CONTRIBUTIONS TO THE BIOLOGY OF THE QUEENLESS PONERINE ANT *DIACAMMA CEYLONENSE* EMERY (FORMICIDAE)

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(With five text-figures)

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Key words: *Diacamma ceylonense*, queenless ant, Ponerinae, Formicidae, Hymenoptera

All ants are generally classified as highly eusocial. However, there are some 100 species of ants belonging to the morphologically primitive subfamily Ponerinae, which lack a morphologically differentiated queen. One or a small number of mated workers (gamergates) function as queens, i.e. they produce male as well as female offspring. Such ant species are of great interest as they provide unique opportunities to understand the causes and consequences of queenlessness. This is the first report of a long-term field study we have initiated on a large population of the queenless ponerine ant, *Diacamma ceylonense* Emery, on the campus of the Indian Institute of Science, Bangalore. Data are provided on the numbers of colonies present during a 213-week period, from which the probable time of colonisation of the site by *D. ceylonense* is suggested. Twenty-six entire colonies were excavated to study the adult and brood composition. While some colonies did not appear to have a gamergate at the time of excavation, others had only one gamergate per colony. Only the gamergate was mated and had well developed ovaries, while all the workers were unmated and had undeveloped ovaries. Excavated colonies had an average of 230 adult females, 2 males and 80 items of brood. The gamergates were indistinguishable from their workers in body size but there was significant variation in the size of workers between colonies. On an average, colonies employed 24% of their workers outside the nest for foraging and other duties. The relative constancy of this proportion permits estimation of total colony size by merely estimating the number of extranidal workers and thus without having to excavate the nests. In the five colonies studied, foragers spent an average of 9 to 23 days of their lives in performing foraging duties. Most foragers remained faithful to one or a narrow range of compass directions, although such directional preferences of all of them put together permitted colonies to exploit resources in all directions.

INTRODUCTION

Eusocial insects are defined as those insects whose colony members exhibit overlap of generations, cooperative brood care and reproductive caste differentiation into a queen caste and a worker caste. Highly eusocial species are those in which the queen and worker castes are morphologically differentiated (Wilson 1971).

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In this scale of social evolution, all ants are generally classified as highly eusocial (Hölldobler and Wilson 1990, Bourke and Franks 1995). However, some 100 species of ants, belonging to the morphologically primitive subfamily Ponerinae, lack a morphologically distinguishable queen. Their colonies consist only of workers (in addition to males of course), one or a few of whom are mated and take on the function of queens, i.e. production of male and female offspring. These mated, reproducing workers are termed gamergates (Peeters 1991). Queenless ants are of great interest for several reasons: (1) They provide an opportunity to understand the conditions under which the queen caste may be lost. (2) In the absence of winged queens, new colonies have to

be necessarily founded by walking gamergates, which must result in a rather unusual population genetic structure. (3) They can be used as model systems to understand how one or a small number of individuals can establish and maintain reproductive monopoly among a group of identical, or nearly identical, individuals. This is a problem that has been extensively investigated with bees and wasps (see Gadagkar 2001 and references therein) but because queenlessness in ponerine ants is evolutionarily derived from the queenright condition (Baroni Urbani *et al.* 1992), a new perspective is expected from a study of these ants.

In this context, the genus *Diacamma* represents a most fascinating example. In *Diacamma*, all females eclose with a pair of club-like thoracic appendages called gemmae. The gamergate mutilates all workers who eclose after her, by clipping their gemmae. Such mutilation results in poorly understood neurological changes in the victims, making them incapable of sexual calling and mating. This unique mechanism by which the gamergate maintains her reproductive monopoly seems to have a built-in mechanism to ensure that a colony does not necessarily die if its gamergate dies. Mutilated workers do not mutilate others so that, upon the death of a gamergate, the next individual to eclose retains her gemmae, mutilates all those that eclose after her and takes over as the next gamergate of the colony (Fukumoto *et al.* 1989, Peeters and Higashi 1989). While this description fits all other species of *Diacamma* examined so far, there does appear to be an exception. There is at least one species in which the gamergate seems to be capable of maintaining reproductive monopoly without mutilating her workers. This species, which was first found at the foot of the Nilgiri hills, and mistakenly identified as *Diacamma vagans* Smith (Peeters *et al.* 1992), is yet to be described. We therefore refer to it here as *Diacamma* sp. from Nilgiri. *Diacamma* sp. from Nilgiri is morphologically very similar to

Diacamma ceylonense Emery, which is abundantly distributed in and around Bangalore. There is a large population of *D. ceylonense* in the so-called Jubilee Garden in the campus of the Indian Institute of Science, Bangalore (13° 00' N 77° 32' E). Such an easily accessible population facilitates observation of colonies in their natural habitats. Most previous work on *Diacamma*, and indeed on most ponerine ants, has been largely restricted to observation in artificial nests in the laboratory, of ants removed far from their natural habitat.

