Competition hierarchy in the ground foraging ant community in a wet evergreen forest (Western Ghats, India): Role of interference behaviour

P. Basu

School of Ecology and Environmental Sciences, Pondicherry University, Pondicherry 605 014, India.
Present address: Centre for Integrated Rural Development, 46, Vinayagar Koil St, Perumal Raja Garden, Reddyarpalayam, Pondicherry 605 010, India

Few studies are available on the role of interference behaviour in structuring competition hierarchy in the ant community. The present study examines the aggressive interference behaviour of different ground foraging ant species in a tropical evergreen forest habitat in relation to the positions different species held in the interspecific competition hierarchy. The territorial species, *Oecophylla smaragdina* was consistently aggressive towards other species and affected their activities even when it was not numerically dominant at the bait. Similarly, species higher in the hierarchy that were more aggressive affected the activities of species lower in the hierarchy at the bait.

INTERSPECIFIC competition in the form of exploitation and interference has been demonstrated conclusively in ants[1]. While evidence like resource partitioning suggests exploitative competition, a number of studies also show the importance of interference interaction in the structuring of the ant community[2–8]. But despite an overall recognition of the presence of interference interactions within ant communities, only a few studies have quantified the interspecific aggression and traced its role in mediating the competition hierarchy in ants. Again many of these studies are from the temperate or sub-tropical zones leaving a lacuna in observations from the resource-rich tropical forest habitats.

This study attempts to correlate the interspecific aggressions with the positions different ground foraging ant species hold in the competition hierarchy and assesses the role of interference competition in mediating competition hierarchy in the ground foraging ants assemblages in a tropical wet evergreen forest in the Western Ghats in Karnataka state (South Kanara district). The following questions were addressed: (i) Do species higher in the competition hierarchy gain dominance in the hierarchy through aggressive behaviour displayed towards species lower in the hierarchy at ephemeral food sources? (ii) How does interference behaviour determine the coexistence of different species in the community?

To answer the above questions, the competition hierarchy was first identified following Schoener's scheme[9]. The hierarchy includes 1) *territorial* species (that defend the foraging area, food and the nesting site), 2) *encounterer* species (that defend the food and the nesting site), and 3) *submissive* species (that defend only their nesting sites). Evidence for the interference competition was sought from the observations on the behaviour of different species at baits (simulating ephemeral food sources) and utilization of the same by different species.

Methodology

The study was conducted in an undisturbed evergreen forest near the Uppangala village located at the boundary between South Kanara and Kodagu district (75°40′22″ E Long. 12°32′35″ N Lat.) in the central Western Ghats. The average annual rainfall in this area is between 3000 and 3500 mm and has 4.5 to 5 dry months[10]. Activities of the species were measured by placing baits within 0.5 × 0.5 m square frames (bait quadrats). The baits were 1) placed randomly at 8 points during 1990 and 1991 and 2) placed at 15 points along 4 transacts (100 m apart) during 1993. Minimum distance between any two bait points was at least 100 m. The study was conducted during the dry seasons of 1990 (February through April), 1991 (February through May) and 1993 (March). Honey solution and dried fish were used as baits. The quantity of the bait items was kept constant and replenished as and when necessary. Only species that frequently visited the baits were considered for analysis. Species that were not territorial but showed more than 10% of the total number of cumulative aggressive behaviours of all species were considered as encounterers and others were considered as the submissive opportunists. If the abundance of a species was 20 individuals during any observation session, it was considered to be dominant in that session and, if only the dominating species was present during any five-minute observation session at a particular bait, was it consid-

ered to be monopolizing the bait. Activities of different species at a bait were monitored at hourly intervals. The 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 individual of another species. An individual would 'attack' another by biting the latter's antennae or mandible. Often an individual 'chased' another from the bait eliciting escape by the latter.

Multiway contingency tables were used to analyse species interactions at the baits. The variables in the contingency tables were chosen keeping the territorial species, one of the encounterer species and one of the submissive species. Species were categorized into abundance classes to avoid zeros in the table. The following abundance scale was used: 0–1 individual = 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.

