THE FORAGING BEHAVIOUR OF THE COMMON ANT, *MYRMICA RUBRA* (L.)

A THESIS

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KEVIN McGLYNN

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ABSTRACT

This thesis describes the foraging behaviour of the ***Myrmica rubra*** and determines the optimality of this behaviour. Food choice experiments determined that foragers' sensitivity to carbohydrates and amino acids was similar to those found in other species. Foragers collected high energy and amino acid rich foods preferentially. Foraging effort was concentrated in the areas which contained honeydew-providing aphid clusters. These high resource patches were also rich in scavenge items and invertebrate prey. The temporal distribution of foraging effort showed seasonal variation and varied with environmental conditions. The irregular pattern of nest exits indicated the influence of recruitment. The movements of foragers could be distinguished from non- foraging movements. There was considerable variation in movement pattern between foragers. Searching success was related to movement pattern. Also environmental stress caused the foragers' movements to change; making them more like successful movements. There were differences between the movements of aphid-tenders and scavenging foragers. Recruitment was an important influence on all aspects of foraging behaviour. It exaggerated the choice made by individual ants in prefering more concentrated and more calorie-rich foods; it also shaped the temporal and spatial distributions of foraging and altered foraging movements. These results showed ***M. rubra*** to be an optimal forager, acting to maximize the benefit (an energetic reward with an amino acid constraint) accrued from foraging. This benefit maximization was evidenced by the selection of prefered food types, the matching of foraging distribution to high resource patches, and by movement pattern. Individual variation meant that some foragers did not conform to optimal foraging predictions (in the short term). However it seems likely that such individual variation allows new food sources to be discovered. If recruitment is used to exploit these new resources the individual variation will have optimized the benefit to the whole colony.

DEDICATION

TO MY FATHER AND MOTHER

ACKNOWLEDGEMENTS

I am pleased to take this opportunity to record my debt of gratitude to Dr. Greg Peakin, my PhD. supervisor, for the patience, encouragement and support I have enjoyed during the course of this study. I also wish to thank other colleagues from the Rachel McMillan building, particularly Doctors Philip Wright and Roger Wotton, for sharing their ideas and encouraging my own. I also thank them for their practical help. I am indebted to my colleagues in ASRD, Belfast, particularly Jean, Tim, Crawford and Bill, for their help in getting this thesis printed. Lastly, I am especially grateful to my parents for their belief in me and support, understanding and encouragement throughout this project (not to mention before and after!). This gratitude extends to the rest of my family, my wife Claire, and to many friends - even the wit who suggested that it would have been quicker (and better?) to have let the ants write the thesis!

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SUMMARY

1. Experiments and observations were carried out on laboratory and field colonies of ***Myrmica rubra*** to investigate four aspects of its foraging behaviour; food choice, temporal and spatial distribution of foraging effort and foraging movement patterns.

2. Ants could detect fructose and sucrose in 0.01M solutions but glucose solutions of this concentration were not responed to. With equimolar solutions a clear order of preference was established; fructose > sucrose > glucose.

3. Ants could detect the amino acid leucine in 0.001M solution.

4. When in direct competition more ants drank 0.1M sucrose than 0.01M leucine although the total number drinking from leucine was the same as when it was in competition with water.

5. Liquid food preferences areinterpretedwithin the optimality framework. The ants try to maximize energy intakewithinthe constraintthattheymust also obtain a certain amount ofamino acids.

6. Food trails were unable to demonstrate a clear preference amongst solid food items by size or by taste. Ants tended to remove smaller items from range offered first.

7. As ther data on choice amongst solids was inconclusive it was difficult to interpret this within an optimal framework. However, the absence of any unequivocal choice can be interpreted as agreement with the prediction that optimal foragers should become less selective asfood density decreases.

8. Foraging activity increases to mid-Summer and then tails off again. There was no obvious diurnal pattern (within the observation period from 9am to 6pm). Activity was generally greater at higher temperatures and at greater light intensities. Light

intensity changes corralated with temperatures changes and is considered unlikely to have influenced foraging activity directly.

9. It was often the case that several foragers left their nest within a few seconds of each other and that such pulses were irregularily interspersed amongst periods of repose. This pattern was probably due to recruitment processes.

10. It was not possible to determine whether the observed patterns of activity were optimal or otherwise because no assessment was made of food availability or of forager success.

11. The role of recruitment in determining the temporal pattern of foraging activity means that many workers did not go out to forage unless there was a high probability that these forays would be successful. Thus recruitment would act as an optimizing mechanism.

12. The distribution of aphid-tenders in the field was optimal as most foragers searched in the areas with aphid clusters. The distribution of scavengers was very similar to that of the aphid- tenders, although some scavengers searched well away from the core area. This pattern could also have been optimal for scavengers if other food resources had the same apatial distribuition as aphids.

13. Laboratory studies quantified small scale movement parameters; ants travelled at about 1cm/sec, changed direction about every 1.5sec with these turns being in the range 20-60' without bias to right or left.

14. Large scale movement pattern was quantified in the field. Ants probably used the same small scale pattern in the field. On average ants travelled a net distance of 14.6cm in 30 seconds although this was very variable. About half of the ants travelled consistently in one preferred direction during their foray. The variability of large scale ***M. rubra*** movements compares with that found in ***Cataglypsis bicolor***.

15. The small scale movement pattern of those ants which found food were different from those which did not; successful ants took significantly fewer turns. This finding is similar to the finding that foragers of ***Cataglypsis bicolor*** which travelled straighter were more likely to find food.

16. In the field the movements of aphid-tenders were different from those of general scavengers. The movements of aphid-tenders from different nests were very similar to each other. Individual aphid-tenders probably make the same kind of movements on successive forays; such individual consistancy has been found in ***Cataglypsis bicolor, Neoponera apicalis*** and ***Messor aciculatus***.

17. Experience of water stress caused the small scale movement pattern to change. Unwatered ants took significantly fewer turns, and these turns were significantly larger. Their movements became more like those of successful ants. The ability to change movement pattern in light of experience can be interpreted as an optimizing mechanism.

18. Foraging movements changed with time into the foraging run for only one nest of nine where the degree of area-restricted searching increased with time elapsed. Early movements served to get the ant to a required location, later moves permitted the ant to search this location thoroughly. This change has also been found in ***Messor wasmanni***.

1. GENERAL INTRODUCTION.

Ants are amongst the most successful products of natural selection whether one considers absolute numbers, biomass, geographical range or ecological impact. Ants are all the more fascinating because all species, Bernard (1968) suggests 7600 species while Brown (in Wilson 1971 p29) suggests that there may be as many as 14000 species of 250 genera in 11 subfamilies of the ant family Formicoidae, display an impressive level of social and behavioural organisation.

The evolution of ant societies intrigued Darwin (1859) for they represented a particular puzzle to the theory he was developing. If, as he postulated, natural selection favoured those individuals which survived to reproduce in the "survival of the fittest"how could sterility have arisen and been perpetuated in such societies?

Yet these too are products crafted by the process of evolution by means of natural selection.

1.1 NATURAL SELECTION IS AN OPTIMIZING MECHANISM.

Cody (1974a) defines natural selection as an optimizing mechanism. In selecting the "fittest" individuals from a population it ensures that the genetic material which codes for the fit phenotypes will be passed on to, and become more frequent in, subsequent generations. These fit individuals are the ones which make the best (=optimal) trade-offs between the conflicting demands of their many interactions with their environment (abiotic and biotic including co-specifics). Thus the phenotypic components which allow such optimal trade-offs should become more abundant in future generations.

The spread of optimal genotypes and phenotypes through a population may be constrained by a number of factors. For instance, different phenotypic components may have equal fitness (e.g. human blood groups) and so their frequency in the population would remain more or less constant (Lewontin, 1974).

It could be that the optimal phenotype is heterozygous (as is the case for the sickle cell anemia gene in regions where malaria is common) and so the population would continually be "restocked" with sub-optimal homozygotes at every generation.

Also new genotypes are always being produced (through mutation, crossing-over of chromosomes, and sexual reassortment) and some of these may give phenotypes which allow better trade-offs than the previous best. This new genetic material would then spread through the population.

Environmental instability can also prevent an optimal phenotype from spreading through the population. This is because conditions may become unsuitable for a phenotype which was very well adapted to the previous regime and was increasing in the population. This scenario is exemplified by the great number of extinct species known only from their fossil record.

The constraints limiting the spread of optimal phenotypes through populations make it possible for some extant phenotypes to be suboptimal. Therefore it is necessary to have some means of examining the optimality of extant phenotypes.

Moreover, examination of the optimality of phenotypes can illuminate the natural selection pressures which have acted to shape the evolution of organisms into their present form.

It is often necessary to restrict the investigation to some specific phenotypic component but in doing so it should not be forgotten that it is upon the whole organism that natural selection acts. The three main ways of examining the optimality of extant phenotypes are outlined below.

1.1.1 COMPARATIVE TESTS.

Comparative tests of optimality involve comparing separate species which have been subjected to the same natural selection pressures. These same selective pressures would have imposed the same conflicting demands and it might be expected that the same optimal compromise would be reached between the various demands in each case. Thus the fittest, and therefore the predominant, phenotype in each situation would be similar. This would result in analagous phenotypes, or phenotypic components being displayed by otherwise distinct organisms.

There are many such examples of the convergent evolution of separate phylogenetic lines towards common phenotypic components, such as the eyes of octopuses and vertebrates. Other examples are provided by Cody's (1974) examination of the bird faunas of oldfield in Texas and Chile and by Maynard-Smith's (1978) finding that sexual dimorphism is more pronounced in harem-holding than in monogamous primates.

1.1.2 INDIVIDUAL VARIATION TESTS.

A very direct way of examining the selection pressures which determine what phenotype will be optimal is to compare individuals with different phenotypes. Kettlewell's (1955, 1956) demonstration that the melanic form of the peppered moth ***Biston betularia*** suffered less from avian predation than the peppered form on soot-covered trees but were more predated on lichen- covered trees clearly shows how different phenotypes have different levels of fitness (assuming that overall fitness is reduced when predation is higher).

Individual variation can also be introduced by experimental manipulation as was the case when Nelson (1964) added a second egg to nests of the gannet ***Sula bassana*** to demonstrate that they were able to rear two young.

1.1.3 QUANTITATIVE TESTS.

In quantitative tests the properties of extant phenotypes are compared with the prediction of some model which is designed to predict how an optimal phenotype might achieve maximum fitness. If a close correspondence were to be achieved between the real and predicted data the model must have correctly incorporated the selective pressures and demands acting upon the phenotype. The model should be discarded if it fails to produce such a match.

Quantitative tests, and optimality models, may cover any aspect of the phenotype. Indeed they are usually restricted to considering only one component of the "optimal" phenotype, a necessary simplification imposed by the complexity of real systems.

Optimality models include some measure which is being optimized. As natural selection favours phenotypes with the greatest inclusive fitness then optimality models, if they are to mimic extant phenotypes accurately, should include inclusive fitness as their optimization criterion. However, as the assessment of inclusive fitness is difficult it is often necessary to consider some approximations of this measure. In some situations individual fitness could be satisfactory (Maynard Smith 1978). However, it is often the case that even this cannot be measured and some more proximate measure must be used. Such proximate measures would include fecundity, frequency of copulation, the number of hosts visited by a parasite, the time spent in search of mates, the area of territory defended, rate of water loss, rate of foodgain, amongst many others. When such proximate measures are used as optimization criteria it is assumed that they are ultimately related to inclusive fitness. The exact nature of the criterion used will depend upon the individual model.

The validity of any particular model can be tested by testing its assumptions. If the crucial assumption that it correctly incorporates the selective forces responsible for the evolution of a phenotypic component can be proved to be incorrect then the model should be discarded. It should be noted that the hypothesis that natural selection acts as an optimizing mechanism is not in doubt.

The appropriateness and usefulness of optimality models can also be tested by comparing their prediction to the real systems they are intended to simulate. If the predictions of the optimality model are indeed reflected by the extant phenotypes then it may be concluded that the selection pressures have been correctly incorporated into the model.

1.2 OPTIMAL FORAGING THEORY.

Optimal foraging theory encompasses a range of models which attempt to predict how foraging behaviour could be optimized in order to afford maximum possible fitness to the animal.

Models might be divided into those where the amount of time and effort devoted to the task is minimized and those where the rate of benefit gain is maximized. Ultimately these two types of model can be fitted to the same framework.

Optimal foraging behaviour rules are more complicated if the animals have to search for food in a patchy environment, or if the animal is obliged to forage from a fixed central place, and to return captured food to this central place.

1.2.1 TIME MINIMIZATION.

Animals must spend some time foraging in order to obtain sufficient rations to meet their needs. However, as there are other demands on the animals' time, there will be pressure to keep this time to a minimum. Hence animals which are able to obtain sufficient rations more quickly might be at a selective advantage.

MacArthur and Pianka (1966) proposed a model considering how a forager may minimize the time it spends foraging through the choice of which prey types to include in its diet. They consider different prey types to contain the same reward for the forager but to be ranked on the basis of the time required for search and capture.

As more lower ranking prey types are included in the diet the mean search time per item will decrease but mean capture time will increase as those lower ranked (more difficult to catch) items are included.