For all these reasons, we have initiated a long-term study of the population of *D. ceylonense* in the Jubilee Garden of the Indian Institute of Science, Bangalore. This is the first report of this ongoing study.

MATERIAL AND METHODS

This study was conducted in the Jubilee Garden, Indian Institute of Science, Bangalore. The site is a plantation of *Acacia auriculiformis*, with a few individuals of *Polyalthia longifolia*, *Tamarindus indica* and *Ficus* sp. The area (about two hectares) was divided into 60 line transects. Initially, an extensive search was conducted to locate the nests of *D. ceylonense*. All nests were marked with sequentially numbered aluminium tags and the tree nearest to each nest was marked with red paint. Every Monday, the nests were monitored for activity and for the occurrence of males. Nests that appeared to be abandoned were checked by inserting a stick inside the nest entrance and waiting for the appearance of workers. In addition, such nests were also monitored for activity during the subsequent 4-5 weeks, before confirming them as abandoned. On the first Monday and Tuesday of every month, the entire study site was searched systematically to record any newly initiated nests. Data thus obtained, during 213 weeks, on the numbers of nests, numbers of newly initiated nests, abandoned nests and number of males, were

analysed in relation to abiotic factors such as maximum and minimum temperatures and total rainfall using the Kendall's correlation coefficient. Climatic data were obtained from the India Meteorological Station, Bangalore. As there was a monotonic increase in the number of nests during the first 120 weeks of study, a linear regression model was fitted to these data which was then used to predict the probable time of colonisation of Jubilee Garden by *Diacamma ceylonense*.

Twenty-six colonies with all individuals and brood were collected from within the Indian Institute of Science campus, but outside the Jubilee Garden. Nest characteristics such as height of the mound, number of brood chambers, depth of the nest and commensals encountered, were recorded for all these nests. Head width and alitrunk length of all individuals were measured in 21 of these colonies. Data on head width and alitrunk length were subjected to one-way analysis of variance to partition variance within and between colonies. In the nine colonies that had a gamergate, one-sample t-tests were performed to compare each gamergate with her workers. In 15 of these 21 colonies (including the nine that had a gamergate), the numbers of mature eggs, width and length of proximal oocytes and the presence (or absence) of sperm in the spermatheca, were recorded for all individuals by dissecting their gaster.

Five other colonies were chosen for observation of the extranidal behaviours. Four of these colonies were observed for four weeks each while one was observed for 55 weeks. Each observation session was of 4-hour duration and was conducted either in the morning (0600 to 1000 hrs), midday (1000 to 1400 hrs) or afternoon (1400 to 1800 hrs). One each of the morning, midday and afternoon sessions were completed in each week, thus yielding 12 hours of data per week, per nest. All new workers seen outside the nest were uniquely marked with quick-drying coloured paint on the thorax or abdomen, starting two weeks before the commencement of observations and continuing throughout the period of observation. All extranidal behaviours visible to the observer, positioned near the nest mound, were recorded. The 852 hours of data thus collected, were used to compute the number of extranidal ants active per day, the number of days for which different ants were active, and the rate per hour at which they performed extranidal activities. When the ants left the vicinity of the nest mound, the compass direction in which they departed was recorded in eight discrete directions namely North, Northeast, East, Southeast, South, Southwest, West and Northwest. When the foragers returned, what they brought back (food, building material or nothing) was noted. The proportion of successful and unsuccessful trips made by foragers who had made at least three trips were then computed and compared. A successful trip was defined as the act of returning to the nest with either food or building material. An unsuccessful foraging trip was one in which the ants returned with neither food nor building material. Data on foraging directions of all active foragers were subjected to Rayleigh's test (Batschelet 1981) of randomness to determine the degree of randomness in the foraging paths, both for individual ants as well as for colonies as a whole.

Another eleven colonies were excavated in an attempt to predict the colony size from the numbers of ants engaged in extranidal tasks. Over a period of three days, all ants seen outside the nest were marked. At least two persons spent 3 hours and 30 minutes each, per day (30 minutes at the beginning of every hour from 0600 hrs-1800 hrs) for three consecutive days, marking the ants. Pilot experiments had indicated that this effort was more than adequate to mark all extranidal ants. On the fourth day the nest was excavated to determine the colony size (these nests were then used for other experiments not reported here) so that the relationship between the number of extranidal ants and the total colony size could be ascertained.