An index of the ability of finding food items by different species was calculated in the following manner: if a species found a food item during the first hour of the 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 1; all other values lay between these two extremes. All the scores for particular species were then summed up to obtain the index of ability of a species in finding out food items.

Results

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 the baits, of which 15 were found in more than 5 cumulative observations (Table 1). This is about the half of the local species pool[10]. Of 15 species, 9 species that frequently visited the baits were classified following Schoener's[9] scheme into territorial, encounterer and submissive species based on qualitative observations. *Oecophylla smaragdina* was found to be the only territorial species. Pheidole sp. 1 and *Tetramorium tortuosum* were the encounterers and the rest were found to be submissive.

Bait occupancy

Although 10 species showed higher abundance, i.e. were dominant at some observation or the other at baits, only 5 species were dominant in more than 5% of the total observations. *Pheidole* sp. 1 occurred at maximum number of baits ($n = 21$, 87.5%) followed by *Aphenogaster beccarii* ($n = 19$, 79.71%). *O. smaragdina* occurred at 16 out of 24 baits (66.67%). *Pheidole* sp. 1 was recorded in maximum number of observations ($n = 420$, 53.98%) followed by *O. smaragdina* (297, 38.17%).

Dominance and monopolization

A total of 305 observations (39.2% of total number of observations) were dominated by some species or the

Table 1. 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
Pheidole sp. 1	87.5	54.0	12.34	5.78
Aphenogaster beccari	79.2	16.4	0.00	0.00
Monomorium sp. 1	66.7	10.7	2.83	0.26
Oecophylla smaragdina	66.7	38.2	3.86	3.47
Phedologiton sp.	29.2	14.6	4.37	0.00
Tetramorium sp. 2	29.2	11.95	0.90	0.00
Crematogaster wroughtoni	29.2	24.81	12.98	1.03
Camponotus compressus	29.2	16.84	0.00	0.77
T. tortuosum	25.0	21.47	1.16	0.13
Camponotus sp. 1	16.7	4.24	1.16	0.77
Crematogaster sp. 2	12.5	4.50	1.16	0.00
Amblyopone sp.	12.5	6.30	1.16	0.00
Leptothorax sp.	12.5	1.93	0.13	0.00
Monomorium sp. 2	8.33	0.90	0.64	0.13
Leptogenys sp. 1	8.33	2.44	0.00	0.00

