2 WAY MODEL	DF	G	p	N
Pheid-Cremat	25	47.21	0.005	259
Pheid-Aph	15	25.19	0.047	522
Pheid-Mono1	25	45.52	0.016	214
Pheid-Phdg	25	58.48	0.001	373
Pheid-Camp1	15	18.85	0.04	179
Pheid-Tetra2	20	43	0.002	132
Cremat-Aph	15	56.16	0.001	132
Cremat-Phdg	25	157.62	0.001	252
Cremat-Camp2	15	96.75	0.001	155
Cremat-Tetra1	25	55.58	0.001	98
Cremat-Tetra2	20	65.17	0.001	222
Mono1-Camp2	15	27.99	0.02	206
Phedg-Camp2	15	84.03	0.001	204
Phedg-Tetra1	25	43	0.001	201
Camp1-Camp2	9	20.2	0.02	156
Tetra1-Camp2	15	29.99	0.01	310
Tetra1-Tetra2	20	31.2	0.052	208

Table 4.9. Density and dispersion of nests of all species.
Number of plots = 15. R = Randomness index
(Clark & Evans 1954).

Plot	Number of Nests/m ²	R	Dispersion
Plot 1	0.17	0.82	Random
Plot 2	0.27	1.24	Over dispersed
Plot 3	0.35	0.8	Random
Plot 4	0.64	0.64	Random
Plot 5	0.31	3.66	Over dispersed
Plot 6	0.33	1.27	Over dispersed
Plot 7	0.31	0.95	Random
Plot 8	0.24	0.91	Random
Plot 9	0.28	1.00	Random
Plot 10	0.30	0.93	Random
Plot 11	0.30	0.94	Random
Plot 12	0.29	1.06	Random
Plot 13	0.32	1.02	Random
Plot 14	0.45	1.20	Over dispersed
Plot 15	0.46	1.17	Over dispersed

Figure 4.10. Distance between con-specifics and hetero-specifics nests (measured from nest maps).



DISCUSSION

Behaviour and Competition Hierarchy.

Interference competition in the form of aggressive interaction between pairs of species has been observed as a frequent phenomenon among ants (Holldobler and Wilson 1990). The coexistence of individuals of different species at a food item are often a function of the degree of aggressiveness of different species. In the present study, *O. smaragdina*, a territorial species was the most aggressive. This species was engaged more in direct aggressive interaction especially 'attack'. Interestingly this species was frequently aggressive at the bait even when they were not numerically dominant. The response of *Pheidole* sp. 1, the next most aggressive species was more in the form of indirect aggressiveness eliciting avoidance and escape from the other species. This was the only species that directed some aggressive behaviour towards the territorial species, *O. smaragdina*.

According to Schoener (1983)'s scheme of classifying a community based on the competitive abilities of different species, maximum number of aggressive interactions are expected from the territorial and the top most species in the hierarchy who would defend their foraging area, food items and the nesting sites. Encounterers, the species next in the hierarchy would defend their food items and nesting sites. The submissive species, lowest in the hierarchy are not expected to show any aggressiveness and would defend only their nesting sites.

Based on this criterion, it was possible to categorize different species that came to the bait regularly and that were also common in the pitfall traps. The most aggressive species in this community was *Oecophylla smaragdina* which is known for their territoriality. The aggressiveness and territorial behaviour of this arboreal nesting species have been amply documented previously. Holldobler (1983) observed the key role of *O. smaragdina* in forming an ant mosaic in tropical Australia.

The two encounterer species in this community were *Pheidole* sp. 1 and *Tetramorium tortuosum*. *Pheidole* sp. 1 were the only species that showed some aggressive behaviour towards *O. smaragdina*. Although *Tetramorium tortuosum* has been categorised in this study as an encounterer based on the number of aggressive behaviours it showed towards other species (the third species showing more than 10 % of the total aggressive behaviours of all species), most of its aggressive behaviour was towards other submissive species and it was definitely lower in its competitive ability than *Pheidole* sp. 1. Both submissive and encounterer behaviour have been documented for the genus *Tetramorium*. (Holldobler and Wilson 1990). Majer (1976 a-c) documented the dominant behaviour of a species of *Tetramorium* in the ant mosaic in Ghana cocoa farm. Brian (1983) reported the same in England.

Of the rest of the species, submissive behaviour has been documented previously for the genus *Aphenogaster*. Members of this genus are not known to fight back effectively when encountered instead they are known to maximize their resource utilization through an efficient recruitment system (Holldobler and Wilson 1990). Species of the genus *Camponotus* have been documented as subordinate species in an ant mosaic in Ghana (Room 1971). Pisarski and Vepsäläinen 1981, Vepsäläinen and Pisarski 1982 documented a species of *Camponotus* as encounterer.