RESULTS AND DISCUSSION

Diacamma ceylonense nests were found to occur quite commonly in the study area. The nests are subterranean, with a distinct mound at the entry of the nest. The mounds are often decorated with dry twigs, leaves, insect and spider exuviae, and occasionally, bird feathers. Moffett (1985) observed that these decorations are used to harvest dewdrops, which the ants drink in the mornings. The excavated nests contained 230.5 ±108.6 adult female ants, 2.3 ±5.3 males, 18.5 ±19.4 eggs, 22.6 ±18.7 larvae and 40.0 ±36.6 pupae. The nests were 63.9 ± 20.6 cm deep under the ground with 4.1 ±1.2 brood chambers and the mounds were 3.2 ±4.1 cm above the ground (Table 1). Males were usually found in the first chamber, closest to the entrance. The next 2-3 chambers had brood and the last chamber at the bottom contained refuse. We often found cockroaches, isopods, crickets, pseudoscorpions, bagworms, grubs, earthworms and a few other ant species in the nests; we presume that these were commensals (Table 2). Nine out of the twenty-one colonies excavated, seemed to lack a gamergate; the possibility that the gamergate was lost during excavation seems unlikely but cannot, of course, be entirely ruled out. The remaining 12 colonies invariably had only one gamergate each. In two nests, one or two individuals other than the gamergate also had gemmae, but only on one side of their thorax; perhaps their mutilation was not

Table 2: Co-inhabitants observed in *Diacamma ceylonense* nests

Commensal	No. of nests in which observed
Cockroaches	12
Crickets	11
Pseudoscorpions	9
Bagworms	3
Grubs	1
Earthworms	1
Isopods	14
Other ant species	1

yet complete. Of the 15 colonies used for dissection, 9 had one gamergate each, while the remaining 6 colonies did not have a gamergate. The number of mature eggs in the gamergates ranged from 0-24 with a mean of 8.78 ±10.28 eggs. None of the workers had developed ovaries and none of them were mated in any of the colonies, including those without a gamergate (Table 1). Thus *D. ceylonense* colonies are monogynous and recent molecular studies suggest that they are also monoandrous but with some serial polygyny (gamergate turnover) (Gopinath 2002).

For both head width and alitrunk length, there was a significant added variance between colonies. In the case of head width, this added variance between colonies was significantly higher than the variance within colonies, while in the case of alitrunk length, this variance was significantly less than the variance within colonies (Table 3). Variance between colonies is

Table 3: One-way analysis of variance of head width and alitrunk length of individuals of *Diacamma ceylonense* from 21 colonies

	Source	DF	SS	MS	F	p
Head width[a]	Among colonies	20	1811.07	90.55	791.42	0.001
	Within colonies	4731	541.31	0.11		
	Total	4751	2352.38			
Alitrunk length[b]	Among colonies	20	1151.20	57.96	94.61	0.001
	Within Colonies	4683	2849.00	0.61		
	Total	4703	4000.19			

[a]Variance between colonies significantly higher than variance within colonies
[b]Variance between colonies significantly lesser than variance within colonies

Table 1: Colony composition and body measurements of the individuals in *Diacamma ceylonense*