The changes in search and pursuit times when new items are added to the diet against the number of kinds of items are plotted in Figure 1.1. As more types of prey are included the reduction in search time becomes less and the increase in pursuit time becomes more. Eventually there is a point of intersection where the reduction in search time equals the

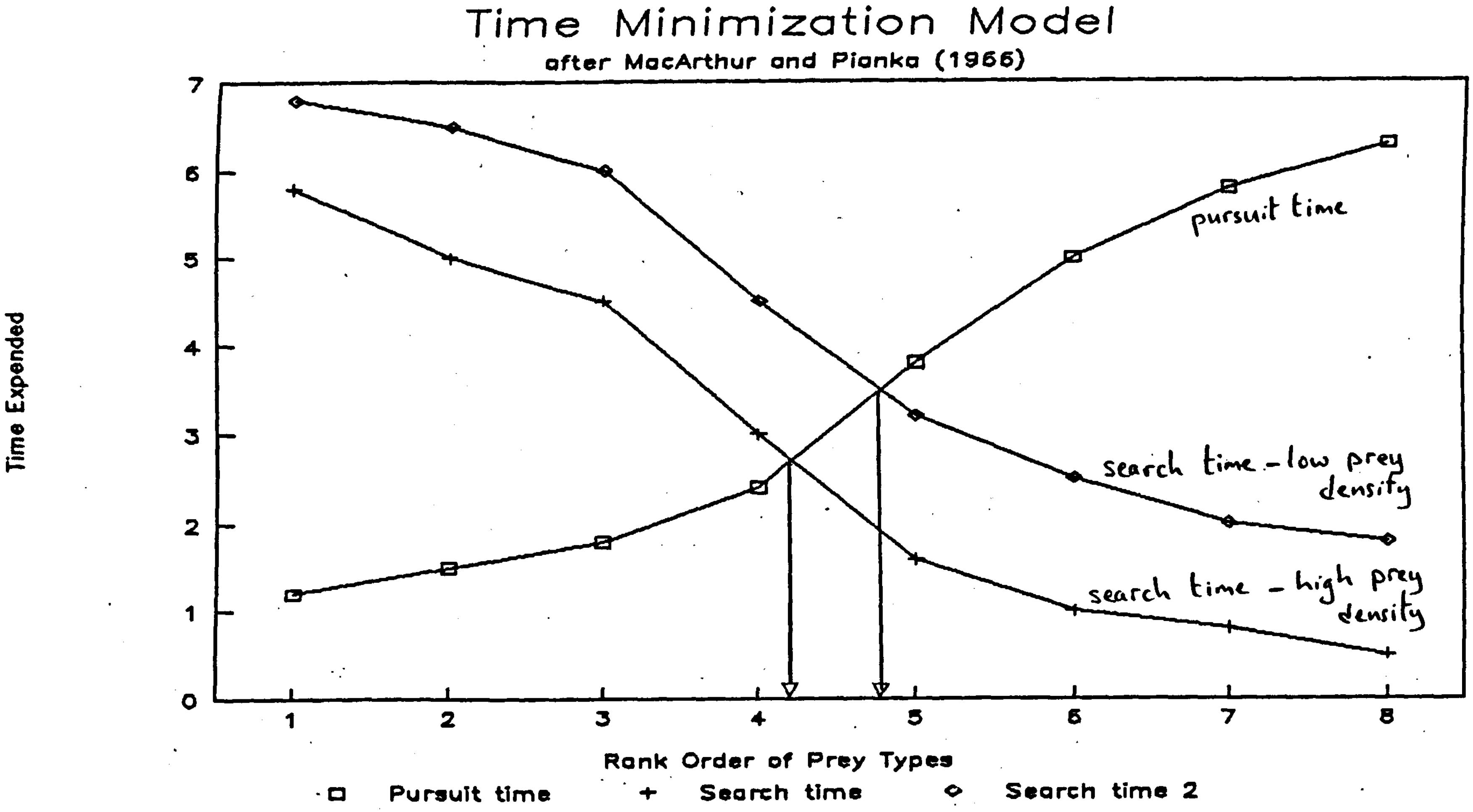


Figure 1.1. Time minimization model. As more prey types are included the time involved in obtaining each items changes. The optimal number of prey types is determined from the point of intersection. (after MacArthur and Pianka, 1966).

increase in pursuit time. Beyond this point of intersection the reduction in search time is less than the increase in pursuit time and so the total time per item will increase. The optimal number of prey types will be that which gives the minimum foraging time per item.

As prey density changes so too will the search time per item. If prey density were to be halved (say) this would double the height of the curve for the change in search time. The point of intersection would move to the right and number of prey types in an optimal diet would be grearter than at higher prey density (see dashed line in Figure 1.1).

1.2.2 BENEFIT MAXIMIZATION.

Another group of optimal foraging models predict that an optimal foraging animal should maximize its net rate at which benefit is accumulated (per unit time). Emlen (1966) proposed that animals maximized their rate of benefit gain as a consequence of the inclusion or exclusion of certain food types in their diet. Emlen proposed that an optimal foraging pattern would give the greatest possible rate of energy gain for the forager.

Emlen allowed that prey type of food had a characteristic calorific value and time cost and could be ranked on the basis of the difference in costs and benefits per unit time. An optimal forager should include in its diet that number of prey types which maximized the difference between benefits and costs per unit time. At high food densities this would be maximized if only the best prey type was included.

However at lower food densities the forager would face longer periods of unsuccessful search. As the time expended increases the overall rate of net energy gain will fall. Under these circumstances the forager should include lower ranking prey types (which should have been rejected at higher prey densities). Thus Emlen's model predicts that an optimal forager should be responsive to changes in overall food density. When prey is abundant it should be very selective and only include the highest ranked prey types but when food density is less it should be less selective.

At any given food density the forager should either include or exclude all items of any given type - it should not display partial preferences. Hughes's (1979) model allowed for partial preferences in that "high energy" prey could be excluded from an optimal diet if they are cryptic (i.e. requires a long time to evaluate or may be misevaluated) or if the predator learns to handle less energetic rewarding prey more quickly (and so increase the rate of reward).

Pulliam (1975) proposed a model which incorporated the need for the optimal forager to include certain essential nutrients in its diet. Such a situation is explored in Figure 1.2. Where there are no nutrient constraints, as in the upper diagram, the optimal combination will be the one which gives the maximum possible rate of energetic gain, which can be achieved by taking all items of one type only all items of both types (i.e. no partial preferences). Where there is a nutrient constraint such that the forager must obtain an minimum amount of nutrients, the forager may then show partial preferences by taking a limited number of a less calorifically rewarding prey.

1.2.3 INTERRELATION OF TIME-MIN AND BENEFIT-MAX MODELS.

Time minimization and benefit maximization models are closely related. The relationship has been modelled by Schoener (1971) and Sih (1984) who conclude that time minimizers should behave as benefit maximizers while foraging. A time minimizer reduces the time required to collect a given ration of food by maximizing the rate at which it is gathered while foraging.

Rapport (1971) provides a graphical interpretation of the same point (see Figure 1.3). In this diagram points giving greater fitness reward are enclosed by "indifference loops", and consumption of more prey moves the forager further away from the axis. A forager at point a (see figure) would benefit by increasing its consumption and so tries to maximize its energy intake. Meanwhile a forager at point b would be a time minimizer; it would not benefit from further consumption, but should consume less.

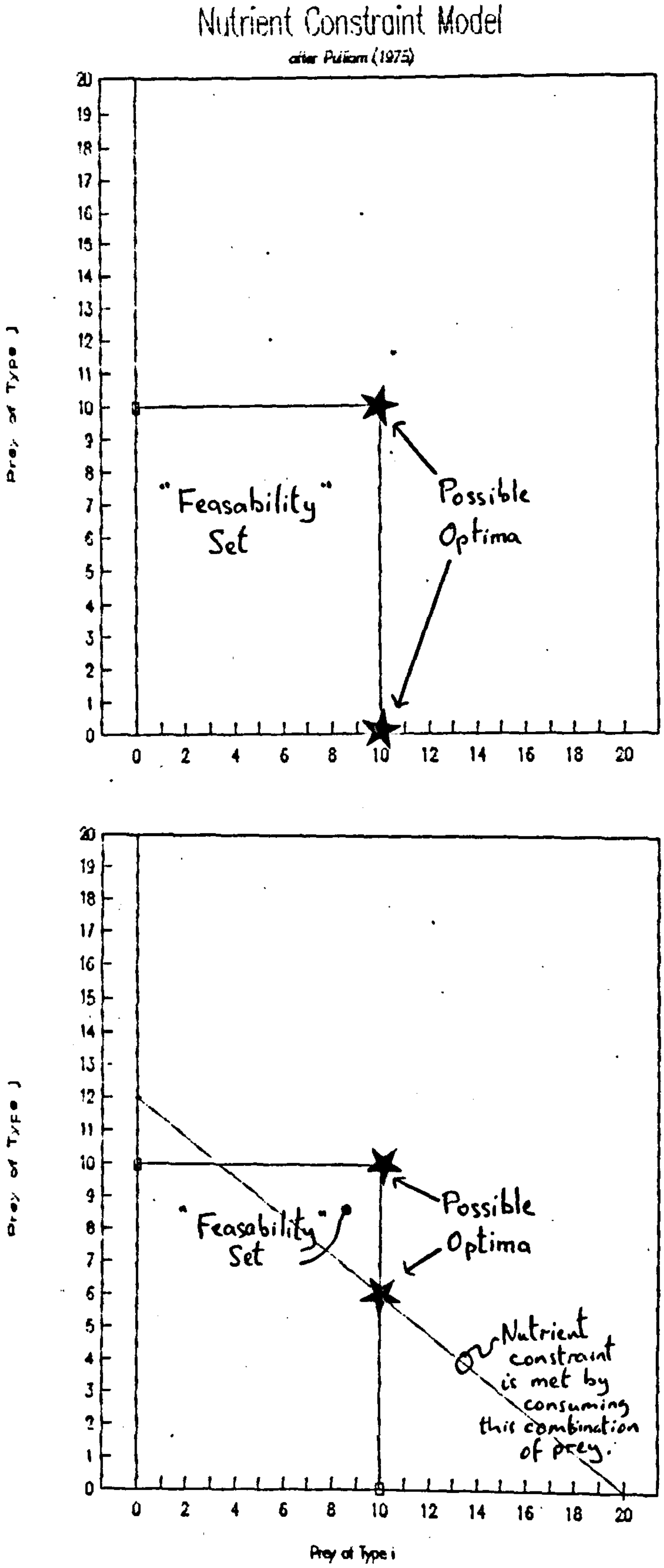


Figure 1.2. Nutrient constraint benefit maximization model where a forager must obtain both nutrient and calorific benefits (after Pulliam, 1975).

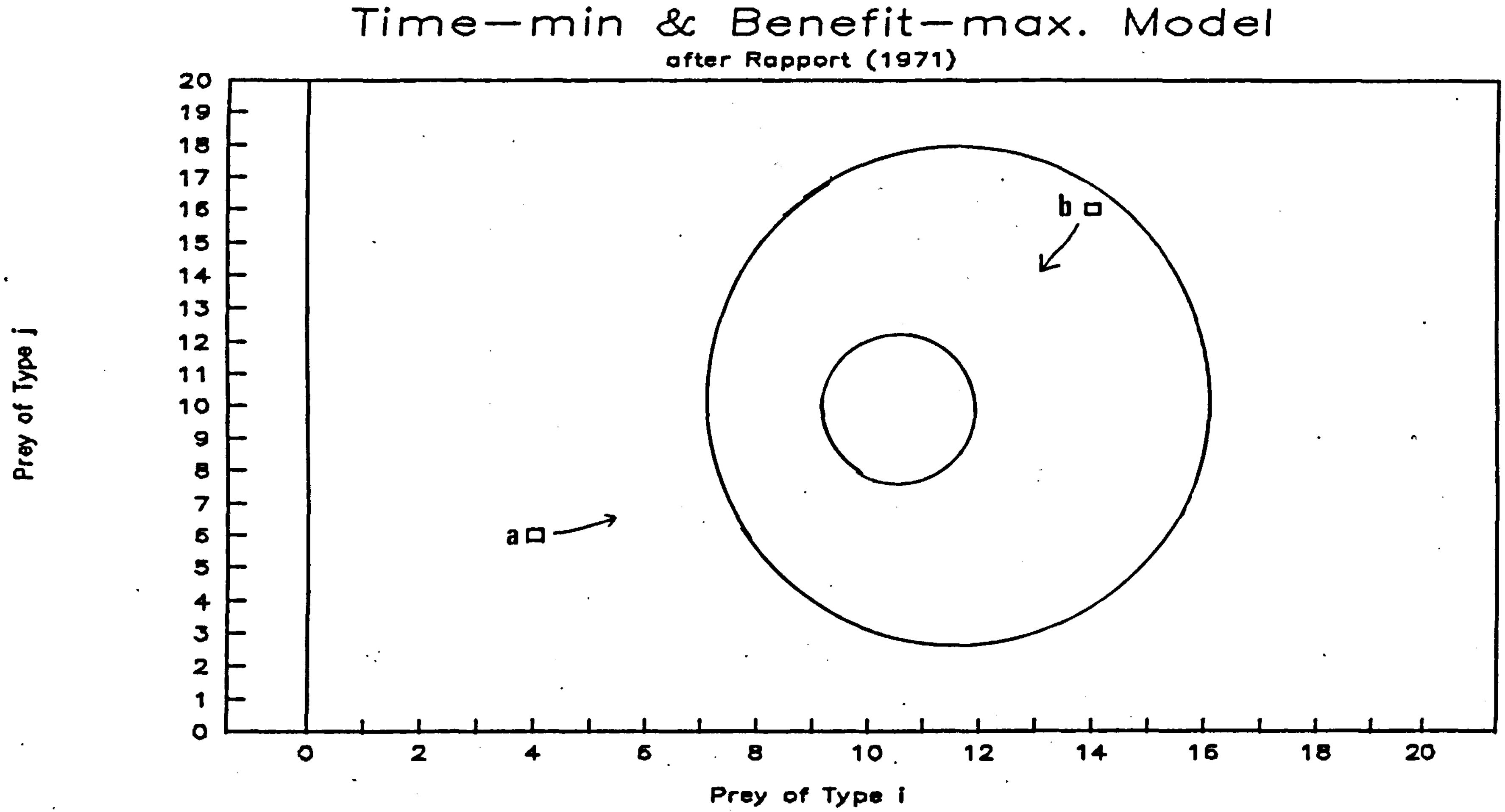


Figure 1.3. Model demonstrating inter-relationship of time-minimization and benefit-maximization models. Points to centre of concentric loops offer greater fitness reward (after Rapport,1971).

1.2.4 FORAGING IN A PATCHY ENVIRONMENT.

Animals are liable to forage in environments where food resources are scattered such that there are areas of high resource availability interspersed with, and grading into, regions with few resources. Such patchy distribution of food resources presents further complications to those investigating optimal foraging behaviour.

MacArthur and Pianka (1966) extended their model to consider how many types of patches of different resource quality should be visited by an optimal forager in order to minimize the time it spends foraging.

As with prey types, patches are ranked on the basis of resource quality, from those which gave the greatest reward per unit time to thosewhich gave the least. The time required to procure an item of prey can be split into time spent travelling between patches and the hunting time spent within patches. These times will change as lower ranking patches are included (Figure 1.4).

The inclusion of poorer patches reduces the time spent travelling between patches but increases the average time spent searching within patches. The optimal number of types of patches is determined as the point where the increase in within patch search time is no longer compensated for by the saving in interpatch travel time.

MacArthur and Pianka's model is simplistic in its consideration of patches which are either visited or not. It allows no insights into the dynamics of how patches are exploited.

Charnov's (1973 unpubl. thesis, 1976) "Marginal Value Theorem" considers the dynamics of patch use by a forager trying to maximize its benefit gain. It considers when the forager should leave a patch as the reward rate diminishes due to the foragers presence in that patch. The situation is presented in Figure 1.5.