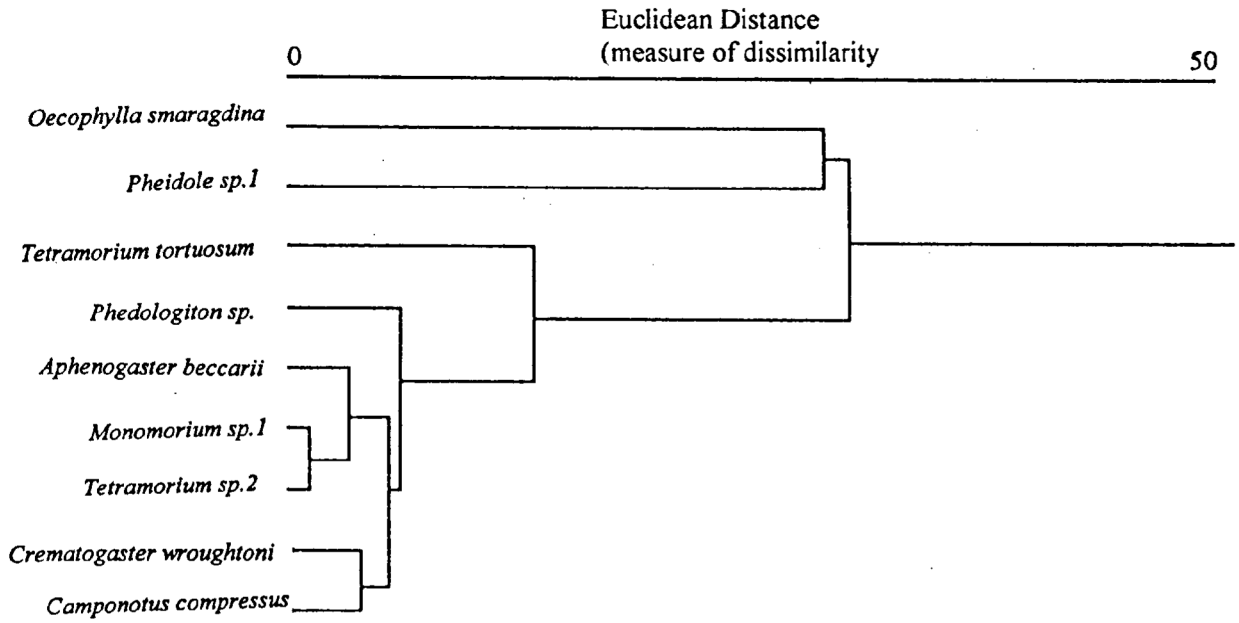

Figure 1. Dendrogram showing resemblances among different species in terms of aggressive behaviour at bait. Dendrogram was made based on the frequency of aggressive behaviour shown by each species at bait.

other. Domination by *Pheidole* sp. 1 (12.34%) and *Crematogaster wroughtonii* (12.98%) was evident. On 104 occasions, one species or the other monopolized a bait (13.37% of the total observations) (Table 1). *O. smaragdina* monopolized 90% of the baits that they dominated (3.47% of the total observations) followed by *Pheidole* sp. 1 monopolizing 46.88% of baits that they dominated (5.87% of the total observations). At some hour or the other during the day, *Pheidole* sp. 1 dominated 71.15% and monopolized the bait 51.92% of the times it arrived at the bait first. Likewise, *O. smaragdina* dominated the bait 60.86% and monopolized the bait 30.43% of the times when it arrived first at the bait.

Aggressive interactions at bait

A total of 371 aggressive interactions were observed during the whole period of experiment. *O. smaragdina* was engaged in the maximum number of direct aggressive interactions (46.01% of the direct aggressive behaviours shown by all species) while *Pheidole* sp. 1 showed the maximum number of indrect threats (37.02% of indirect threat shown by all species). Most of the aggressive behaviours of *O. smaragdina* were directed towards *Pheidole* sp. 1 while most of the aggressive behaviour of *Pheidole* sp. 1 were directed towards *T. tortuosum*. All the species other than *O. smaragdina* and *Pheidole* sp. 1 clustered together when the dendrogram was drawn based on the 'Euclidean distance' between species calculated from the frequency of different aggressive behaviours shown by different species (Figure 1). *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

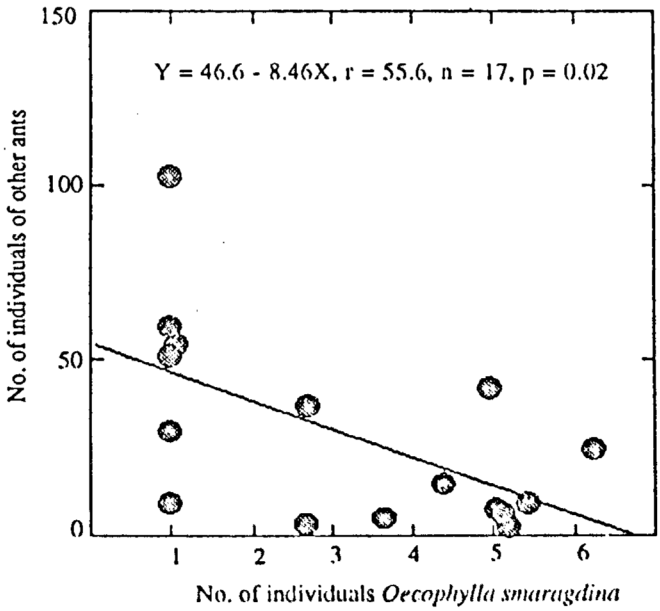

Figure 2. Relation between the number of individuals of *Oecophylla smaragdina* and that of other species at baits.

in the form of eliciting 'avoidance' were higher than direct interactions – 'attack' and 'chase'.

No significant correlation was found when the number of individuals of different species were correlated with the number of aggressive behaviours shown by each of these species at different baits.