Date of collection	Colony code	No.of females	No.of males	No.of eggs	No.of larvae	No.of pupae	Depth of nest (cm)	Height of mound (cm)	No.of brood chambers	Head width[a] (mm)	Alitrunk length[a] (mm)	No. of mature eggs[b]	Width proximal oocyte (mm)	Length of proximal oocyte (mm)
25.11.93	D-1	292[c]	0	[d]	11	15	50	0	4	—	—	—	—	—
25.01.94	1	341	0	0	13	15	50	6	3	1.99 ±0.05	3.91 ±0.14	—	—	—
24.02.94	2	499[e]	0	0	23	78	150	0	5	2.29 ±0.03	4.51 ±0.10	—	—	—
31.03.94	3	319	3	[d]	51	110	75	0	3	2.26 ±0.09	4.54 ±0.16	—	—	—
27.04.94	4	140[e]	0	28	20	30	50	0	2	2.02 ±0.06	4.14 ±0.15	—	—	—
24.05.94	5	158	8	8	29	15	65	0	4	2.02 ±0.06	4.10 ±0.14	—	—	—
28.06.94	6	420[e]	0	36	55	103	55	0	4	2.00 ±0.05	4.14 ±0.16	—	—	—
28.07.94	7	220[c]	0	42	51	45	65	5	5	—	—	—	—	—
23.08.94	D-2	184[c]	0	14	13	3	65	0	4	—	—	—	—	—
31.08.94	8	251	0	46	31	35	45	7	3	2.03 ±0.07	3.97 ±0.20	0	0.31 ±0.06	0.98 ±0.39
28.09.94	9	286	1	66	66	64	50	0	6	2.06 ±0.08	4.10 ±0.16	13	0.37 ±0.13	1.03 ±0.38
27.10.94	10	91	0	0	8	18	70	0	4	2.01 ±0.06	4.07 ±0.18	0	0.43 ±0.17	0.95 ±0.49
15.11.94	11	161	0	33	0	12	60	0	3	2.00 ±0.05	4.06 ±0.16	0	0.29 ±0.04	0.73 ±0.29
06.12.94	12	138[e]	0	0	0	0	60	10	5	2.05 ±0.07	4.20 ±0.15	—	—	—
18.01.95	13	18[e]	0	0	0	0	60	10	2	2.10 ±0.07	4.25 ±0.16	—	—	—
07.02.95	14	250	0	3	1	0	50	5	5	2.07 ±4.29	4.29 ±0.14	3	0.38 ±0.04	1.31 ±0.14
08.03.95	15	293	13	33	33	55	85	0	5	2.04 ±0.07	4.23 ±0.17	16	0.46 ±0.03	1.4 ±0.05
05.04.95	16	180[e]	0	35	10	23	80	0	7	2.02 ±0.08	4.18 ±0.14	—	—	—
17.05.95	17	131	1	24	21	38	60	0	3	2.03 ±0.08	4.15 ±0.17	24	0.43 ±0.08	1.27 ±0.25
16.06.95	18	297	10	44	26	75	65	0	4	2.06 ±0.08	4.26 ±0.13	23	0.4 ±0.06	1.33 ±0.21
13.07.95	19	269	22	0	11	130	60	0	5	2.06 ±0.08	4.32 ±0.23	0	0.63 ±0.08	0.25 ±0.04
25.07.95	D-3	237[c]	0	0	9	11	50	10	5	—	—	—	—	—
23.08.95	20	200[e]	0	9	35	49	40	8	4	2.00 ±0.05	4.21 ±0.14	—	—	—
13.09.95	21	312[e]	0	11	34	53	65	5	4	2.06 ±4.28	4.28 ±0.17	—	—	—
15.09.95	D-4	262[c]	0	11	36	64	70	8	5	—	—	—	—	—
27.10.95	22	45[e]	1	0	0	0	65	10	2	2.06 ±0.08	4.32 ±0.14	—	—	—
MEAN		230.5 ±108.6	2.3 ±5.3	18.5 ±19.4	22.6 ±18.7	40.0 ±36.6	63.9 ±20.6	3.2 ±4.1	4.1 ±1.2	2.04 ±0.07 (n=4751)	4.16 ±0.21 (n=4703)	8.8 ±10.3		

[a]Up to 9% of the individuals were not used for head width and alitrunk length measurements in some colonies; [b]mature eggs - those which were about to reach the main duct; [c]Body measurements not done; [d]Eggs not counted; [e]Colony without gamergate; All gamergates dissected were found to have sperms in the spermatheca.

likely to have a genetic basis and variance within colonies, a nutritional basis. As expected from the fact that the gamergate is simply an unmutilated worker, in 17 out of 18 tests (9 colonies, each tested for head width and alitrunk length), the gamergate was not significantly different in body size as compared to the workers in the colony (one sample t-test; Table 3).

The number of active nests steadily increased from the commencement of this study (December 1993) up until 120 weeks. After that the number of active nests decreased to an extent (Fig. 1a). In our 213 weeks of study, we recorded a total of 117 nests, active at one time or another. Although new nests were initiated and abandoned throughout the study period, initiations usually outnumbered abandonings during the first 175 weeks, while abandonings outnumbered initiations during the next 38 weeks (Fig. 1b,c). Twenty-one out of 117 nests were active throughout the 213 weeks of observations. Given that they were already present at the beginning of the study, they must have been older than 213 weeks. Males were few in number but were recorded more or less throughout the year (Fig. 1d). Climatic data are depicted in Fig. 1e. There was a positive correlation between minimum temperature and number of nests initiated ($\tau = 0.26$ at $p<0.008$) and abandoned ($\tau = 0.38$, at $p<0.0001$). There was also a positive correlation between rainfall and number of nests initiated ($\tau = 0.43$ at $p<<0.01$) and abandoned ($\tau = 0.39$, at $p<0.0001$) and number of males ($\tau = 0.29$, at $p<0.005$). Maximum temperature showed no such correlation.