Interference Competition and Coexistence

Result from the present study clearly shows the presence of a competitive dominance hierarchy. *O. smaragdina* the 'territorial' and most aggressive species in the community had a negative effect on the activity of any other species at baits as the cumulative number of individuals of other species depended on the number of individuals of *O. smaragdina*. Significant three order interaction models also indicated that *O. smaragdina* affected the interaction between an encounterer species and a submissive species in the presence of *O. smaragdina*. The other aggressive and 'encounterer' species *Pheidole* sp. 1 affected the activities of other 'submissive' species at the bait as apparent from the two way species association models. The second



encounterer species *Tetramorium tortuosum* also affected the activities of two species, one among which is its congeneric. Similarly, with a few exceptions, species next in the hierarchy influenced the activities of the species lower in the order. Behaviourally, *O. smaragdina* showed maximum number of overt aggressive behaviour such as 'attack' and 'chase' and; *O. smaragdina* was also the only species that 'attacked' any other species, but abundance wise it was not always the most abundant species at the bait which is possibly the reason why no correlation was found between the total abundance of a species and the total number of aggressive behaviours shown by it. However *Pheidole* sp.1, the species which showed the next maximum number of aggressive behaviour was present abundantly at the bait. It dominated and also monopolized a bait for the maximum number of times. Interestingly the submissive species could coexist with the territorial species as predicted but was affected by the encounterer species. The fact that the activities of the submissive species were not affected by *O. smaragdina* indicates that they could coexist with the top territorial species while the activity of encounterer species *Pheidole* sp. 1 was affected by the former. The regression models with *O. smaragdina* and other submissive species however had a negative slope which indicates that the activities of the submissive species reduced in the presence of *O. smaragdina*. Vepsäläinen and Savolainen (1990) demonstrated that submissive *Myrmica* sp. could coexist with territorial *Formica* spp. Occasional coexistence of submissive with the dominants has been found to be affected by morphological differences, colony sizes and foraging area. Fellers (1987) found significant reduction in the activity of the submissive species in presence of dominant species.

Species which found a bait faster showed more aggressiveness towards other species. In most of the cases food was found faster either by *Pheidole* sp.1 or *O. smaragdina* the territorial species. Both these species by definition are expected to defend their food item. It was hence likely that there was a correlation between rate of food finding and aggressiveness.

Ants live in a highly competitive environment as they live in long lived colonies with many workers thereby amplifying the intensity of competition (Savolainen and Vepsäläinen 1988) and the competition pressure in the ant community has been described to be closer to vertebrates than to any other insects (Schoener 1986). In this highly competitive environment, the coexisting ant species are expected to show divergence in their resource utilization pattern as predicted by the competition theory. The divergence could either be on their food choice or selection of nesting space. These divergences in turn, are also expected to be reflected on the morphology and behaviour of the competing species. While a number of studies are available showing partitioning of resource by the competing ant species, the importance of interference competition has been re-emphasized recently in this regard. As pointed out by Savolainen and Vepsäläinen (1988), the behaviour of the encountering individual foragers would determine which species would coexist and insight into the interactions among individuals of specific populations can hence elucidate community relationship.. Presence of aggressive dominant species in a given community and the response of other species towards it will lead to separation of resource utilization mode of the other species and the coexistence of species would depend on the relative successes of the other species in maximizing their resource utilization in the presence of a top competitor. Aggression from the dominant species can reduce the fitness of submissives by:

- 1) restriction of foraging activity in terms of reduction in forager density and foraging area (Yasuno 1965),
- 2) reduction in food harvesting (Lynch et al. 1980, Reznikova 1982),
- 3) decreased production of sexuals (Pontin 1961,1963, Boomsma and Vanloon 1982).

In this regard, it is often easy to visualize a linear competition hierarchy determined by the aggressiveness of the top species in the hierarchy.



Depending on the strength of overt aggressiveness of the top species, the species lower in the hierarchy would adopt different foraging strategies or take to different habitat/micro-habitat. Andersen (1992) has shown that species diversity in ant community is determined by the success of the dominant species. The present study did not address the aspect of habitat/micro-habitat shift of the species lower in the hierarchy, but examined their foraging strategies as influenced by behavioural interactions from the top territorial species at baits. While the abundance of the encounterer species were affected by the abundance of the territorial species the best strategy for the submissive species was to adopt an opportunistic strategy in exploiting resources in the presence of territorial by taking to stealthy behaviour even though their abundances were affected by the territorial species.

Exploitation and Overlap in Resource Use by Different Species.

Exploitation: *Oecophylla smaragdina* and *Pheidole* sp. 1, the two top most species in the hierarchy were most efficient in finding the bait. *Pheidole* sp.1 found a bait item during the first hour of setting bait for the maximum number of times followed by *O. smaragdina*. These two species also have high values for the 'index of food finding'.