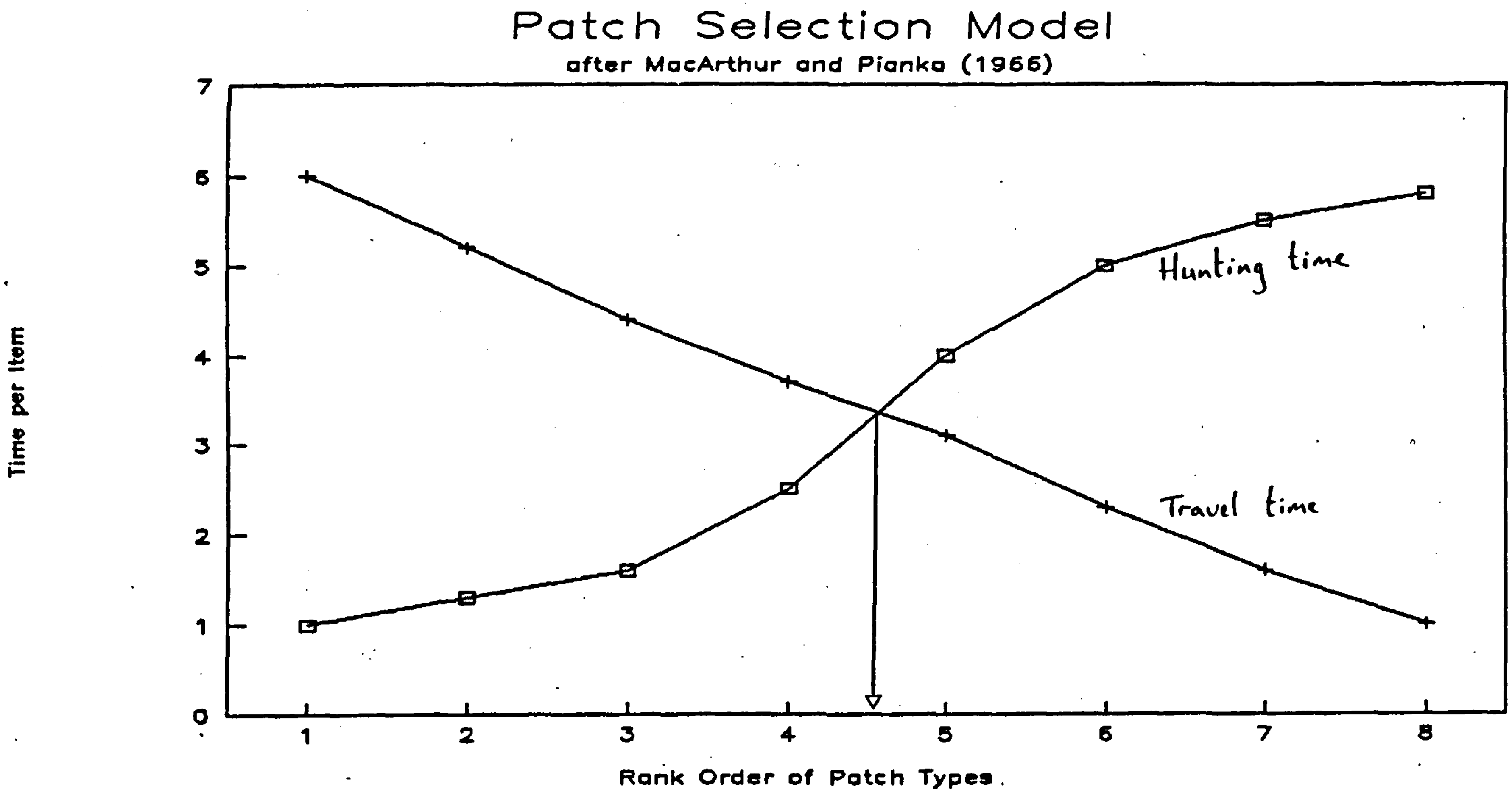


Figure 1.4. Patch choice model. As more patch types are included the time involved per item changes. (after MacArthur anad Pianka, 1966).

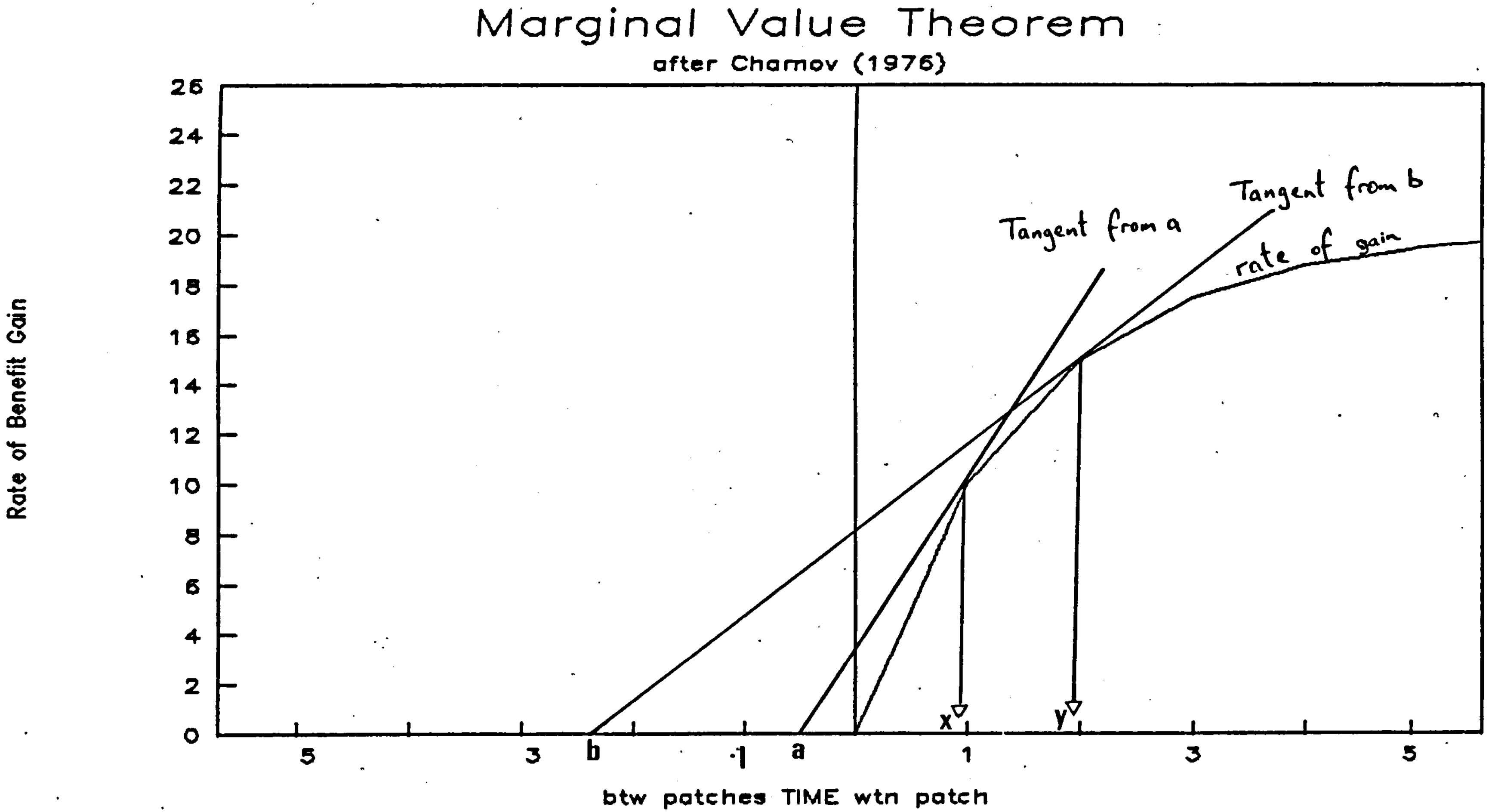


Figure 1.5. Marginal Value Theorem model demonstrating optimal use of a patchy environment. When travel time between patches is greater the forager should spend longer within each patch (after Charnov, 1976).

The Marginal Value Theorem predicts that an optimal forager should remain longer in better patches. When interpatch travel time is greater the overall rate of benefit gain must fall but the forager will harvest more from each patch.

These same optimal decision rules for patch exploitation have been derived independently by Krebs et al. (1974), Oaten (1977), Parker and Stuart (1976) who considered an optimal strategy to locate mates, and, Cook and Hubbard (1977) who considered parasites finding suitable hosts.

1.2.5 FORAGING FROM A FIXED CENTRAL PLACE.

Some animals are obliged to return food to a central place before it is consumed (e.g. to a refuge to feed offsprings). Such "Central Place Foragers" incur additional costs which have significant implications when considering the optimality of their foraging behaviour.

Schoener (1979) considered diet selection in CPFs. He concluded that as foraging costs increase with distance then items considered profitable close to the central place might not be profitable further from the nest. Therefore optimal central place foragers should be more selective in taking only the best types of food when further from their nest.

This result has been found independently by Orians and Pearson (1979) whose model was revised by Lessels and Stephens (1983). They also found that with increasing food density the forager's expected rate of energetic reward increases with the effect that only higher quality food items should be included in the diet. (This was also the case for non-CPFs).

Orians and Pearson also consider patch use by CPFs and conclude that whilst a rich patch far from the CP may give the same expected rare of energy return as a poor patch nearby the opposite is not the case. Therefore only better quality patches should be used further from the nest.

1.3 EUSOCIAL INSECTS.

Ants are particularly useful animals with which to study the optimality of foraging behaviour. This is because the division of reproductive labour within their colonies means that the sterile individuals (workers) which engage in foraging do not have conflicting reproductive demands. Moreover, as it is usually the case that there is a further division of non-reproductive tasks between workers, the foraging workers do not have to perform any other non-reproductive tasks.

These features are shared with other insects which live in eusocial societies.

1.3.1 EUSOCIALITY.

Eusociality, or true sociality, is displayed by all species of ants, some species of bees, some species of wasps (all within the order Hymenoptera where societies are predominantly female) and by the termites (making up the order Isoptera where both sexes are present).

Eusocial societies are characterised by three features:-

i/ there is a division of reproductive powers between individuals, where some individuals (workers) are unable (or less able) to reproduce while other individuals have full reproductive potential (reproductives queens and males). These sterile workers may differ from their parents in a variety of phenotypic components.

ii/ individuals cooperate in caring for the young (of other individuals), and,

iii/ there is an overlap of generations such that worker offsprings assist their reproductive parents with reproduction and help in caring for their young.

All ant species function at this highest level of sociality. There are bees and wasps which display some but not all of these characters; these lower levels of sociality are discussed by

Michener (1969) for bees and by Evans (1958) and Evans and West- Eberhard (1973) for wasps.

There exists an unusually high degree of genetic relatedness between the individual members of eusocial Hymenopteran societies due to their haplo-diploid mechanism of sex determination (Dzerion's rule 1845 in Wilson, 1971). Sisters (most society members are female) share 75% of their genetic material. Thus workers could pass on more of their genetic material to future generations if they helped their mother queen to produce more sisters than if they were to produce offsprings of their own. This peculiarity may help to explain how eusociality has arisen in the Hymenoptera (Hamilton, 1964) but it is not sufficient on its own to explain the evolution of eusociality for the termites, all of which are eusocial do not use this mechanism.

1.3.2 DIVISION OF NON-REPRODUCTIVE LABOUR.

Even when they are relieved of reproductive duties there still remains a great range and variety of non-reproductive activities to be performed by the workers. Some idea of the range of tasks to be performed can be seen from the behaviour repertoire of workers of the acorn ant ***Leptothorax curvispinosus*** as compiled by Wilson and Fagen (1974) and which is outlined in Table 1.1.

In the majority of species studied the non-reproductive tasks are further divided between groups of workers such that different sets of workers do different things. Such "polyethism" is usually based on size or age differences or on both.

Size polyethism has been found in many species where markedly different-sized workers are found, such as ***Pheidole hortensis*** where Calabi et al. (1983) compiled behavioural repertoires of minor and major workers. Minors performed 25 tasks while majors did 6, with only self-grooming and trophollaxis being common to both.

Such size polyethism is common in ***Pheidole*** for when Wilson (1984) investigated 10 species he found similar division between minors and majors in all cases. Size polyethism is

BEHAVIOURAL ACT	NO. OBS	FREQUENCY
1 Self-grooming	465	0.2370
2 Antennal tipping	24	0.0122
3 Allogroom worker	84	0.0428
4 Allogroom queen	5	0.0025
5 Carry egg	30	0.0153
6 Lick egg	50	0.0255
7 Carry larva	248	0.1264
8 Lick larva	354	0.1804
9 Assist larval ecdysis	11	0.0056
10 Feed larva solid food	66	0.0336
11 Carry pupa	24	0.0122
12 Lick pupa	95	0.0484
13 Assist eclosion of adult	16	0.0082
14 Lay egg	5	0.0025
15 Regurgitate with larva	152	0.0775
16 Regurgitate with worker	126	0.0642
17 Regurgitate with queen	27	0.0138
18 Fight queen or workers	18	0.0092
19 Lick wall of nest	27	0.0138
20 Forage	57	0.0291
21 Feed on honey	11	0.0056
22 Feed on solid	34	0.0173
23 Carry dead insect	5	0.0025
24 Carry dead nestmate	5	0.0025
25 Carry live nestmate	3	0.0015
26 Handle nest material	8	0.0041
27 Stridulate	12	0.0061
TOTAL	1962	1.0

Table 1.1. List of behavioural acts observed in repertoire of **Leptothorax curvispinosus** workers and number of times and relative frequency each act was witnessed (from Wilson and Fagen, 1974).

not restricted to this genus for it is also found *in Aneuretus* **simoni** Traniello and Jayasuriya (1975), (Wilson 1976), ***Zacryptocerus varians*** Cole (1980),**Camponotus** ***Zacryptocerus varians***(subgenus ***Colobopsis***) species Cole (1980), ***Atta sexdens*** Wilson (1980a), and even in ***Leptothorax longispinosus***, which is considered to be monomorphic (the largest workers are 60% bigger than the smallest), by Herbers and Cunningham (1983).

A number of investigations have revealed how workersshow sequential behaviour changes with worker age. There are a great many examples of temporal polyethism. Temporal polyethism has been found in ***Myrmica scabrinodis*** and in ***M. rubra microgyna*** (**=ruginodis**) (Weir 1958a,b), in ***Formica polyctena*** by Otto (1958a), in the fire ant ***Solenopsis invicta*** by Sorensen et al. (1983), and in ***Pogonomyrmex owyheei*** by Porter and Jorgensen (1981). In every case workers progress from "indoor" duties such as tending the queen and brood to "outdoor" activities such as nest defence and foraging as they mature.

This behavioural change has associated physiological changes. Workers' ovaries degenerate as they age (in ***Formica polyctena*** Otto 1958a) and the capacity to lay eggs is also reduced (in ***Myrmica ruginodis*** Weir 1958b and in ***M. rubra*** Smeeton 1981, 1982b). Porter and Jorgensen (1981) suggest that foragers are a "disposable" caste because they are the oldest. They reason that the colony would suffer less if an old worker, nearing the end of its lifespan, was lost doing some dangerous outdoor task than if a young worker was lost.

1.3.3 MEETING THE COLONY'S NEEDS.

It is very much the case in eusocial societies that the sterile workers operate for the benefit of the entire colony, not for themselves as is the case in solitary animals. For instance foragers gather food not just to meet their own metabolic needs but also, and more importantly to satisfy the dietaryneeds for maintenance, growth amd reproduction, of the queen(s), larvae and the rest of the workers.

The colony's food demands are liable to change over time. A major reason for such changes is the status of the brood. In some species it is possible to examine colonies and to find all stages of brood to be present. In such cases there would be no marked changes in the demand for food. Wilson (1959a) reports that most tropical rainforest ants have aperiodic brood populations.

In temperate latitudes the change of the seasons may determine how brood development patterns. This is the case in ***Cataglypsis cursor*** as Cagniant (1979) has demonstrated (see Figure 1.6) where all developmental stages occur in one summer. In ***Myrmica rubra***, Brian (1957a)has reported that it takes two years to complete all the developmental stages (see Figure 1.7).

The brood cycles which has the most dramatic effect on foraging behaviour is undoubtably that of the army ants, where the alternation of nomadic and statary phases is correlated to the presence or absence of larvae (see Figure 1.8).

1.3.4 SELECTIVE PRESSURE ACTS ON STERILE INDIVIDUALS.

Darwin (1859) realised that in eusocial societies natural selection acts upon the reproductive individuals, and that those which are helped by sterile workers produce more offsprings. Thus there is a pressure for reproductives to produce workers with characteristics which make them better helpers. Again this selection pressure will have an optimizing effect in that it will produce a worker-force which is best able to do ALL of the non-reproductive tasks.