Since the number of nests increased steadily during the first 120 weeks, a linear regression model was fitted to the data (Fig. 2). The model is highly significant. Extrapolating backwards in time, using the slope and its 95% confidence interval, we may hypothesize that the Jubilee Garden was colonised by *D. ceylonense* some 85 to 113 weeks before the beginning of the study, i.e. between September 1991 and May 1992 (Fig. 2).
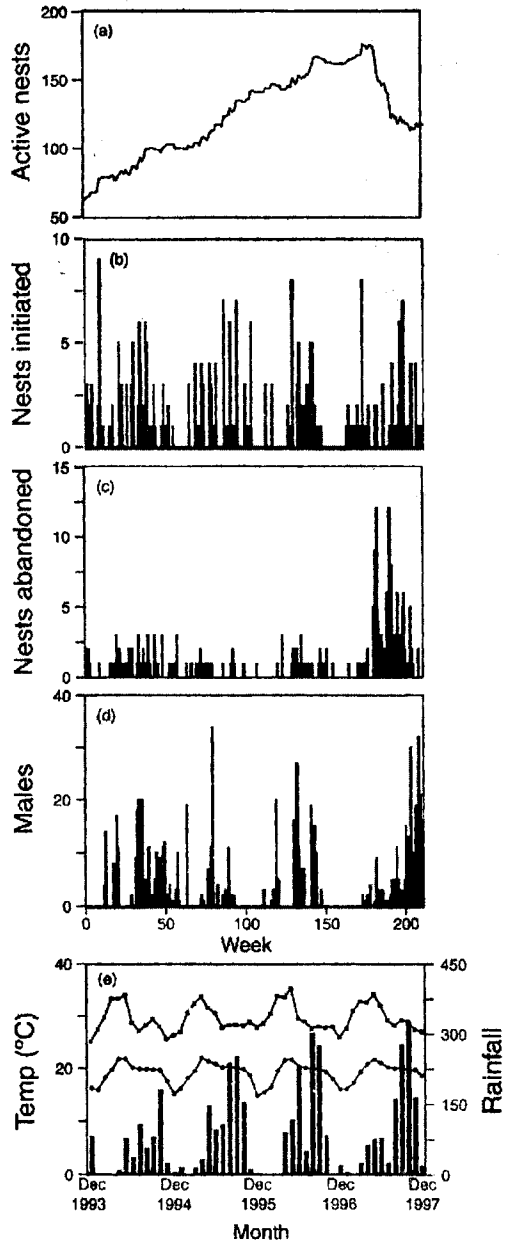

Fig. 1: The number of (a) active nests, (b) nests initiated, (c) nest abandoned, (d) males and (e) mean monthly rainfall (bars), mean monthly maximum temperature (upper line) and mean monthly minimum temperature (lower line), during the 213 weeks of census of the Jubilee Garden population of *Diacamma ceylonense*
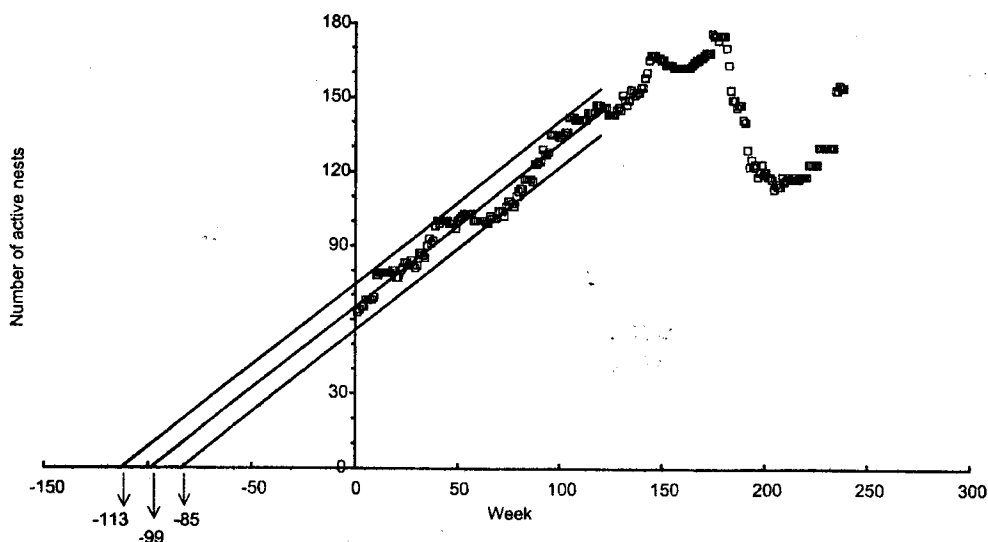
Fig. 2: Number of active nests from the 120-week data was used to fit a linear regression model which was extrapolated backwards using the slope and its 95% confidence intervals, to estimate the probable time of colonisation of Jubilee Garden by *Diacamma ceylonense*