Relation between activity of territorial species and the activities of other species

Abundance of *O. smaragdina* significantly affected the total number of individuals of all the other ants at the bait which included both encounterer and submissive species ($Y = 46.6–8.46X$, $R^2 = 0.31$, $N = 17$, $p = 0.02$) as evident from the negative regression slope (Figure 2). Regression between the abundance of *O. smaragdina* and the species richness and diversity of other species at any given observation was found to be non significant. *O. smaragdina* affected the abundances of *Pheidole* sp. 1 and *C. wronghtoni* but, it did not affect the abundances of the other submissive species, except *Camponotus compressus* (Table 2).

Species association at the bait

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 interactions between different pairs of submissives.

Association between most of the submissive species and the encounterer species was dependent on *O. smaragdina*, the territorial species (Table 3). *Pheidole* sp. 1 and *C. wroughtoni* affected the activities of most of the submissive species (Table 4). However, interactions among the submissives in most cases were not significant.

Table 2. Relation between the abundance of *Oecophylla smaragdina* and the encounterer and submissive species. $N = 778$. Only significant regression between *O. smaragdina* and other species have been shown

Independent variable (Y = *Oecophylla smaragdina*)			
Dependent variable (x)	Model	R^2	p
Pheidole sp. 1	13.613–0.64 x	0.013	< 0.01
Crematogaster wroughtoni	9.582–0.395 x	0.011	< 0.01
Camponotus compressus	0.323–0.013 x	0.013	< 0.01

Table 3. Effect of the territorial species on the interactions bet the encounterer and submissive species

Best model	*df*	*G*	*p*
O.sm–Pheid–Aph	6	45.02	< 0.0
O.sm–Pheid–M1	15	37.33	< 0.0
O.sm–Pheid–Phg	120	1739.57	< 0.0
O.sm–Pheid–T1	18	58.31	< 0.0
O.sm–Pheid–T2	16	29.87	< 0.0
O.sm–Pheid–C2	6	23.67	< 0.0

G, Likelihood ratio χ^2 statistic. The first species in the model is torial, the second one is the encounterer and the third one i submissive species. A significant three-order interaction mean association between the encounterer and a particular submi species is dependent on the presence of territorial. O.sm, *Oecop smaragdina*; Pheid, *Pheidole* sp. 1; Phg, *Phedologiton* sp.; T1 *tramorium tortuosum*; T2, *Tetramorium* sp. 2; M1, *Monomoriu* 1; C2, *Camponotus compressus*.

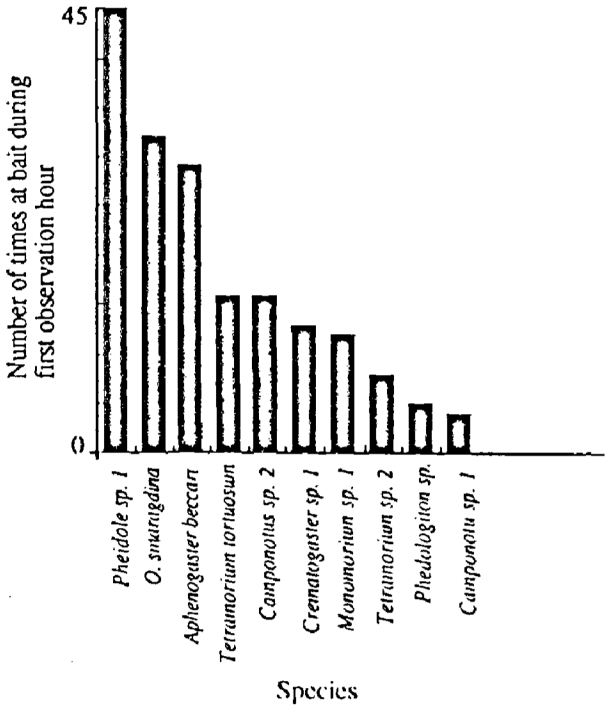

Figure 3. Frequency of occurrence of different species durir first hour of observations. Total number of observations = 778.

Rate of food location and behaviour

In the maximum number of experiments *Pheidole* arrived at a bait during the first hour of observa followed by *O. smaragdina* (Figure 3). *Pheidole* s was the fastest species in finding out food items lowed by *A. beccarii* and *O. smaragdina* (Figur Species which arrived at the bait during the first ho observation were the most aggressive ($r =$ $p = 0.05$) (Figure 5). Species quicker in finding c bait (higher score for the ability to find a food item) showed more number of aggressive behav ($r = 0.635$, $p < 0.05$).