It should be noted here that although *O. smaragdina* and *Pheidole* sp. 1 had high mean abundance scores they did not dominate baits frequently. While *O. smaragdina* dominated only 3.47 % of the total observations *Pheidole* sp. 1 dominated only 12.34 %. Both these species have efficient recruitment mechanisms. Their high mean abundance in comparison to most of the other submissive species however imply their numerical superiority at the bait. *Oecophylla* is known to have a highly sophisticated recruitment system mediated by the secretion from their 'extra ordinary' rectal gland as well as secretion from Dufour's gland and sternal gland which have strong attracting and settling effect (Holldobler and Wilson 1990). Aided by this efficient recruitment system and their massive worker force *O. smaragdina* is hence highly capable of discovering and exploiting new food item. The other dominant species in the community - *Pheidole* sp.1 also maintains large

colony is capable of mass recruitment. Their ability to group retrieve large food items (personal observation) also increases their efficiency as exploiter. *Tetramorium tortuosum*, the other encounterer species was not as efficient in finding out a bait during the first hour of observation. But this species also have an efficient mass recruitment system and therefore has greater exploitative ability. Among the submissive species, *Aphenogaster beccarii* was efficient in finding out a food item during the first hour of observation. Although they have a small worker force, nest density of this species is quite high in the study area and a high forager density per unit area enables this species to find out a bait as soon as it is set. This species is also capable of recruiting quickly to large and profitable food items (personal observation). Although they are poor competitors in the presence of dominant territorial or encounterer species they maximize their efficiency by arriving at the food source first. Their ability to use tool in retrieving liquid food item (Vide chapter 1) also increases their efficiency to exploit food. This ability of this species has also been reported by Fellers (1987). Although, *Tetramorium* sp. 2 and *Crematogaster* sp., *Monomorium* sp.1 and *Phedologiton* sp. are able to mass recruit workers at food item, they were poor competitors. These species never recruited large worker forces in the presence of dominant species and can probably be termed as 'insinuator' species who uses the resource 'stealthily' even in the presence of dominant species without eliciting aggressive response from them (Wilson 1971, Fellers 1987).

High degree of overlap among most of the species pairs in utilizing foods of different sizes and types, especially the common food types 'insects', 'seed' indicate that most species were able to utilize most of the food items and were generalists. The utilization curves of different species show that most of the species were able to collect food items between the size range of below 1 mm to 8 mm. No species other than *O. smaragdina* and *Pheidole* sp. 1 and *Aphenogaster beccarii* were however able to utilize food items of size more than 8 mm. Both *O. smaragdina* and *A. beccarii* have large body size and were hence capable of large food items. *Pheidole* sp.1 although

has a small body size were able to retrieve larger food item because of their group retrieval system. All the species except *Monomorium* sp.1 and *Camponotus compressus* preferred 'insect' food item. Preference for proteinaceous food items in generalist ants has been recorded by Savolainen and Vepsäläinen (1988). *Camponotus compressus* had a clear preference for liquid food items eg. nectaries.

Resource utilization: The present study shows overlaps in collecting foods of different types and size among different species. Within each type also there were overlaps in collecting foods of different sizes belonging to that type. The same is true for each size class of food where there is considerable overlap in utilizing different food types belonging to that size class. However, significant no overlaps (diet separation) were also observed in some cases. Interestingly, encounterer *Pheidole* sp.1 partitioned their food type with territorial *O. smaragdina* as they utilized seeds and other vegetative materials at a greater frequency than *O. smaragdina*. This differentiation between *Pheidole* sp. 1 and *O. smaragdina* is predictable within the framework of 'competition hierarchy' as these two species are two close competitors in the hierarchy the later being excluded from the bait by *O. smaragdina*. All the other species that came to the bait are food generalists or scavengers which has been reported as a common phenomenon in other communities too although dietary specialization has also been reported at times.

Studying resource utilization pattern and resource partitioning has probably been one of the most popular topic among ecologists in the recent past (Schoener 1974, 1983). Fellers (1987) reported high overlap in a community of wood land ants and equated that with intensity of competition. It has also been shown in other social insects. Although a number of studies have demonstrated it in ants (Davidson 1977b, Hansen 1978, Bernstein 1979, Plowman 1981, Torres 1984b), not much is known about the resource utilizations of the complex ground foraging ant community of tropical forests.

Partitioning with regards to food type and size has been demonstrated by Torres (1984a).

Does this high overlap indicate strong competition? : As has been mentioned earlier in this chapter, high overlap in resource use has often been equated with the strength of competition. This would be true for this food generalist ant guild if food was limited.