Diacamma ceylonense workers are individual, diurnal foragers with directional fidelity within a narrow range of directions (as seen from our observations given below). Their major food consisted of termites, although bugs, cockroaches, grasshoppers, crickets, spiders and other species of ants were also observed being brought to the nest on some occasions. Prey, however large, was never retrieved in groups, but there was some cooperation among the workers near the nest to manoeuvre it through the nest entrance. Foraging continued for most of the day on colder days, but was restricted to the mornings and evenings only, on warmer days. Foraging was suspended during heavy rains although some extranidal tasks like nest cleaning and shifting of materials around the nest increased soon after rainfall. On finding an item of prey, the forager paralysed it by stinging and returned with it to the nest quickly and in a short, more linear path as compared to the often long-winding path it had followed during its outward journey. When a termite nest or trail was discovered, the successful forager made repeated trips to the same source.

The mean number of active individuals seen outside the nest during any 4-hour observation session varied from about 6 to 32 and the mean foraging life span of workers ranged from 9 to 23 days (Table 4). Foraging was the most frequently performed extranidal activity. In four out of five

Table 4: Number of active animals per observation session, and foraging life span in five colonies

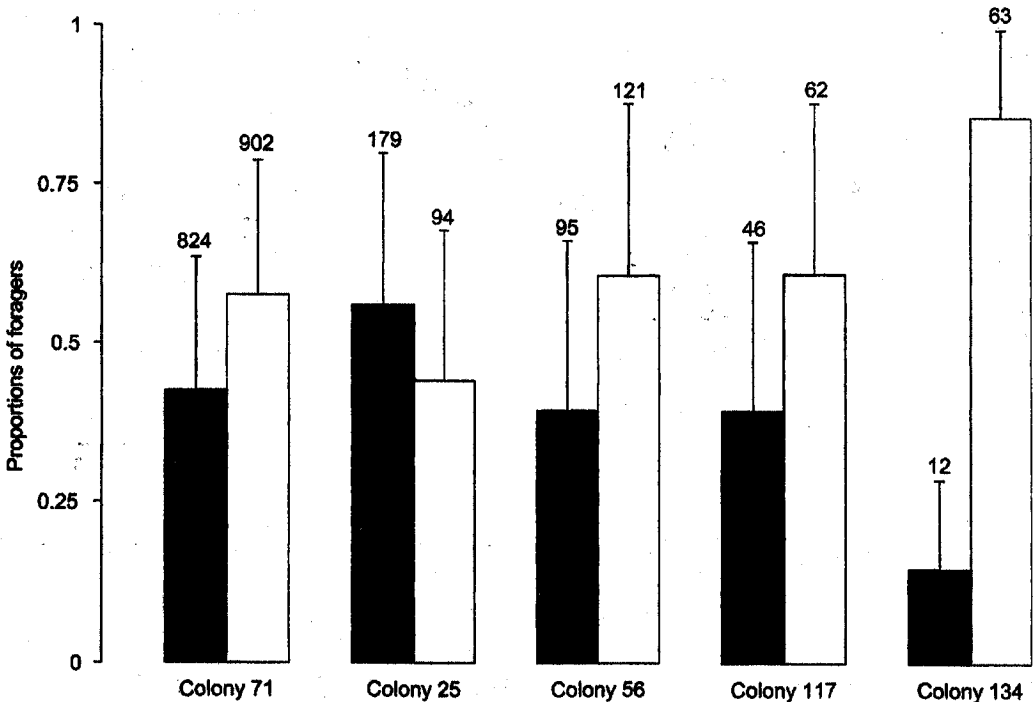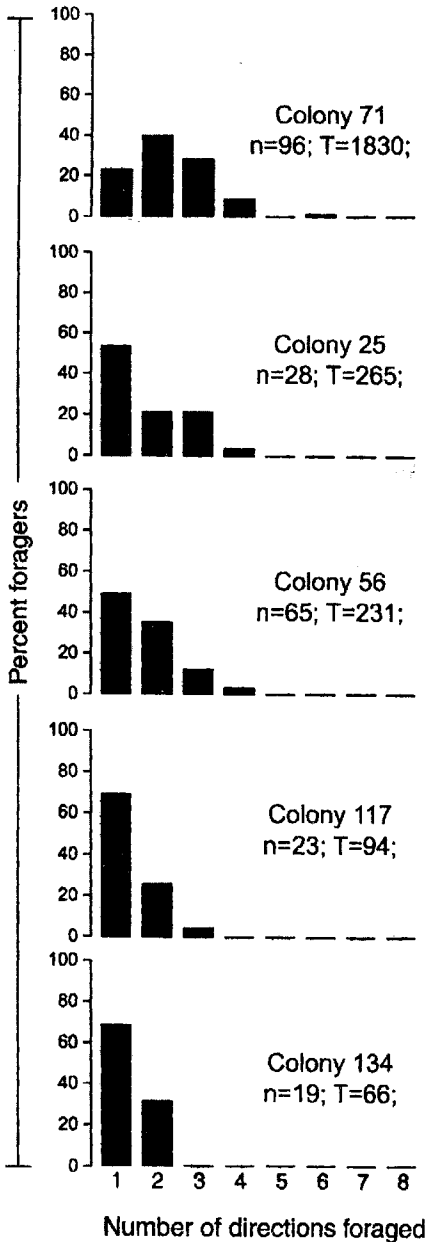| Nests	No. of sessions & No. of days observed	No. of active animals/session[a] Mean ±SD (Range)	Foraging life span in days Mean ±SD (Range)
071	165 sessions; 385 days	6.7 ±3.6 (1-17)	23.3 ±22.2 (1-154)
025	12 sessions; 26 days	17.2 ±2.2 (11-21)	13.2 ±10.2 (2-26)
056	12 sessions; 27 days	32.3 ±8.0 (22-51)	9.0 ±7.6 (2-27)
0117	12 sessions; 26 days	12.9 ±3.7 (5-18)	12.9 ±8.7 (2-26)
0134	12 sessions; 23 days	16.2 ±5.5 (4-22)	15.5 ±6.1 (2-23)