Table 4. Interactions between the (i) encounterer species (*Pheidole* sp. 1) and the other submissive species and (ii) interactions between different submissive species. A significant two-way association signifies that the activities of one species is affected by the presence of the other species at the bait

2-Way model	*DF*	*G*	*p*	*N*
PH–CR	25	47.21	0.005	259
PH–APH	15	25.19	0.047	522
PH–M1	25	45.52	0.016	214
PH–PHDG	25	58.48	0.001	373
PH-CAMP1	15	18.85	0.040	179
PH–T2	20	43.00	0.002	132
CR-APH	15	56.16	0.001	132
CR-PHDG	25	157.62	0.001	252
CR–CAMP2	15	96.75	0.001	155
CR–T1	25	55.58	0.001	98
CR–T2	20	65.17	0.001	222
M1–CAMP2	15	27.99	0.020	206
PHDG–CAMP2	15	84.03	0.001	204
PHDG–T1	25	43.00	0.001	201
CAMP–CAMP2	9	20.20	0.02	156
T1–CAMP2	15	29.99	0.01	310
T1–T2	20	31.2	0.052	208

G, Likelihood ratio χ^2 test statistic; *N*, Total number of observations at those baits where particular species pair was found; PH, *Pheidole* sp. 1; CR, *Crematogaster wroughtoni*; APH, *Aphenogaster beccarii*; M1, *Monomorium* sp. 1; CAMP1, *Camponotus* sp. 1, CAMP2, *Camponotus compressus*; T1, *Tetramorium tortuosum*; T2, *Tetramorium* sp. 2; PHDG, *Pheidologiton* sp.

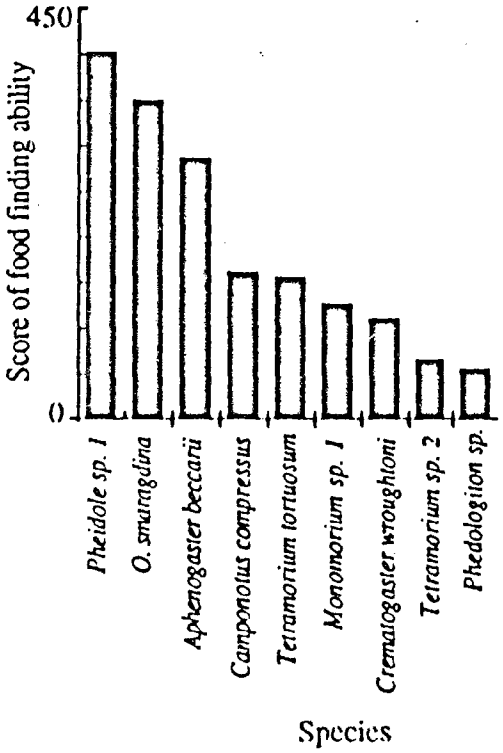

Figure 4. Score of food-finding ability of different species. Calculated as follows: if a species found a food item during the first hour of observation it was assigned a score of 6 and consecutively if a species found a food item during the sixth hour of observation it was assigned a score of 1. All the scores for a particular species for all the experiments were summed up to obtain a final score.

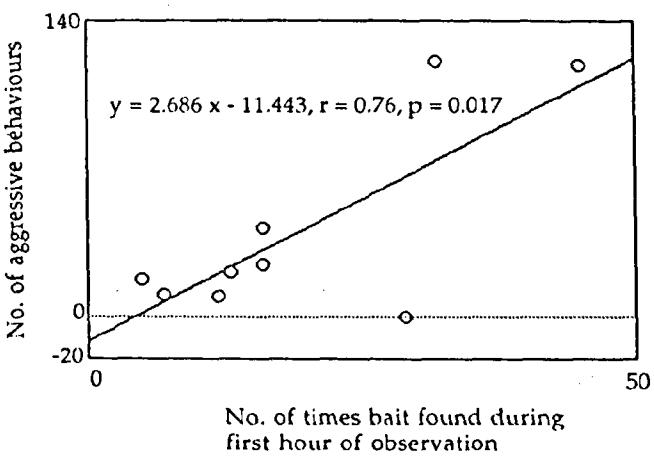

Figure 5. Relation between number of times each species came at a bait during the first hour of observation and number of aggressive behaviour shown by it. Total number observations = 778.