Foods for the generalist scavenging species are highly ephemeral and random and finding a food item is highly probabilistic for these species. Direct estimation of the availability or abundance of food for this scavenger guild is hence not easy and we have to infer from the indirect evidences whether food is abundant for these ants. Schoener (1982) suggested that interference behaviour among coexisting species would indicate limitation of food. Another evidence would be the rate of scavenging. An increased rate of scavenging of food items would indicate limitation of food items (Fellers 1987). As observed in the present study there was high interference on the simulated food item. The rate of food removal was also high as discrete food items like pieces of dried fish or honey placed as bait attracted ants within 10 to 30 minutes after placing the bait in the study area (personal observation). Fellers (1987) concluded food limitation by looking at the above two lines of evidences. Whitford et al. (1976) and Fellers (1987) found high overlap values (> 0.70) in communities of competing species. Overlap values between most of the species pairs in the present study also followed the same range. There are hence indications that there is competition for food among the species that commonly interacted at the bait.

Is There Any Correlation between Exploitative and Interference Abilities.

As is apparent from the present study, species which are stronger in interfering with other species are also better in exploiting resources. *O. smaragdina* and *Pheidole* sp.1, the two topmost species in the behavioural hierarchy were the two most efficient exploiters at baits. Both these species

dominated baits for the maximum number of times and were also fast in arriving at baits than any other species. Submissive species, poorer in combating other species were also poorer exploiters at the bait and optimized their cost of coexistence with the stronger species by adopting opportunistic strategy of exploiting food. Cost of interference from the species higher in the behavioural hierarchy would be in the reduction of the foraging activity and *vis a vis* the amount of food items brought to the nest. Other studies also support this observation. Reznikova (1982) found increase in the amount of food item brought to the nest by *Formica cunicularia* when nests of *F. pratensis*, it's superior competitor was removed from the area. Yasuno (1965) reported an increase in the foraging area in *Formica japonica*, a submissive species after the nests of *F. yessensis*, it's superior competitor was removed from the area. Presence of dominant *Prenolepis imparis* reduced the food harvested by subordinate *Aphenogaster rudis*.

Nest Dispersion .

There was no clear evidence of uniform nest distribution in this community and nests were found to be randomly dispersed in more number of plots when nests of all the species were considered. The plots showing overdispersion were more in a rocky terrain and presumably, did not offer suitable nesting sites for the deep ground nesting ants.

As pointed out by Rytí and Case (1992) from a simulation study, it is not always logical to infer interspecific competition from the overdispersion or randomness of nests as spacing of colonies is affected both by the interspecific interactions as well as colony birth and death rates. As suggested by them, random spacing of colonies is possible even in an interacting community if the nest density is low or for colonies where interactions between established colonies are stronger than the effects of colonies on nest establishment. They also predicted that inter-nest distance between heterospecifics will be smaller than that between the conspecifics if interspecific competition is not strong. Result from our study show that inter-nest distance between heterospecifics are smaller than the conspecifics.

This would be indicative of the lesser intensity of competition in the study area.

Previous studies have also attributed overdispersion to the presence of one or more territorial species in the community (Levings and Traniello 1981, Majer and Camer-Pasci 1991) and habitat suitability (Doncaster 1981, Herbers 1989). Territorial species kill foundress queens of the other species and at times of the same species. Hence, the presence of a dominant territorial species in a locality by would cause nests of other species to be uniformly distributed. Most of the territorial species recorded in the tropics are arboreal and species mosaic in tropical arboreal ants is hence common (Majer and Camer-Pasci 1991). In this community the only territorial species was *O.smaragdina* and although they forage on the ground, they essentially nests in the canopy.

The fact that the heterospecific nest distance is smaller indicates that even the submissive species could coexist with the stronger ground nesting species in the community. This is also evident from the fact that nests of the strong encounterer species *Pheidole* sp.1 were closer to the hetero specifics which are essentially the species lower in the hierarchy and in almost in all the cases submissives. Savolainen and Vepsalainen (1988, 1989) found the submissives to coexist with the stronger territorial and encounterer species in the community.

Interspecific Competition : Does It Organize This Community?

There was obvious evidence of interference competition exerted by the territorial and the encounterer species which in turn affected the exploitative ability of the species lower in the hierarchy, although no evidence of resource partitioning was apparent. The strength of competition was not enough to influence the inter colony spacing of most of the species. Strength of competition in organizing community has been related to the success of the territorial species (Savolainen and Vepsalainen 1988); The territorial species in my study was arboreal nesting and was not an obligate ground forager. It

was hence likely that the presence of this species in the area did not affect the nest dispersion of other species. Some degree of a vertical partitioning of the foraging area between *O. smaragdina*, the arboreal nesting territorial species and the next stronger encounterer species *Pheidole* sp. 1 which is an obligate ground forager may be suggested. However, the high degree of interference and wide overlap in food choices of different species indicates the important role of interference competition in this community. Presence of territorial species in the community has been seen previously to have organizing role and has often been seen to form mosaics (Room 1971, Savolainen and Vepsäläinen 1988, Adams 1990, Andersen 1992).