[a]1 session = 4 hours

Fig. 3: Proportions of successful (shaded bars) and unsuccessful (blank bars) trips made by foragers in five colonies (numbers above bars are the numbers of successful/unsuccessful trips)

colonies (Fig. 3; Mann Whitney U test; Colony 71, 56 and 134 at p<0.001, and Colony 117 at p<0.05), the number of successful foraging trips was significantly less than the number of unsuccessful trips In one colony (Fig. 3, Colony 25), foragers were somewhat more successful in retrieving prey items, but the number of successful and unsuccessful trips did not differ significantly from each other (Mann Whitney U test, p>0.05). Foragers who had made at least three trips were used for this analysis. The proportions of successful and unsuccessful trips were computed for each worker and then averaged across workers in each colony.

Many foragers seemed to be faithful to certain foraging directions (Fig. 4), although the colony itself seemed to have foragers covering all directions. Rayleigh's test of randomness confirms that in all five colonies studied,

individual foragers were non-random with respect to the directions in which they made foraging trips, but that the colony as a whole (with all its foragers put together) was random in this regard. In each colony, even the most random forager was less so than the colony as a whole (according to Rayleigh's test of randomness, p<0.05, see Fig. 5). The mechanism by which the foragers achieve such collective randomness, in spite of individual non-randomness, remains to be investigated.

Experiments in which all the ants seen outside the nests were marked before nest excavation demonstrate that the number of ants seen outside the nest is a reasonably constant proportion of the total colony (24.39% ±9.63%) (Table 5). This information can be used to approximately infer colony size without necessarily having to excavate nests. Besides helping to avoid unnecessary excavation of nests,

Fig. 4: Frequency distribution of numbers of foragers who foraged in different numbers of direction in five colonies

Colony 71 n=96; T=1830;

Colony 25 n=28; T=265;

Colony 56 n=65; T=231;

Colony 117 n=23; T=94;

Colony 134 n=19; T=66;