The worker-force can achieve this through size and temporal polyethism which reduces the variety of tasks which each individual must do and so allows spatial and behavioural specialism. This opens up the possibility of the workers phenotype becoming optimized to perform a particular activity.

Ant foraging behaviour provides a excellent opportunity for the investigation of the

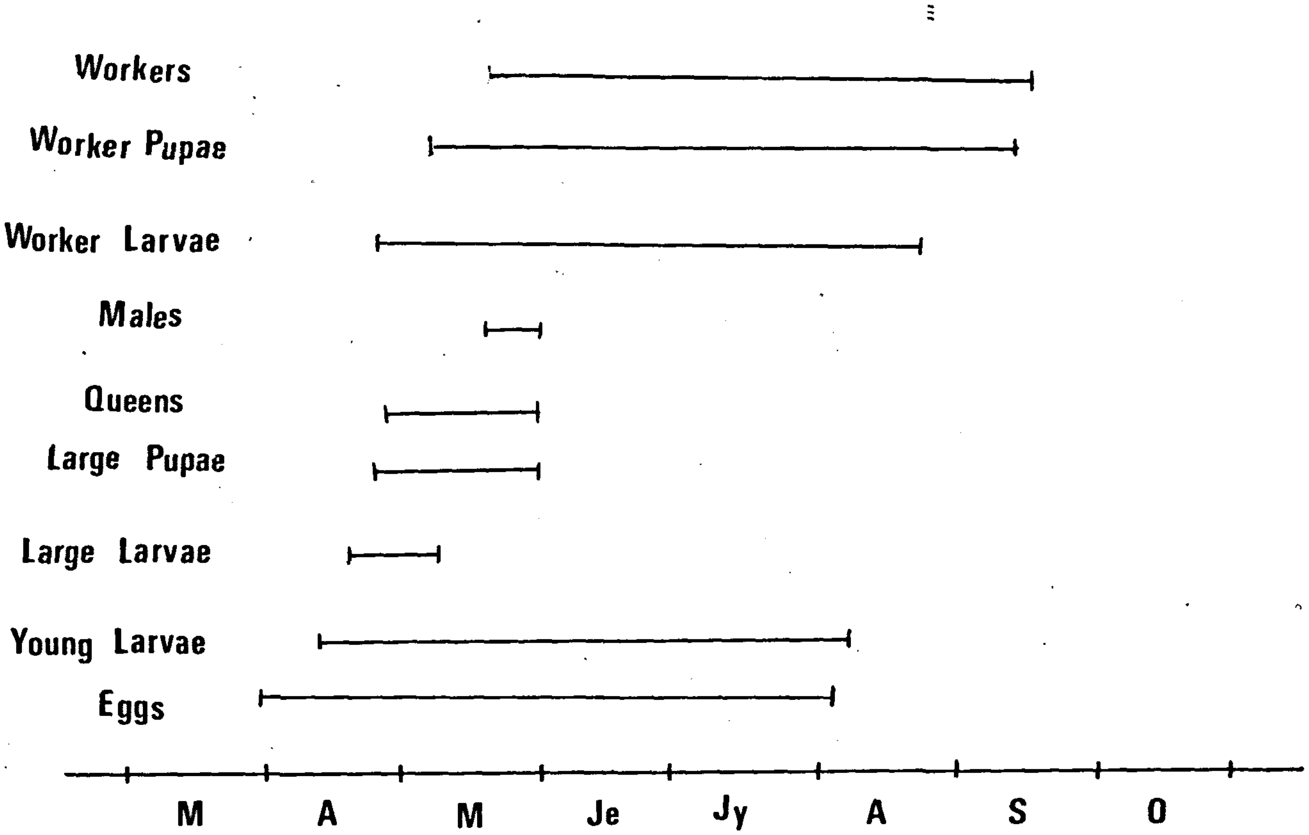


Figure 1.6. Annual brood cycle of <u>Cataglypsis cursor</u> (after Cagniant 1979).

├──┤ Marks period when a particular stage is present

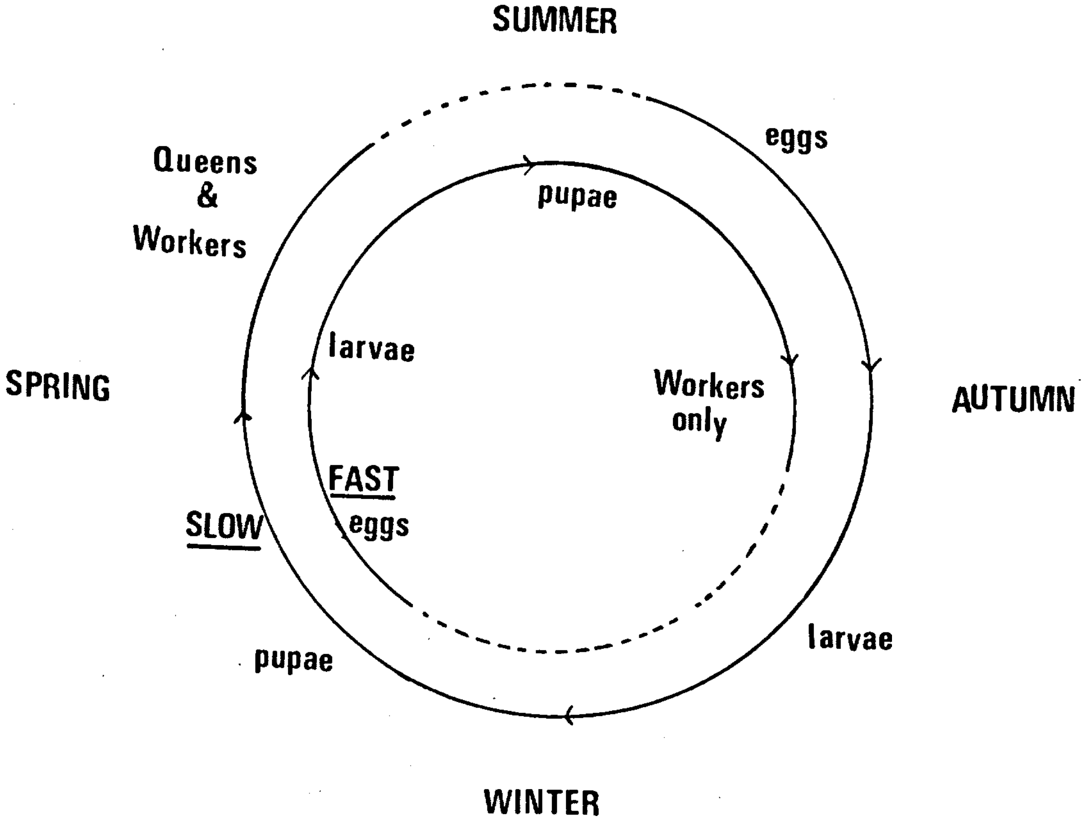


Figure 1.7. "Fast and slow" brood cycles in Myrmica (after Wilson 1971).

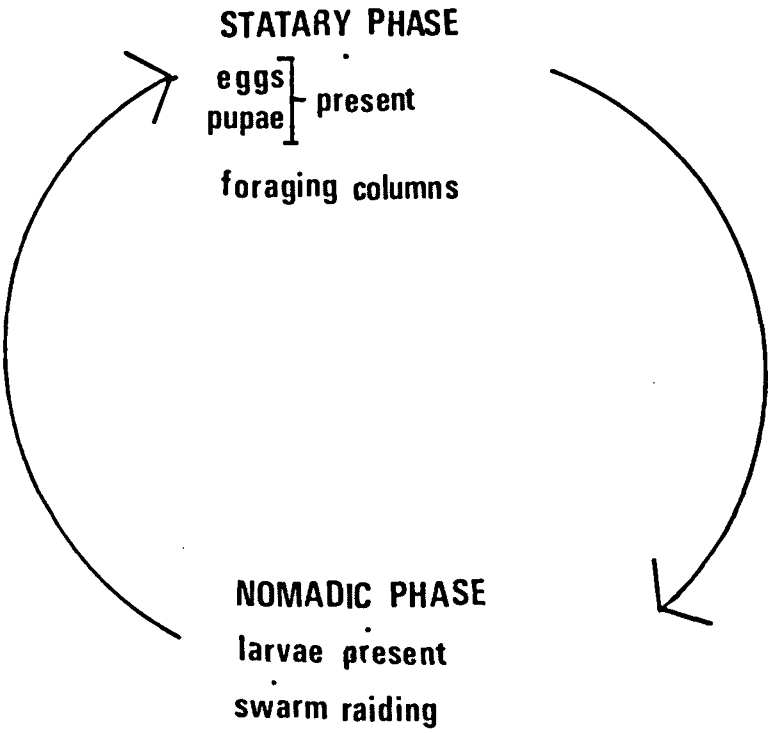


Figure 1.8. Cylce of stataty and raiding phases in army ants (after Wilson, 1971).

optimality for it is a conspicuous activity performed by the oldest workers which have effectively lost whatever residual reproductive potential they may have had when younger and are freed from other non-reproductive chores.

That is not to say that foraging behaviour can be seen in complete isolation from other aspects of colonial life. The status of the colony is variable, and such changes as do occur in the physiological state of the colony, the state and age structure of the brood, the size of the total worker population, and so on, and such factors have many important implications for foraging demands and response.

1.4 ANT FORAGING BEHAVIOUR.

It is very much the case that individuals forage not just to meet their own requirements, as is the case for solitary animals, but to meet those of the entire colony. In as much as this is a permanent situation, eusocial insects are unique among animals.

Ants, as a group, exploit a great range of food sources with and use a variety of foraging strategies to exploit these. These strategies might be graded from those where foraging workers operate independently of other foragers, as is the case in the ponerine ***Neoponera apicalis*** (Fresneau 1985) and in ***Cataglypsis bicolor*** (see for example Schmid-Hempel, 1984) to those where large numbers of workers operate in close association with each other. This is the case where ants forage along well defined trails (e.g. ***Formica rufa***, Skinner 1980a), columns (e.g. ***Atta cephalotes***, Lewis et al. 1974a) or in swarms (e.g. ***Eciton burchelli***, Franks and Fletcher 1983).

Of course there will be some degree of overall coordination at the colony level even in those species where individual workers forage independently of each other. This is due to that fact that these workers are foraging from, and for, the same colony; therefore separate individuals will be in receipt of the same physiological and behavioural cues as each other.

The degree of persistance of the cooperation (or of its absence) may depend upon ecological circumstances, particularily the availability and distribution of suitable foodstuffs. It is also mediated by recruitment signals communicated between foragers.

1.5 RECRUITMENT COMMUNICATION.

Wilson (1971) defines recruitment as communication that brings nestmates to some point in space where work is required. The most celebrated form of recruitment exhibited by social insects is undoubtably the "waggle-dance" of honeybees discovered by Karl von Frisch (1967 and references therein). No communication of this complexity has been identified in ants but there does exist a wide range of recruitment systems in operation.

In the simplist cases the recruitment signal is merely a chemical released when a forager encounters food. This is found in the ponerine ants ***Odontomachus troglodytes*** (Longhurst and Howse, 1978) and ***Bothroponera soror*** (Longhurst et al., 1980), as well as in ***Pogonomyrmex badius*** (Wilson 1971 p247).

A somewhat more complicated form of recruitment communication is found in the process of "tandem-running". In this form of recruitment one worker, upon discovering food, returns to the nest where it recruits a nestmate which follows it back to the food. Only one nestmate is recruited at a time. Tandem-running was first described by Hingston (1929) in the Indian formicine ant ***Camponotus sericus***. Tactile communication is certainly used in tandem running and in some situations it would appear that pheromones are also used. Tandem running is also observed in ***Cardiocondyla venustula*** (Wilson 1959b).

The most elaborate form of chemical communication used by ants is considered to be the use of pheromonal trails (Wilson 1971 p248) In this system successful foragers release pheromones as they travel between the food and the nest. These pheromones persist sufficiently to allow naive recruits to follow the trail of pheromones until it locates the food. Pheromonal trails allow many recruits to find the food.

Pheromonal trails are used by the ponerine ant ***Megaponera foetens*** (Longhurst and Howse, 1979), ***Tetramorium caespitum*** (Verhaeghe, 1977), ***Tetramorium impurum*** (Verhaeghe, 1982) amongst many others.

Many ants display mechanisms which allow the amount of recruitment to be controlled, and may permit the response to be matched to the nature of food source. For instance Breed et al. (1987) found that in the ponerine ant ***Paraponera clavata*** the intensity of recruitment is related to the quantity of food found.

Similarily Jaffe (1985) has shown that in ***Solenopsis saevissima*** the magnitude of the recruitment response, controlled by the amount of pheromones laid on the trail, is determined by the number of ants which lay trails on the way back to the nest.

Crawford and Rissing (1983) have shown that single foragers of ***Formica oreas*** are able to convey sufficient information to their nestmates to allow discrimination between different food sources.

Cammaerts, in a series of studies (1977, 1978, 1980a, 1980b), has shown graded recruitment behaviour in ***Myrmica rubra*** and ***M. scabrinodis*** and Cammaerts and Cammaerts (1980) have investigated recruitment in ***M. sabuleti*** and ***M. ruginodis***.

She showed that workers drink pure water without recruitment but used pheromone trails and "invitation" behaviour to summon recruits from the nest to sugar solutions. The intensity of the invitation behaviour and the number of ants recruited increased with sugar concentration.

Recruitment behaviour was different when solid prey were found. Foragers returned small prey to the nest where their invitation behaviour caused recruits to leave the nest, but these recruits went in all directions from the nest. When a forager found a large prey it returned to the nest and recruited nestmates which followed her in a definite trail back to the prey.

2. FOOD CHOICE

A major area of optimal foraging theory concerns the selection of the items which make up the diet from amongst the range available. As some materials are likely to be more valuable than others then consumption of the former in preference to the latter is likely to afford a greater fitness reward to the forager (or rather to its colony). Where this is the case, natural selection will have shaped the foraging components of phenotypes to ensure optimized diet selection behaviour.

Ants, as a group, eat a massive range of foodstuffs and consume virtually every possible food type. Table 2.1 presents some examples of the breadth of some species' diets.

The nutritive value of different food types will depend on their composition; they will contain different amounts of carbohydrate, protein, lipid, other nutrients and undigestible material. There may exist great variablilty in the composition of items within the same class.

Honeydew, a common item in the diet of many species, is a very complex mix of materials. The honeydew of ***Myzus persicae*** contains sugars, amino acids and lipids as well as minerals, vitamins and other organic molecules such as plant hormones. The most common sugars found in honeydew are sucrose, fructose and glucose. Eleven amino acids have been found; alanine, asparagine, aspartic acid, glutamine, glutamic acid, leucine or isoleucine, phenylalanine, proline, serine, theorine and valine (Auclair, 1963). Lipids account for 12-16% of the dry weight of ***M. persicae*** honeydew (Strong 1963, 1965). Twenty fatty acids have been identified ranging from C4 to C20 compounds with palmitic acid being the most common.