Discussion

Behaviour and competition hierarchy

Interference competition expressed as aggressive interaction between pairs of species has been observed as a frequent phenomenon among ants[1]. The coexistence of individuals of different species at a food item is often a function of the degree of aggressiveness of different species. The observations from the present study also indicate a crucial role of aggressive interference behaviour rather than numerical dominance at the food source in determining the hierarchy in a community. *Pheidole* sp. 1 dominated the maximum number of baits in terms of abundance, monopolized the maximum number of baits that it dominated, was the first to locate a bait for the maximum number of times and dominated and monopolized a bait for the maximum number of times when it was the first to locate the bait. But it did not prove its superiority in terms of aggressive interference interaction over *O. smaragdina*. *O. smaragdina* established its superiority in the hierarchy by showing the maximum number of aggressive behaviour towards other species. The aggressive behaviour shown by it towards *Pheidole* sp. 1 was also far higher than the reverse. 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 which slightly contradicts a previous finding by Andersen[8] who showed a strong positive correlation between abundance and aggressive behaviour of the dominant species. The response of *Pheidole* sp. 1, the next most aggressive species was more in the form of indirect aggressiveness, i.e. by eliciting avoidance and escape from the other species.

Based on Schoener's scheme[9] it was possible to categorize different species that came to the bait regularly. The most aggressive species in this community was *O. smaragdina* which is known for territoriality[1]. The aggressiveness and territorial behaviour of this arboreal nesting species have been amply documented previously. Holldobler[1] 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 *T. tortuosum*. *Pheidole* sp. 1 was the only species that showed some aggressive behaviour towards *O. smaragdina*. Although *T. tortuosum* has been categorized 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 shown by 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*[1]. Majer[11–13] documented the dominant behaviour of a species of *Tetramorium* in the ant mosaic in Ghana cocoa farm. Brian[14] reported the same from England.

Among other species, submissive behaviour has been previously documented 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 systems[1]. Species of the genus *Camponotus* have been documented as subordinate species in an ant mosaic in Ghana[15], while Vepsalainen and Pisarksi[16] documented a species of *Camponotus* as encounterer.

Interference behaviour and coexistence

Results from the present study clearly show 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 when it was present. 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 *T. 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 the maximum number of overt aggressive behaviour such as 'attack' and 'chase' and *O. smaragdina* was the only species that attacked any other species. 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 amount of aggressive behaviour shown by it. However *Pheidole* sp. 1, the species which showed the second maximum number of aggressive behaviour, was present abundantly at the bait. It dominated and also monopolized a bait maximum number of times. Interestingly, the submissive species could coexist with the territorial species as predicted in Schoener's scheme[9] 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*. Vepsalainen and Savolainen[17] demonstrated that submissive *Myrmica* sp. could coexist with territorial *Formica* sp. Occasional coexistence of submissive with the dominants has been found to be affected by morphological differences, colony size and foraging area. Fellers[18] found significant reduction in the activity of the submissive species in the 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 being encounterer and territorial respectively, are expected to defend their food items. It was hence likely that there was a correlation between rate of food finding and aggressiveness.

As ants live in long-lived colonies with many workers, the intensity of competition is amplified[6]. Schoener[19] described the competition pressure in the ant community to be closer to vertebrates than to any other insect. In this highly competitive environment, the coexisting ant species would be expected to show divergence in their resource utilization pattern as predicted by the competition theory. The divergence could be either due to their food choice or selection of nesting sites. These divergences are in turn expected to be reflected on the morphology and behaviour of the competing species. While a number of studies are available demonstrating partitioning of resources by the competing ant species, the importance of interference competition has been reemphasized in this regard[6,8]. 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[6]. Presence of aggres-

sive dominant species in a given community and the response of other species toward it will lead to a separation of resource utilization mode of the other species and the coexistence of species would depend on the relative successes of other species in maximizing their resource utilization in presence of a top competitor. Aggression from the dominant species reduces the fitness of the submissives by: (i) restriction of foraging activity in terms of reduction in forager density and foraging area[20]; (ii) reduction in food harvesting[21,22]; (iii) decreased production of sexuals[23–25].