Percent foragers

Number of directions foraged

n = number of foragers observed
T = total number of trips observed

Table 5: Colony size and percentage of extranidal ants

Colony code	No. of extranidal ants marked	Colony size	Percentage of foragers
DC28	69	457	15.10
DC29	89	376	23.67
DC30	135	593	22.77
DC31	23	192	11.98
DC42	23	121	19.00
DC47	47	145	32.41
DC52	47	271	17.34
DC53	24	137	17.51
DC64	60	145	41.38
DC65	39	103	37.86
DC66	12	41	29.26
Mean ±SD	51.6 ±35.9	234.6 ±171.6	24.39 ±9.63

the proportion of foragers is in itself a useful parameter in many kinds of studies (see for e.g. André *et al.* 2001, Gopinath 2002). Investigations to determine intra-colony genetic relatedness using microsatellite markers, population genetic structure using both nuclear and mitochondrial markers and the mechanism of mutilation of the gemmae are in progress and would form the subjects of future publications.
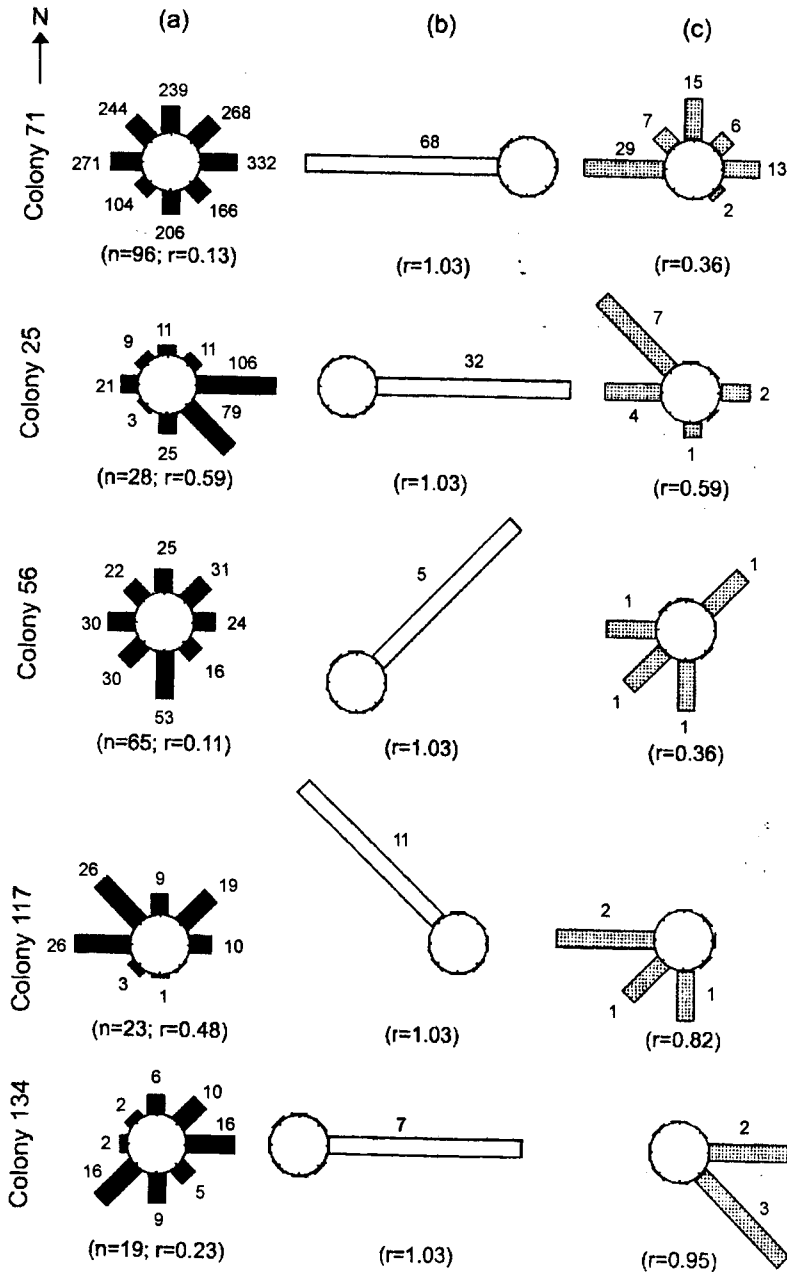
n = no. of foragers for the colony as a whole; r = randomness
Bars are proportions of number of trips made by forager(s) in different directions. Values beside each bar indicate the number of trips made by one or more foragers (in a) and one forager (in b and c).

Fig. 5: Foraging direction for (a) colony as a whole, (b) the most non-random forager and (c) for the relatively most random forager, in the five colonies studied.

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