Beattie (1985) reviews the various analyses of extrafloral nectar, another common food source, which reveal that they contain sugars, amino acids, lipids and other organic compounds such as alkaloids and phenolics. The predominant sugars are again sucrose, fructose and glucose (Bentley 1977) with raffinose, arabinose, xylose and rhamnose occasionally present. The three main sugars have been found in the extrafloral nectar of a

SPECIES: **Myrmecocystus mimicus Wheeler**
SOURCE: Holldobler (1981)
METHOD: 1747 ants observed as they returned to nest
DIET: 53% termites, 10% other insects or insect parts, 1% seeds, 36% nothing in mandibles.

SPECIES: **Novomessor cockerelli**
SOURCE: Whitford et al. (1980)
METHOD: booty collected from returning foragers
DIET: 46% arthropods (or parts thereof), 38% seeds, 8% flowers and petals.

SPECIES: **Novomessor albisetus**
SOURCE: Whitford et al. (1980)
METHOD: booty collected from returning foragers
DIET: 6% arthropods (or parts thereof), 40% seeds and fruits, 4% leaves and stems, 6% flowers and petals, 23% combination of faeces, rabbit skin, porcupine quills and bird feathers.

SPECIES: **Formica subnitens Creighton**
SOURCE: Ayre (1959)
METHOD: 1138 items collected from returning foragers
DIET: 44% ants, 22% Coleoptera, 4.6% Lepidoptera, 4.5% Diptera, 4.8% Homoptera, 4% Orthoptera, 3.3% Hemiptera, ALSO exudates of Ponderosa pine, honeydew from 10 species of ap[hid.

Table 2.1. Some examples of the variety of food stuffs in ant diets.

variety of plants. Twenty-two amino acids have been detected in extrafloral nectar, although the average number is 14.7 +/- 5.09 (reviewed by Baker et al. 1978). Little is known of the lipid content of extrafloral nectar but lipids have been found in 15 of 85 plant species examined.

2.1 DIETARY CHOICES.

Not all species comsume such a wide range of food types. Many individual species collect a limited range of food types and consequently have reduced diets. This narrowing of the range of food types may be a reflection on the range of food available to that species under those conditions rather than any actual preference or choice made by the ant.

However, there are many cases where individual species show clear preferences for certain food types, even when other potential foods are available. Such preferences may be due to a complex array of characteristics such as size, mass, palatability, defensive mechanisms and compounds, and chemical composition. The food preferences may change over time as different food sources become available or as the food requirements of the colony change. One example of preference is provided by the army ant ***Neivamyrmex nigrescens***, an active predator of termites and other ants in desert-grassland habitats in Arizona and New Mexico. Around 16 species of ant are taken as prey by these army ant colonies but colonies of ***Pheidole*** species are raided more frequently than their relative abundance would suggest. Whilst ***Pheidole*** species made up about 45% of the total number of ant colonies in the study area, 93% of the colonies raided were of ***Pheidole*** (Mirenda et al. 1980a). They suggest that the preference is probably due to the absense of efficient defensive or evasive mechanisms which make ***Pheidole*** an "easy prey".

An example of changing preferences is provided by Haskins and Haskins (1950) who found that when larvae were absent ***Myrmecia gulosa*** foragers are predominantly nectivorous but when larvae are present foragers take insects and other arthropods by scavenging and active predation. This change must surely relate to the changing food requirements of the colony caused by by larval demand.

That ant species use the physical properties of potential food as a selection criterion is well established. Such a selection process would seem to occur in the four sympatric species reported by Traniello (1987). He collected forage items returned by foragers of ***Lasius neoniger, Formica schaufussi, Monomorium minimum*** and ***Myrmica americana*** and found that there was a significant correlation between the size of prey collected by each species and worker size in each species (Table 2.2 Chi-sq.=151.69, df=6, p<0.002 for individually returned prey, my calculation from Traniello's data).

Now these species also practised group-retrieval of prey items and this would extend the size range of prey upwards in each case.

Size is also a selection criterion in ***Pogonomyrmex rugosus*** and ***P. barbatus*** as Davidson (1978) has shown. He provided colonies of these seed-harvesters in the Chichuahuan desert with extra rations of crushed barley seeds which had been sieved into distinct size classes.

In one experiment six colonies of ***P. barbatus*** were exposed to patches of small (0.7mg), medium (2.7mg) and large (9.8mg) seeds, and the first 200 seeds returned were recorded. In the12 replicates of this test it was found that the majority of seeds taken were of the intermediate size (Chi-squared 141.42, df=2, p<0.001 for sum of 12 tests, my calculation from Davidson's data).

In another experiment seven colonies of ***P. rugosus*** were exposed to patches of four seed sizes (0.7mg, 2.7mg, 9.8mgand 32.6mg). Each test was replicated at four distances from the nest entrance (3m, 6m, 9m and 12m). The first 100 seeds returned in each test were recorded. In 38 of 40 tests, seeds of size three were taken preferentially, although some seeds of all sizes were taken at all distances. The preference for size three because more pronounced with increasing distance from the nest. As distance increased significantly fewer seeds of size two were taken. Similarily less seeds of size four were taken with increased distance but this change was not found to be significant. Too few seeds of the smallest size were taken at any distance for comparison to be made.

Species	M.minimum	L.neoniger	M.americana	F.schaufussi
	Worker charcateristics			
Body Weight	0.1+-.01	1.5+-.03	2.2+-.05	6.8+-.08
Head Width	0.5+-.02	0.9+-.03	1.1+-.03	1.5+-.04
	Individually retrieved prey			
Mean	0.06	1.5	2.5	12.2
s.d.		2.6	2.9	18.8
Range		0.1-7.5	0.2-15.4	0.3-65.3
No.	174	95	91	184

Table 2.2. Relationship between forager size and size of individually retrieved prey in four sympatric ant species (from Traniello 1987). Body weight in mg +/-s.d., head width mm +/-s.d. For **M. minimum** mean prey size was estimated from as 0.06mg from the total weight of 174 prey items collected (therefore no s.d. or range available).

A similar size preference has been demonstrated for the European seed harvester ***Messor capitatus*** by Baroni-Urbani and Nielsen (1990) who offered crushed wheat seeds of different size classes (0.5-1.0mm diameter, 1.0-2.0mm, 2.0-3.0mm and 3.0-4.0mm) to field colonies. They counted the number of ants attracted to contiguous patches of each size classes (2m from nest) at 2 minute intervals. (They took this as a measure of the attractiveness of each seed type - the actual numbers removed might have been a better measure). It was observed that more ants were found with the 3.0-4.0mm seeds, indicating that this was the prefered size.

Weight is another characteristic which can be used in diet selection. It was found to be used when Baroni-Urbani and Nielsen presented a laboratory colony of ***M. capitatus*** with artifical seeds (inert styropore spheres soaked in sugared water and coated in flour) of 5.0 to 5.5mm diameter which had been loaded with lead weights of 8, 65, 130, 300, 450, 600 and 800mg.

When they plotted the number of ants attracted against the seed mass they found that this fitted a parabolic function (the fit was statistically significant) with a maximum around 400mg.

This prefered weight was some ten times the mass of a wheat seed, one of the prefered natural seeds collected by field colonies. This reinforces the idea that preferences are determined by a complex array of criteria.

The chemical composition of food items is another characteristic used by foraging ants to establish an order of preference of which foods to collect and return to the nest. Taste is likely to be the main characteristic when the forager encounters liqud food because the parameters of size, shape, and mass are inapplicable.

Glunn et al. (1981) investigated food preferences of the fire ant ***Solenopsis invicta*** by offering colonies three kinds of liquid food and recording the rate at which ants accumulated to drink. The sum of the number of ants present was counted at 1 minute intervals for the next 15 minutes from the time of the first encounter was used as an estimate of preference.

Ten field colonies were presented with 1M sucrose, rat serum and unrefined soy oil. There was much heterogeneity between the colonies in their responses to these foods; three prefered oil over the other foods, one prefered serum, while five prefered oil and serum equally. When the recruitment data from the ten colonies was pooled the overall pattern of preference was (from the most prefered) oil, serum, sucrose. A similar heterogeneity emerged from tests with 31 standardized laboratory colonies when 16 different preference patterns emerged.

A more homogenous preference pattern emerged from Schmidt's (1938) study of response to sugar solutions in three ant species; ***Lasius niger, Myrmica rubida*** and ***M. rubra***. These species discriminated between different concentrations and between different sugars, with sucrose being accepted at lower concentrations than fructose or glucose, see Table 2.3.

Similarily, Sudd and Sudd (1985) have shown that foragers of ***Formica lugubris*** in Yorkshire show preferences for sucrose solutions of different strengths. They pipetted drops of solution (from 1.2M down to a control of distilled water) into the paths of individual ants as they foraged along the branches and twigs of trees. More ants drank when stronger sucrose solutions were available.

When they performed such tests between April 14 and June 15 they found that the median effective concentration (i.e. the concentration at which 50% of ants would accept, and 50% refuse, the solution) was around O.15M although some fluctuations were found from day to day.

When they extended their observations from Spring to Summer they obtained evidence of a remarkable change in preference. Over the course of 1 week in June the concentration of sucrose which elicited drinking in 50% of ants rose sharply from 0.15M to 0.9M. This change coincided with the Summer production of the apterous aphids which this species

Species	Lasius niger	"Myrmica rubida"	Myrmica rubra
Sucrose	0.005M	0.0025 - 0.00125M	0.006M
Fructose	0.15	0.03125	0.02
Glucose	0.125	0.03125	0.02

Table 2.3. Acceptance thresholds for three sugars in three ant species; from Hassett et al. (1950) using data from Schmidt (1935).

Lipid	Antennate	Examine	Pick-up	Remove	TOTAL
1,2-Diolein	25 (25)	6 (3)	28 (7)	80 (10)	139
1,3-Diolein	10 (10)			4 (1)	14
Monolein	17 (17)				17
Oleic acid	18 (18)	4 (2)	4 (1)	16 (2)	42
Ricinoleic acid	29 (29)	2 (1)	4 (1)		35
Un-treated	12 (12)				12

Table 2.4. Response of **A. rudis** foragers to teflon beads impregnated with lipids . Scoring system is explained in text, number of observations are given in brackets. Data on 12 other standard lipids are excluded from table; they all yielded scores of less than 35.

tended. Thus when this new better food resource because available foragers only returned sucrose solution of higher concentrations to their nest.

Ants can also discriminate between different lipids. This capacity was revealed by Marshall et al. (1979) in ***Aphenogaster rugis***. They presented foragers with inert "teflon" beads which had been impregnated with various lipids and observed their responses. These responses were scored 1 - for brief antennation, 2 - for examination of the seed, 4 - for picking up the seed, and, 8 - for removing the "seed". The total response was taken to be the sum of these scores. In different tests the beads were impregnated with different lipids (either standards or extracted from the eliasomes of actual seeds). The responses to the range of lipids is summarized in Table 2.4. It is obvious from this that the ants responded to some lipids but not to others.

The use of taste as a characteristic in determining food preferences is not restricted to liquid foods. Leaf-cutter ants use taste (undoubtably in conjunction with other criteria) in determining which plants it will forage from. Leaf-cutters are something of a special case for they select food not for direct consumption but to be used as a substrate for fungal growth in the nest; the fungi are then used as a food source for the colony.

The fact that leaf-cutters make foraging choices is demonstrated by the Mexican leaf-cutter ***Atta mexicana*** which selectivly attacks six plants from the range available in the Sonoran desert (Mintzer 1979). Of these, four are perennials and two were annuals. When the annuals appeared the ants seemed to ignore the perennial plants.

Similarily ***Atta cephalotes*** in Costa Rica only attacks a restricted subset of the total range of available plant species. Over a period of 5 months Berish (1986) observed the plants being attacked and carried out a chemical analysis of the plant tissue.

Less than 10 of the 300 or so available plants were commonly attacked although most plants in the vicinity of nest were sampled. ***Gmelia*** was the most prefered when available, but if it is not available then cassava was predominant amongst the plants attacked.

Chemical analyses of the plant tissues revealed that the average composition of nitrogen was 2.3-3.1% (of dry mass). However, in the commonly cut plants the nitrogen content was 4-5.8%. The prefered plants also had a higher composition of phosphorus than the average. The content of manganese and of aluminium was lower in the cut plants. It is known that nitrogen and phosphorus promote fungal growth while manganese and aluminium can interfer with the enzymes of amino acid synthesis (at least in higher plants). The foragers would seem therefore to be selecting the best substrate for fungal growth.

As well as colony level diet selection there can also be individual selectivity. This has been found to occur in ***Pogonomyrmex rugosus***, for example, by Rissing (1981) who found that colonies harvested a mixture of seeds of the three grasses (Kentucky blue-grass, orchard grass and ryegrass) which he made available. He found that different (marked) individuals were consistent in harvesting the same species of seed, and this individual preference lasted for several days. Thus individuals displayed selectivity whilst the colony, as a whole, did not.

2.2 THE OPTIMALITY OF DIETARY CHOICE.

The fact that some species of ant make choices in the selection of some of their food means that they possess some phenotypic component or components which allow such selections to be made. These components will have been shaped by natural selection and therefore will have been optimized. But what are the selection pressures which have shaped these components? What optimization criterion do they maximize?

The prediction that optimal foragers should maximize their rate of energy intake, or if this is translated to the case of eusocialinsects, that the foragers should act so as to maximize the rate of energy intake into the colony is met by, for example, the behaviour observed in ***Myrmica rubra*** and **Formica oreas** by Cammaerts (1977, 1978) and Crawford and Rissing (1983) respectively where foragers recruit more nestmates to stronger sugar solutions. It is also met by ***Pogonomyrmex occidentalis*** which recruited at a greater rate when seed patches were closer to the nest, when patch size was increased, when seed density was increased and when seed size was increased.

Similarily, the preference pattern revealed by Schmidt (1938) would seem to support the idea of maximizing the rate of energy gain. If the phenotypic component determining taste thresholds was shaped to allow the foragers to maximize the colony's rate of energy gain then it would be expected that the foragers would be most sensitive to the sugars with highest calorific content. The acceptability series ran sucrose, glucose=fructose; this reflects the calorific content of the sugars; sucrose 3.92cal/g, fructose 3.73cal/g and glucose 3.72cal/g (Mitchell, 1981).

Further support is provided by the observations of Sudd and Sudd (1985) that a greater proportion of ***Formica lugubris*** foragers accept sucrose solutions of higher concentrations.

Pyke, Pulliam and Charnov (1977) suggest that if net energy gain is to be maximized then more profitable items should be included in the diet, at the expense of less profitable items, more frequently as food density increases. This prediction is supported by the behaviour of ***F. lugubris*** where foragers' acceptance thresholds for sucrose solutions increase when rich honeydew becomes available (Sudd and Sudd, 1985).

Orians and Pearson (1979) suggest that as foraging costs increase (through increased travelling time from the central place) the forager should be more selective in choosing forage items if it is to maximize it net rate of energy gain.

This prediction is supported by Davidson's (1978) experiment on ***P. barbatus*** where smaller seeds (relative to the most prefered size) were taken less frequently when food was presented further from the nest.

Conflicting results, however, are provided by Baroni-Urbani and Nielsen's (1990) work on ***Messor capitatus*** and by Taylor (1977) on ***Pogonomyrmex occidentalis***. They found that the distance of a food find from the nest did not influence dietary choice.

Indeed, the prediction that food preferences should be more pronounced when foraging costs increase is rejected by Traniello et al.'s (1984) finding of how diet selection in ***Formica schaufussi*** changed with temperature.