In this regard, it is often easy to visualize a linear competition hierarchy determined by the aggressiveness of 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/microhabitat. The present study did not address the aspect of habitat/microhabitat 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 was 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 species by taking to stealthy behaviour even though their abundance was affected by the territorial species.

While the present study showed the total number of individuals of the encounterer and submissive species being regulated by the territorial *O. smaragdina*, the evidence for the regulation of species diversity and species richness by the territorial species in the present community was not clear.

1. Holldobler, B. and Wilson, E. O., *The Ants*, Harvard University Press, Cambridge, 1990.
2. Adams, E. S. and Traniello, J. F. A., *Oecologia*, 1981, **51**, 265–270.
3. Holldobler, B., in *The Biology of Social Insects* (Proceedings of the Ninth International Congress of IUSSI, Boulder, Colorado, 1982) (eds Breed, M. D., Michener, C. D. and Evans, H. E.), West View Press, Boulder, 1982, pp. 312–317.
4. Holldobler, B. and Lumsden, C. J., *Science*, 1980, **210**, 732–739.
5. Levings, S. C. and Traniello, J. F. A., *Psyche*, 1981, **88**, 265–319.
6. Savolainen, R. and Vepsalainen, K., *Oikos*, 1988, **51**, 135–155.
7. Galle, L., in *Social Insects and Environment* (Proceedings of the 11th International Congress, IUSSI, Bangalore) (eds Veeresh, G. K., Mallik, B. and Viraktmath, C. A.), Oxford-IBH, New Delhi, 1990, pp. 706–707.
8. Andersen, A. N., *Am. Nat.*, 1992, **140**, 401–420.
9. Schoener, T. W., *Am. Nat.*, 1983, **122**, 240–285.
10. Basu, P., *Biotropica*, 1997, in press.
11. Majer, J. D., *J. Appl. Ecol.*, 1976, **13**, 145–155.
12. Majer, J. D., *J. Appl. Ecol.*, 1976, **13**, 123–144.
13. Majer, J. D., *J. Appl. Ecol.*, 1976, **13**, 157–175.
14. Brian, M. V., *Social Insects: Ecology and Behvioural Ecology*, Chapman and Hall, New York, 1983.
15. Room, P. M., *J. Appl. Ecol.*, 1971, **40**, 735–751.
16. Vepsalainen, K. and Pisarksi, B., *Am. Zool. Fennici*, 1982, **19**, 327–335.
17. Vepsalainen, K. and Savolainen, R., *J. Anim. Ecol.*, 1990, **59**, 643–654.
18. Fellers, J. H., *Ecology*, 1987, **68**, 1466–1478.
19. Schoener, T. W., in *Community Ecology* (eds Diamond, J. and Case, T.), Harper and Row, New York, 1986, pp. 556–586.
20. Yasuno, M., *Sci. Rep. Tohuku Univ.*, 1965, **31**, 181–194.
21. Lynch, J. F., Balinsky, E. C. and Vail, S. G., *Ecol. Entomol.*, 1980, **5**, 353–371.
22. Reznikova, J. I., *Behaviour.*, 1982, **80**, 84–95.
23. Pontin, A. J., *J. Anim. Ecol.*, 1961, **30**, 47–54.
24. Pontin, A. J., *J. Anim. Ecol.*, 1963, **32**, 565–574.
25. Boomsma, J. J. and Van Loon, A. J., *J. Anim. Ecol.*, 1982, **51**, 957–974.

ACKNOWLEDGEMENTS. This study was supported partly by a fellowship from the UGC. French Institute of Pondicherry partly provided the infrastructure during the study. Sincere thanks are due to Dr Priya Davidar for her invaluable support all through this study and to Nambi for his assistance during a crucial phase of the field experiment. Critical comments on the manuscript from Drs Priya Davidar, K. N. Ganeshaiah, Francois Houelier, Rani and C. P. Geevan have immensely helped this paper.