They offered either 6mg or 32mg cockroaches to foragers and recorded their response. At room temperature they found that the foragers prefered the larger ones and rejected the smaller ones. But they found that as they altered temperature between 15 and 35'C (the normal foraging range in this species) that preferences changed. Foragers were much less likely to reject the small roaches at higher temperatures ($p<0.0005$).

They also measured ants' oxygen consumption rates at different temperatures and found that this measure of metabolic cost increased with ambient temperature. Thus as the ants costs (including foraging costs) increased they became more likely to select less rewarding items. Thus rather than becoming more selective as costs increased these ants became less selective.

The behaviour of ***Novomessor cockerelli*** and ***N. albisetus*** when provided with extra food conflicts does not maximize the colony's energy intake. When they are provided with extra food they respond by increasing the number of foragers travelling to the food source (Whitford et al. 1980). This change is greater when the extra rations are of tuna or corned beef than when extra oats are provided. Oats have the greater calorific content, therefore if the ants were to maximize the colony`s calorific intake they would respond more to oats, the opposite of what was in fact observed. However, tuna and corned beef contain more protein, the foragers would therefore seem to be maximizing their intake of protein. In this case their behaviour would still be optimal, but a new optimization criterion is required.

The leafcutter ***Atta cephalotes*** seems touse food selection criteria which services yet another optimization criterion for it serves to produce the optimal substrate for fungal growth. By cutting leaves predominantly from plants with high nitrogen and phosphorus contents but with low manganese and aluminium levels (Berish 1986) they manage to provide their fungi with excellent conditions for growth.

In other cases it is not possible to determine what criterion might be being optimized. For instance, Baroni-Urbani and Nielsen (1990) investigated the preference of ***Messor capitatus*** for seeds from different plants, and tried to determine what criterion determined the order of preference. They had established that crushed wheat seeds of a certain size were prefered over other size, and that artifical seeds of a certain mass were prefered over other weights, but could not explain the preference range displayed for seeds from locally occuring plants on the basis of these criteria.

In field trials they offered crushed seeds (2.0-3.0pm diameter) of wheat and other seed types to colonies and counted the number of ants attracted to each seed array. This response was compared to a standard response, that produced when only wheat was available. They calculated a number of the physical and chemical characteristics of the seeds tested to see if differences in these determined choice. Their results are summarized in Table 2.5. No correlation was found between any of the seed characters and the number of ants responding.

2.3 FOOD CHOICE IN *MYRMICA RUBRA*.

The diet of ***Myrmica rubra*** has received some mention already. Schmid (1938) has found that sucrose solutions are acceptable at 0.0066M and that fructose and glucose are acceptable at 0.02M. Cammaerts (1977, 1978) observed foragers drinking pure water (a dietary item?) and sucrose solutions of various concentrations up to 1M, and collecting Drosophila and cockroach pieces.

Brian (1977 pp53-5) summarizes the diet of ***M. rubra*** to including aphids, springtails, fly larvae, adult flies, spiders and many other small creatures. Also foragers from colonies living in acid grassland collected seeds of tormentil, ***Potentilla erecta. M. rubra*** is also known to tend aphids, for example, Dreisig (1988) records foragers tending ***Aphis acetosae*** L. on the upper parts of the stems and within the infloresences of the dock, ***Rumex acetosa*** L.

The object of this part of my study is to determine what foods are included in the diet of ***M. rubra***, to investigate the selection processes (if any) involved in including these food types, and to explore the optimality of any such choice.

Test Seed species	Weight Fresh	Dry	% Water	J/mg dry wt.	% N	Relative response
Foeniculum vulgare	3.0	2.8	6.8	24.2	2.86	0.6
Zea mays	163.7	152.8	7.1	19.2	1.78	0.9
Ocimum basilicum	1.1	1.1	6.4	23.8	3.31	5.8
Petroselinum hertense	1.8	1.7	6.9	25.2	3.43	15.6
Spinacea oleracea	9.1	8.4	7.8	19.2	3.64	54.1
Lactuca sativa	0.7	0.7	4.6	28.1	4.59	74.8
Raphanus sativus	8.8	8.4	4.7	27.6	5.49	93.5
Secale cereale	24.4	22.5	8.1	17.8	1.44	98.2
Triticum sativum	34.3	31.7	8.2	18.9	1.92	100.0
Avena sativa	20.2	18.9	7.1	19.8	2.45	111.9
Linus usitatissimus	7.0	6.7	5.3	27.6	3.90	146.0

Table 2.5. Physical and chemical characteristics of seeds used in preference tests and the response they elicited from ants. Wheat standard elicited 100% response. All values are means.

3. FORAGING ACTIVITY

The amount of effort that a colony dedicates to foraging at any particular time is another phenotypic component which will have been shaped by the forces of natural selection. It seems intuitive that an optimal foraging activity pattern would be one which matches activity to reward. Thus the colony should forage most when it is most likely to be rewarding and forage least when the chances of obtaining a reward are smallest.

The colony's food requirements at any particular time must also be taken into consideration when considering optimal foraging activity patterns. It would be advantageous to the colony if foraging activity could be increased in line with food demand (assuming that the time and energy saved when not foraging could be used elsewhere).

Foraging activity does in fact show great fluctuations with time, particularly with respect to annual and diurnal cycles. In some cycles the amount of activity fluctuates between periods when there is no activity at all and periods of high activity. In other, less extreme, cases there is always some activity right throughout the cycle, albeit reduced at some times.

The variations in the amount of foraging activity are, in many cases, controlled by the environmental conditions imposed upon the colony. Such restricting conditions may be considered as constraints on this phenotypic component.

3.1 ACTIVITY CYCLES.

A fine example of annual cycling of the amount of foraging activity is provided by ***Lasius neoniger*** in the northern temperate region (Massachusetts). By counting the number of ants entering and leaving the nest Traniello (1987) found that foraging started in mid-April, increased to its maximum value by the end of June and then declined through July and August. By September foraging had declined to about five percent of the maximum.

This pattern is typical of species in the region for when Traniello counted nest exits and entrances in three other species (***Myrmica americana, Formica schaufussi*** and ***Monomorium minimum***) in the same habitat he found that they displayed much the same annual pattern, although there were some differences in the exact timing of peaks between the species.

A similar pattern of seasonal activity has been found in five species of ***Myrmica (sabuleti, scabrinodis, sulcinodis, rubra*** and in Dorset. When Elmes (1982) recorded the number of ants caught in pitfall traps between September 1976 and December 1979 he discovered that the number of ants caught (and by implication the amount of foraging activity) increased through Spring to a peak in mid-Summer and declined through Autumn. A few ants were caught through the Winter.

He plotted cumulative frequency curves from February (the month with lowest activity) to January and found that, on average, 50% of the annual activity had occured by June 29 - i.e. by this time half of the year's foraging had occured. On average 95% of foraging activity took place between the middle of April and the end of September. In the particular case of ***M. rubra*** 2.5% of foraging had occured by mid-April, 50% by the begining of August and 97.5% by the start of October. Ninety-five percent of the colony's foraging activity occured in a period of 165 days between mid-April and October.

A similar range of foraging times has been observed in ***M. scrabinodis*** in Yorkshire by Pickles (1935). He made direct observations of foraging ants throughout the year. His last observation of foraging ants in 1932 was made on October 23; foraging resumed on March 26 of the following year. He did not observe any foraging between these dates.

Talbot (1946) investigated diurnal activity cycles of three species in Michigan and found that their activity patterns were quite different. Her counts of exits from and entrances to ten nest of ***Formica incerta*** revealed that this species did not forage at night, then foragers began emerging from the nests during the morning and activity reached a peak in mid-afternoon and declined again thereafter.

The absence of nocturnal foraging is shared by ***Catalypsis bicolor*** in Greece as is revealed by Harkness's (1977) counts of the number of foragers entering and leaving nests. Typically the number of exits and entrances built up from zero in the early morning towards a peak in the region of 180 to 210 per hour by 10am. The activity would remain in this peak range (with some fluctuation) til about 3pm whereupon activity would decrease to reach zero again at about 8pm.

Talbot found in Michigan that ***Lasius neoniger*** foraging occured primarily at night. The rate of exits and entrances then slowed during the morning to reach a low ebb for several hours during the afternoon. In some cases activity ceased altogether in the afternoon.

Another example of nocturnal bias in foraging activity is provided by ***Atta cephalotes*** in Guyana. Cherrett (1968) counted the number of ants moving along foraging trails from the nest and found that most foraging occured during the night while very few foraged around noon.

Talbot's counts of foragers entering and leaving nests of ***Myrmica americana*** revealed that there were two peaks in the daily activity pattern. She reported that "On many days workers were going in and out of the nest during the entire 24 hours, but they were usually most numerous during during midmorning and again in early evening. When activity ceased it was during the afternoon."

Similarily when Levieux (1979) counted the number of foragers departing from two colonies of ***Messor galla*** in the Ivory Coast he found that there were two sharp peaks of activity separated by periods of repose. Activity occured between 7 and 10am and again between 4 and 6pm, when peaks of c280 and 150 ants per minute and fell to zero at other times.

Twin peaks were also found in the four species, ***L. neoniger, F. schaufussi, M. minimum*** and ***M. americana*** studied by Traniello (1987) in Massachusetts.

Daily patterns of activity are prone to change depending on the season. For instance, Levieux (1983) noted in ***Myrmecia eumenoides*** in the Ivory Coast that foraging during the rainy season occured right throughout the day whilst at the height of the dry season foraging was confined to two periods, from 5-10am and from 4-11 pm.

Changes in daily activity pattern between seasons have also been noted for ***Atta mexicana*** in the Sonoran desert, Mexico. Mintzer (1979) observed that in December ants of this species foraged in daylight from 9am to 6pm. In March ants continued to be active during the day (but on two of eight days activity slackened on most foraging trails in early afternoon). By July foraging had became distinctly nocturnal.

Jensen (1977) also noted changes in daily activity pattern in ***Formica pratensis***. His counts of the number of foragers leaving the nest revealed that on cool cloudy days there was a single diurnal peak of activity between 10am and 4pm. However, on hot sunny days there were two peaks, one in the morning between 6am and 9am and the second between 1pm and 4pm.

3.2 ENVIRONMENTAL CONSTRAINTS AND CONTROLS.

Temperature is a very obvious constraint on whether foraging may occur or not. It can constrain foraging if it is too high or too low. This is illustrated by Bernstein's (1974) work which established the temperature ranges within which three species foraged. ***Pogonomyrmex californicus*** foraged at temperatures between 32'C and 53'C, **P. rugosus** foraged between 23'C and 46'C while ***Veromessor pergandei*** foraged within the range 18'C to 39'C.

In some species it is found that different temperatures initiate and terminate foraging bouts. Mintzer (1979) has determined that in Winter the foraging bouts in **Atta mexicana** were initiated in the morning when air temperature exceeded 12`C and that leaf- cutting ceased when temperature fell to 14'C in the evening and all activity had ceased when it fell to 11'C. In Summer, when the maximum daytime temperature reached 39'C, foraging bouts started when temperature dropped below 32'C in the evening and ceased as temperature rose to 29'C in the following morning. This relationship between temperature and foraging activity is presented in Figure 3.1.

The influence of temperature extends beyond controlling whether foraging can occur or not, for temperature can often be related to the intensity of foraging at any particular time. This relationship is exemplified by Traniello's (1987) research which found that maximum foraging. **schaufussi** activity occured at 20'C in ***L. neoniger*** and ***M. americana***, occured at 24'C in ***F. schaufussi*** and at 30'C in ***M. minimum*** in Massachusetts.

Similarily in Michigan, Talbot (1946) was able to relate air temperatures to foraging activity in ***Lasius neoniger, Formica polyctena*** and ***M. americana***. Each species had a different temperature when their foragers were most active; 13'C, 30'C and 23'C respectively.

Temperature is not the only environmental factor to constrain foraging activity. The influence of humidity has been illustrated by Schumaker and Whitford (1974) who found that in the Chichuachuan desert the foraging activity of ***Trachyrmyrmex smihi neomexicanus*** stopped whenever saturation deficits were greater than 35g/m3.They also found that the sympatric ***Formica peripilosa*** continued to be active up to a maximim saturation deficit of 52g/m3.

There is some conflicting evidence as to whether light intensity exerts control over foraging activity. Hodgson (1955) suggested that, in *Atta* ***cephalotes***, foraging bouts were initiated when light intensity exceeded 3.2lux (from observations over 22 days, 18 of which were wet and overcast).

However, Lewis et al. (1974b) determined that ***A. cephalotes*** could initiate foraging at any time of the day or night. Some foraging bouts started when the light intensity was as low as 0.02lux (starlight), whilst others started when the light intensity was 100000lux (noonday sunlight). It seems unlikely therefore that light intensity is an important cue in determining foraging times in this species at least.

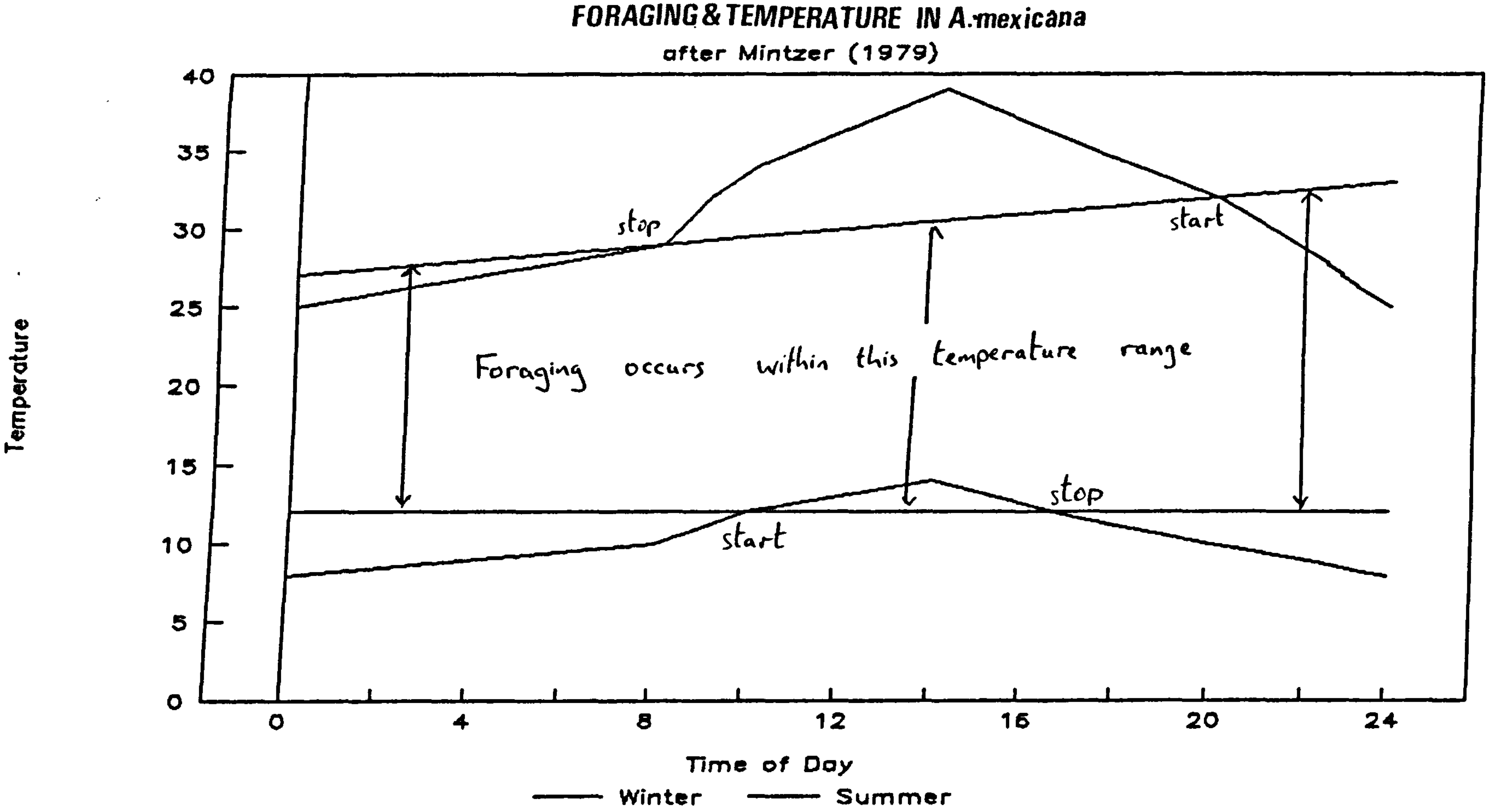


Figure 3.1. Influence of temperature of foraging regimes in *Atta mexicana* (after Mintzer 1979).

There are some more convincing documented cases where foraging activity is related to light intensity. For instance, the two peaks of foraging activity in ***Messor galla and M. regalis***, observed in the rainy and dry seasons in sudanese savanna in the Ivory Coast by Levieux (1979), can be related to changes in light intensity.The first peak occured in early morning (7-10am) when light intensity had climbed quickly to 100lux and ended before it reached 1000lux. The second peak occured in the late afternoon (4-6pm) as light intensity fell from 1000 to about 100 lux again and ceased when it fell below 100lux again.

Similarily Skinner (1980a) also found that the pattern of foraging activity in ***Formica rufa*** (number of foragers per minute on trails) reflected the circadian pattern of light intensity change.

It is difficult to establish a causal link between light intensity and foraging activity because light intensity is positively correlated to other environmental factors, notably temperature, which, as had already been demonstrated, exerts a strong influence on foraging activity.

Rainfall can also influence foraging; it has been observed to delay the onset of foraging in *A.* ***cephalotes*** (Lewis et al., 1974b) when other conditions were favourable. They also observed that when rain started after a foraging bout had commenced,the ants dropped their burdens and either ran back to the nest or sheltered. Persistent rain stopped foraging altogether.

Pickles (1935) reported that strong winds reduced foraging in ***F. fusca,*** **L.** (=***Acanthomyops) niger*** and ***M. scabrinodis***; he observed on several occassions that foraging in these species was negligible on days of gale force wet winds in Yorkshire, "on visiting the ants on a brilliantly sunny, boisterous day, I have been disappointed in not finding a single ant of any of the species walking about".

3.3 INTERNAL CONTROLS.

In addition to the external environmental factors which can influence foraging activity there is an array of influences from within the colony which affect foraging activity.

Cammaerts' (1980a) work on ***Myrmica rubra*** and ***M. scabrinodis*** shows that there must be some control independent of environmental factors for, under controlled laboratory conditions, she found that the number of workers in the foraging area showed a diurnal pattern. There was a peak of activity between 5am and 10am, followed by a long period of reduced activity and a period of on activity around 2am. The peak of activity was more pronounced in the case of ***M. scabrinodis***.

Internal influences must also have been responsible for regulating the activity pattern in ***Atta cephalotes***, for in Lewis et al.'s (1974a) study in Trinidad it was found that neighbouring colonies, obviously exposed to the same physical environmental conditions, foraged at different times of the day. One colony initiated foraging between 2pm and 7pm, another between 9am and 8pm and a third started foraging between 7am and 4pm (these ranges include 90% of foraging starts from 76 observations). Data were not sufficient to carry out a significance test.

The condition of the brood is one internal influence known to affect foraging activity. This is most dramatically demonstrated by the army ants. During their statary phase, when eggs and pupae are present and larvae absent, foraging activity consists of a series of raiding columns radiating outwards from their temporary nest. This changes drastically when the larvae emerge and new adults eclose. Then the entire colony moves off in a nomadic phase where foragers capture any food items which come into their path (#1.3.3).

The physiological state of the colony or the degree of hunger also influences foraging activity. Cosens and Toussaint (1986) investigated foraging activity patterns in laboratory colonies of ***Formica aquilonia*** (Yarrow). They established a regime where 10ml of 10% sugar solution was provided at 10am each day. A constant pattern was then observed; i/ an initial increase in numbers of foragers at the sugar site over a period of 1.5 hours reaching a maximum of c56 ants/count, ii/ a subsequent decline in numbers over a similar time period to about 20 ants/count and iii/ the maintenance of this level of foraging activity until about 6pm by which time the sugar solution was exhausted.

Cosens and Toussaint then altered the feeding regime. When they reduced the daily ration to only 5ml of sugar solution they found that on the on the first day the pattern was as before but the sugar was exhausted quicker. On subsequent days the number of ants on the site increased dramatically, from maxima of 58 to 90 to 121 ants/count. Thus the colony responded to a period of relative starvation byincreasing the number of foragers active.

When the sugar deficit was corrected by providing greater volumes of sugar solution the pattern again changed. In this case less foragers went to drink from the solution. This reinforces the suggestion that the amount of foraging activity is related to the food requirements of the colony.

Recruitment will also influence foraging activity for ifone forager discovers a good food source it may recruit other foragers. This obviously increases the number of foragers active. This response was seen in ***Formica aquilonia*** in the case cited immediately above, and is also found in a great may other species (see #1.5 above).

3.4 OPTIMAL ACTIVITY PATTERNS.

There are several mechanisms which may be employed to match foraging activity patterns with food rewards within the constraints imposed by environmental factors.

One mechanism is to maintain regular and reliable food sources. In protecting clumps of aphids the ants are guaranteeing that foraging trips will bring rewards if the aphids are visited. Indeed where ants construct "shelters" for aphid clusters they may be creating favourable micro-environments. This could allieviate, to a degree, some of the environmental constraints.

Another optimizing mechanism which matches foraging activity to food reward is recruitment. Recruitment may be viewed as a mechanism which allows the colony to switch from periods of low activity to phases of high activity. This is an optimizing mechanism as minimal expenditure is incurred for most of the time, this being in the form of a few experienced scouts searching out food sources. And yet, when it is established that extra expenditure is likely to be rewarded, it allows for periods of increased expenditure. Recruitment might also allow the intensity of the response to a food find to be mediated by the colony's current dietary requirements, with "hungry" reserves being more responsive to recruitment signals.

The responsiveness of foragers to food availability is well demonstrated in ***Novomessor albisetosus*** and ***N. cockerelli*** by Whitford et al. (1980). When they supplied extra rations of rolled oats to colonies they found that the number of foragers involved in foraging bouts increased. Counts, typically of 1-4 foragers returning to the nest per minute (during morning and afternoon foraging bouts) were found to increase by a factor of two or more when the extra rations were presented. They found that when the extra rations were of ground beef or tuna fish that the amount of activity increased even more, counts of over 20 foragers returning per minute were made.

Moreover, when ground beef or tuna were made available the duration of foraging bouts was extended. Normally morning activity stopped at 10am, but foraging periods were extended to 12 noonand exposed the ants to temperatures in excess of 40'C. These were outside their normal range and approached lethal temperatures.

3.5 FORAGING ACTIVITY IN *MYRMICA RUBRA.*

Myrmica rubra would seem to display a foraging activity pattern typical to temperate species. Elmes (1982) has established that it forages primarily in the Summer (95% of activity occurs between mid-April and early October), although some activity seems to occur through the Winter months. It is primarily a diurnal forager although, as Brian (1977 p68) has noted, foraging continues into the night in hot sunny weather.

This study sets out to explore further the foraging activity pattern of ***M. rubra***, to determine how environmental factors influence foraging activity and to question whether the pattern serves to optimize the food return to the colony.

4. SPATIAL DISTRIBUTION OF FORAGING EFFORT.

Ant colonies exploit food resources from the area surrounding the nest. Workers emerge from this fixed central place to forage and they return food to this central place in order to satify the needs of the entire colony. This rule needs to be qualified in some cases (during their nomadic phases army ants return food to a "moving" central place and colonies with more than one nest site have "multiple" central places) but these need not concern us unnecessarily here.

The manner in which ants exploit the surrounding area can be examined at two levels. At the colony level the use of the available area by the entire forager force can be explored. It is possible for the total foraging effort of a colony to be clumped, regularily distributed or randomly dispersed over the potential foraging area.

This applies equally to all central place foragers but eusocial insects provide a special case because the fact that there are many individuals foraging from the colony makes it possible for all parts of the area to be used simultaneously. In effect the large number of foragers may serve to make the colony "omnipresent".

At the individual level the use of different areas by individual foragers can be addressed. Just as for the foraging effort of the entire colony, it is possible that the foraging effort of individual foragers could be clumped, randomly distributed or regularily dispersed over the available area.

4.1 PATTERNS OF COLONY USE.

The forager force of some species would seem to use all parts of the potential foraging area more or less equally. Fresneau (1985) found this to be the case in ***Neoponera apicalis*** when he marked individual foragers from three colonies and followed their foraging trips over a period of one month. This revealed that foraging occured in all directions from the nest and at all distances up to a radius of about 30m.

In other cases there appears to be clumped distributions of foraging effort. This clumping is most obvious in species with single foraging trails, but is not restricted to such species. Clumping might only be temporary.

Species using foraging trails, columns or group foraging will expend a great amount of foraging effort in the places where the trails lead to but little elsewhere. This is certainly the case in statary phases of the army ant ***Eciton burchelli*** which send out single raiding columns. Franks and Fletcher (1983) report that these columns are about 6m wide and extend for an average of 89m (+/-41m) from the temporary nest; giving an area of 534m2 in receipt of a disproportionate amount of foraging effort at any time. However the spatial distribution of foraging effort in this species shifts between consecutive days of the statary phase (lasting 15 days). Franks and Fletcher observed that, on average, these raids shifted by 123' between days and that these shifts were consistently clockwise or anticlockwise. Franks and Fletcher calculated that 100% of the foraging area out to 14.3m would be searched and 30% of the area to 89m would be covered. Thus although foraging effort was clumped at any particular time the entire area around the temporary nest was searched during the statary phase.

A similar pattern of short-term clumping also occurs in ***Veromessor pergandei*** where foragers travel along a single trail and do not leave it to forage individually until they reach the distal 10m or so (Bernstein 1971 in Carroll and Janzen 1973). These foraging columns change direction between consequtive foraging periods in the Mohave desert (Bernstein, 1971, Rissing and Wheeler, 1976 and Went et al., 1972).

The amount of clumping may be reduced if there are more than one foraging trail but Cherrett (1968) found a clumped spatial distribution of foraging effort around a colony of ***Atta cephalotes*** in Guyana which used nine foraging routes simultaneously. He assessed foraging effort as the number of ants on trails and the number of foraging sites served by trails and foundthatmost foraging occured in the ESE and SSE sectors.

He also found that the distance distribution of foraging effort was non-random. Considerably less foraging than would be expected occured within the first 32m from the nest and beyond 62m from the nest, with maximum foraging effort being found between 32m and 47m from the nest.

In this case also the trails, and the areas receiving a disproportionate amount of foraging activity, shifted over the course of his study. Both the directional and the distance distributions of foraging effort changed from late October to early December. However, the aggregate of the distributions for the total period (of 58 days) still revealed clumping.

Clumping of foraging effort can also be observed in species which do not use foraging trails. For instance Holldobler and Wilson (1978) found a clumped distribution of foraging workers in the foraging arena (of approx 1m2) of a laboratory colony of ***Oecophylla longinoda.***

Wehner et al. (1983) found a clumped distribution of foraging effort around field colonies in ***Cataglypsis bicolor***. They followed individually marked foragers on foraging excursions and recorded their position every 30 seconds and used these "fixes" to calculate the distribution of foraging effort. They found that the colony's foraging effort was clumped in areas closer to the nest and also in some directions. Harkness and Maroudas (1985) also found that the distance distribution of foraging effort fell off with distance from the nest.

Wehner et al. found that at a site in Greece 90% of foraging time was spent within a radius of 13m from the nest (from 54 foragers followed for a total of 990 mins) while in Tunisia 90% of foraging time was spent within 33m (35ants, 1442 minutes) from the nest. (Individuals' foraging trip duration were 2.8 times longer in Tunisia).

4.2 PATTERNS OF INDIVIDUAL USE.

It has been found in several cases that individual foragers concentrate their foraging effort into restricted portions of the colony's total foraging area. That is to say that they return consistently to these areas on successive foray for a considerable part of their foraging life.

This clumping of individuals' foraging effort has been found in the ponerine ant, ***Neoponera apicalis*** by Fresneau (1985). He followed marked foragers and observed that individuals displayed a high degree of fidelity to specific parts of the foraging area. A total area, centred on the nest, with a radius of 20 to 30m was covered by foragers; this was made up of a "mosaic" of individual foraging areas of about 30m2. Thus individuals showed directional and distance specialisms.

Similar clumping of individual's foraging effort occurs in three species studied by Dobrzanaska`s (1958). He marked foragers of ***Formica rufa*** **L.,** ***F. pratensis*** L. ***and F. truncicola*** Nyl. within a 20x20cm portion of their foraging areas. These marked individuals were resighted at the same location indicating that they foraged in this area consistently. Dobrzanaska concluded that in these species there occured a "secondary partitioning" of the foraging area between individual foragers.

The best documented example of individual foragers concentrating their effortsinto aparticular part of the foraging area is provided by studies on **Cataglypis bicolor**. Harkness (1977) follwed marked individuals and found that they displayed "area-restricted" foraging. He found that the extent of area-restricted foraging was determined by the individual's behaviour whilst foraging; those which licked plant surfaces covered a smaller area than those which searched for scavenge items. This behaviour was repeated on successive forays.

Harkness and Maroudas (1985) followed marked individual *C. bicolor* foragers, marking their position every 10 seconds throughout several consecutive foraging trips and found that the each restricted its foraging to a sector covering an angle of about 40' from the nest.

Schmid-Hempel (1984) also demonstrated that *C. bicolor* foragers tended to return to the same locations on consecutive forays. He found that individuals differed in the persistance with which researched the area again; some "vigorously scoured small areas" while others "quickly moved over extended areas". He demonstrated that the intensity of researching could be increased if foragers obtained a food item on their previous foray. This increased localization of the individual's foraging distribution was found to be greater at greater distances from the central place.

It is also possible that individual foragers show no site specialism and search over the entire area used by the colony. I do not know of any case where such a pattern has been positively documented. However Dobrzanska's (1958) finding that in ***Myrmica scabrinodis, Tetramorium caespitum*** or ***Leptothorax acervorum*** marked foragers were not resighted in previously visited areas strongly suggests that individual spatial specialism is lacking in these species.

It is the case in the African seed harvester ***Messor regalis*** that foragers do not always exploit the same area. In this species foraging pattern changes from column foraging when food is abundant to individual searching when food is scarce. It is possible that individuals might show specialism during periods of food scarcity but this would disappear if the colony switched to column foraging.

4.3 OPTIMAL SPATIAL DISTRIBUTION.

The mechanisms which determine the space use patterns outlined in the foregoing examples could have been optimized by natural selection, for natural selection will favour mechanisms which allow colonies to make the "best" use of the surrounding area.

Cody (1974) considered the extra time and energy expenditure experienced by central place foragers as they travel to and from their nest and concluded that, in a uniform habitat, the area foraged should be circular in order to maximize the difference between benefits and costs.

However, the habitat is unlikely to be homogenous and there are many factors which will conflict with the "desirability" of a circular foraging territory. For instance, strong competition between neighbouring colonies would tend to produce hexagonal foraging areas for regular hexagons represent the closest possible form of packing in two dimensions. Indeed the restricting influence of the presence of neighbours can be seen in the foraging areas mapped for ***Pogonomyrmex badius*** in an old- field in North Carolina by Harrison and Gentry (1981) and in ***Formica rufa*** in deciduous woodland in England by Skinner (1980a).

Similarily predation pressure can influence the utilization of the potential foraging area, such that foraging effort is reduced in areas of high predation pressure. This has been found to be the case in ***Lasius pallitarsis*** (Provancher) by Nonacs and Dill (1988, 1991).

The distribution of food resources would also be expected to have a very strong bearing on the distribution of foraging effort around the central place. If these distributions could be matched then foragers would have the greatest chance of finding and returning food to the colony, and the colony would be more successful. Indeed natural selection should favour mechanisms which match the distribution of foraging effort to the distribution of food.

Andersson (1978) considered how an "optimal" (solitary) central place forager should distribute its time (=foraging effort) over the surrounding area in a habitat where food is uniformly distributed. In his model an optimal forager was one which for which the marginal cost of foraging was equal throughout the area, i.e. the change in costs or reward which the forager would experience if it spent another unit of time searching in one direction at a specific distance should be the same as that experienced in any other direction or distance. Thus he predicts that "the optimal search time (=foraging effort) per unit area should decrease linearily with distance from the central point".

Andersson's model considered the distribution of a solitary animal, but I believe that it can be extended to eusocial insects simply by considering the sum of the distribution of foragers rather than that of the single forager.

The prediction of Andersson's model appears to be met by *C. bicolor* for, as Wehner et al. (1983) and Harkness and Maroudas (1985) have found, foraging effort was concentrated close to the nest and decreased with distance from the nest. The prediction is contradicted by *A. cephalotes* where Cherrett's (1968) found that foraging effort was greatest between 32m and 47m from the colony (food may not have been uniformly distributed).

Clumped food resources might be permanent or renewable in which case their spatial distribution will be fixed. This allows ants exploiting these resources to match their foraging effort distribution to that of the food. For instance, the distribution of aphids clusters, and certainly of trees, is fairly constant. The trails of *F. rufa* serve to channel foragers to trees where aphid clusters are to be found. Moreover, the trails shift, and the spatial distribution of foraging effort changes, as aphid clusters on other trees begin to be exploited (Skinner 1980a,b).

If clumped food resources are not reliable then this sort of matching is not possible. However recruitment provides an excellent mechanism to allow foraging effort to be matched to short-term food distributions. Scouts first determine the position of food and then a bout of recruitment ensures that much foraging effort is targeted on the position of the find.

Charnov's (1976) Marginal Value Theorem considers the distribution of foraging effort between patches with different resource availabilities (see #1.2.4 above). This may be applied to the spatial distribution of ant foraging effort if a correction is made for the fact that ants are central place foragers and that many individuals engage in foraging.

Now Charnov's model did not consider central place foragers. Therefore it is necessary to add the costs of between the central place and the patch to the foraging costs (as in Orians and Pearson's (1979) Central Place Foraging model, #2.3).

In Charnov's model the (solitary) forager spends time in a patch where food is available; the longer it remains in the patch the more food it finds but as it does so it depletes the resource so that the rate it which the forager receives reward decreases with the time the forager spends in the patch. An optimal forager should leave the patch as the "marginal" rate of reward falls to that which is expected from the entire habitat.

This situation can be translated to the case of eusocial insects by considering the number of ants foraging in a patch and the frequency with which they go there. As more ants go more frequently to the same area they deplete the food reserve of that area and so the colony's rate of reward decreases. If Charnov's model were to be applied to ants then the foraging effort allocated to an area should decrease as the colony's rate of reward from that area decreases to the rate of reward from the whole foraging area.

This prediction would seem to be met, at least qualitatively, by those column raiding species where the column shifts, such as ***E. burchelli*** (Franks and Fletcher, 1983) and ***V. pergandei*** (Rissing and Wheeler, 1976), presumably as the resource is depleted, to new areas with undiminished food resources.

4.4 DISTRIBUTION OF FORAGING EFFORT IN *MYRMICA RUBRA*.

I know of no studies which have been carried out to determine the spatial distribution of foraging effort in ***Myrmica rubra***. Therefore I propose to investigate how the potential foraging area around the nests of ***M. rubra*** are exploited. I ask what criteria might be optimized by such a distribution and what constraints might be in play.

5. FORAGING MOVEMENT.

The pattern of ant foraging movements may be determined by natural selection forces. One would expect that a pattern which gives the highest food encounter rate would be favoured.

In some cases, for example where foragers move along clearly demarked trails directly to food sources or where recruited ants follow pheromone trails to a food source (see #1.5), this supposition would seem to be supported. Indeed these seem to be very efficient mechanisms for ensuring that foragers encounter food.

In other cases, such as when individual foraging occurs, the supposition is harder to support. Yet these individual foragers will also have been subjected to selection pressures to make their search pattern effective in encountering food items.

5.1 MOVEMENT SIMULATIONS GIVE INSIGHT INTO OPTIMAL PATTERNS.

A number of researchers have produced simulations of the movement process which serve to shed some light onto what a random movement pattern would be like and at the same time to determine what an optimal pattern would be like. Many of these mathematical models consider only the consequences of random movement patterns, such as the likely distribution of prey encounters (e.g. Rogers, 1972; Paloheimo, 1971a,b; Cain, 1985).

Cody (1971) and Pyke (1978a) produce simulation models which immitate the pattern of movement and predict values for movement parameters which can be tested against actual observations.

In Cody's (1971) computer simulation model the foraging animal was considered to move between points in a grid, with each move being of a fixed length (one grid unit). The direction of movement, which could change at every step, was the controlled variable. In movement simulations the probability that the animal would move ahead, turn right, turn left, or go backwards were controlled.

Cody's simulations showed that the movements which maximized coverage of the "foraging area" had a probability of moving ahead of 0.6-0.7 and of moving backward of 0.05. With such walks over 70% of grid points were visited at least once. Such movements also gave the most even distribution of visits to grid points (very few were not visited and very few were visited more than five times. The lowest coverage was obtained when the probabilities of going ahead, back, right or left were equal (all p=0.25).

Pyke's (1978a) computer simulation model was very similar to that of Cody in that it also considered the effects of varying the directionality of movement whilst keeping the length of moves constant for a forager moving between points in a grid.

Pyke introduced a further variable not included in Cody`s model; he considered "boundary behaviour" which determined what the animal did when it reached the boundary of the grid. This was considered to be a partially reflecting surface where the probabilities of going right, left or backwards were approximately equal.

The main difference between the models was that Pyke defined an optimal path as one which minimized path recrossing (simulating returning to sites where prey have been depleted) rather than maximizing coverage of grid points. Pyke's movement simulations revealed that path recrossing was minimized when the difference between the probabilities of going forwards and going backwards (assuming that the probabilities of going right and left are equal) was between 0.8 and 1.0 (depending on the size of the grid).

Thus Cody's and Pykes`s models both predict that high directionality should be a component of an optimal movement pattern.

Of course, directionality is only one of the parameters required to characterize a movement path. Long movelengths, for instance, might also be included in a path which minimizes the chances of a forager returning to a depleted site.

However it is not always the case that highly directed movements would be advantageous. For instance, if food was located in discrete patches, then an optimal movement pattern would be one that would keep the animal within the patch until it was exploited and then move quickly and directly to the next patch. [Smith (1974a,b) has shown that thrushes turn more often and move shorter distances after they have found an earthworm, presumably in the expectation that there will be other worms in the same vicinity.]

Highly directed movements would not necessarily be best for central place foragers, such as ants, for these would take the forager far from its nest and so increase its costs as it travels to and returns food from distant sites.

5.2 FORAGING MOVEMENTS OF ANTS.

There have been very few studies carried out to investigate the movement patterns employed by individual forager ants searching for food. In 1973 Carroll and Janzen, in their review of the "Ecology of Foraging by Ants" stated that "we do not know what the search pattern of an individual looks like with respect to the pattern of food items". Since then some advance has been made in detailing the search paths of individual ants.

Gordon (1982) carried out a very detailed study of the movement patterns of workers of the red imported fire ant ***Solenopsis invicta***. She video-recorded the movements of ants as they walked over glass sheets (11x11cm) which had been newly introduced to the nest boxes of seven laboratory colonies. These recordings were of 10 second durations. She then simplified the movements by considering every ants position every 0.41 seconds (10 frames); the simplified path was considered as a series of straight lines joining these "fixes".

Gordon classified paths into four classes on the basis of their speed, the tendency for consecutive straight line segments to be in the same direction (=directionality) and the interactions with other workers. Type 1 movements included frequent antennal contacts with other workers, i.e. two or more antennal contacts per 10 second. In Type 2 movements the ant stays still for more than 0.41 seconds at least twice in 10 second segment, the ant moves slowly, and initiates no antennal contacts. Ants 0making movements of Type 3 moved in a slow meandering path, usually with 3-6 or more steps per actual centimeter walked (6 steps/cm is speed of 0.41cm/second). Ants with Type 4 paths were direct (i.e. few turns) and rapid (often three or less steps/cm, about 0.74 cm/second), and no more than one antennal contact in the 10 seconds.

Gordon found that the proportions of ants making movements of each type varied significantly between colonies ($p<0.001$). These proportions also varied over time elapsed (since the glass sheet was introduced); more trails of types 2 and 3, and less of types 1 and 4, were observed when a longer period had elapsed ($p<0.05$, comparing movements at 30, 105, 180, 225 minutes).

She also found that different sized workers (the fire ant displays considerable size polymorphism) were liable to employ different movement patterns. She removed workers making movements of each type from four colonies and measured their head widths and found that ants making type 1 movements were invariably the largest, those making type 2 movements were usually (in 3 of 4 colonies) the smallest ($p<0.001$).

Although Gordon's investigation was not specifically of foraging movements, her findings do serve to demonstrate that different movement patterns can be identified and separated.

Foraging movements patterns have been observed in the primitive ponerine ant, ***Neoponera apicalis***, a species where individuals forage independently of nestmates and do not recruit to food finds. Fresneau (1985) found that the routes leading each forager to its individual foraging area (individuals display site specialism, see #4.2 above) were very stable and precise.

Each forager, as it left the nest, started out in the direction of the final destination and continued to display high directionality until it reached its target area. For those individuals which consistently foraged closer to the nest the phase of high directionality was shorter. When a forager reached its target area, which covered about 30m2, it switched to using looping movements with low directionality.

A similar pattern is evident in ***Cataglypsis bicolor***, another species where foragers operate independently of each other and without recruitment. Such observations have been made by Harkness and Maroudas (1985), by Wehner, Harkness and Schmid-Hempel (1983), and, by Schmid-Hempel (1984).

Harkness and Maroudas (1985) marked the positions of individually marked foragers and compared the positions of these fixes to the predictions of their "flexible chain" movement model. In this model the length of links was kept constant abd the direction between links was a controlled variable.

They found that the location of fixes from actual foraging movements matched fairly well to their flexible chain model if the direction change at fixes were selected at random. The match was enhanced if the size of the direction change at links was restricted for a certain distance from the nest. That is to say, the match was better if a period of more directed movement was followed by a phase of less directed movement.

As this is the pattern used by real ***C. bicolor*** ants, Harkness and Maroudas concluded that the ants "seem to have adopted a search pattern which shows some characteristic features of random search, but which is modified to give also a more rapid penetration into the surrounding terrain".

A similar change in individual foraging movements with time is also found in ***Messor wasmanni*** **Collingwood**, even though this species sends out a single column of foragers, 2.5-5cm across extending for 10-20m, along which there is a flow of as many as 150 ants per minute. At the end of the column the foragers spread out over an area of 2-3m diameter. Individuals only searched a small fraction of this area, typically 0.5m2.

Harkness and Isham (1988) followed individually marked foragers throughout thier forays, "fixing" their positions at either 30 second or 2 minute intervals. On leaving the nest there was a phase of long movelengths (c 1m in 30 seconds) with high directionality. Then, on reaching the end of the column, there was a phase of short movelengths (c25cm) and many turns of great magnitude giving low directionality (from theirfigure 2).

These movements can be interpreted as optimal; the directed movements are the best way of getting foragers to search in an area where food is likely to be encountered whilst the undirected movements are the best way to search the area intensively. Furthermore the later undirected movements ensure that the forager will not travel too far from its central place, and this will limit the extra costs involved with foraging at greater distances.

Any problems which may arise due to the depletion of resources is avoided, in the case of ***N. apicalis*** and ***C. bicolor*** by having different foragers exploiting different areas, and in the case of ***M. wasmanni*** by shifting the direction of the column between days.

Schmid-Hempel (1984) observed the foraging movements of individually marked workers of ***C. bicolor*** in an area of 20x20m which was 8m from the nest. By restricting his observations to this distance from the nest he will have excluded much of the early phase movements.

He simplified foraging movements by considering the paths to be made up of a series of straight line segments joining "fixes" of the ants' location at 10 second intervals. For quantitative analyses of these paths he calculated a straightness index (=clumping index) which was a measure of the similarity of the directions of beeline segments joining the fixes. [This is a "circular" statistic see Appendix 1. The clumping index falls within the range 0 to 1; the higher the more similar the segment directions will be.]

Schmid-Hempel found that different foragers' trails have different clumping index values, indeed a wide spectrum from extremely directed to very tortuous was represented. Moreover, the paths of individuals on (two) consecutive days were found to have the same straightness index of foragers' paths ($p=0.05$). Thus foragers' movements were consistent over this large portion of their foraging career (average life expectancy for foragers was 6 days).

Schmid-Hempel demonstrated that different movement patterns afforded different levels of success to the forager. He found that the movements of those foragers which found some food items during their foray were straighter than those which were unsuccessful (clumping index 0.56 v 0.42, $p<0.01$).

Schmid-Hempel also demonstrated that movement pattern can change depending on the experience of the forager in finding food. In an experiment he offered different rewards, cheese pieces and flies, to foragers 12m from the nest, and recorded the paths taken in subsequent foraging trips. This revealed that ants persisted more in researching an area after receiving cheese (i.e. lower clumping index) thanafter obtaining a fly.

In another experiment, marked foragers were given cheese pieces at 12m and 32m from the nest, on separate days, and their subsequent foraging excursions were recorded. Schmid-Hempel found that the ants showed more tortuous paths (lower clumping index) after finding food at the more distant places.

This flexibility and the tendency to research the site of a previous success might explain why, in another experiment, clumped food was harvested more quickly than the same amount of food in a uniform distribution.

Schmid-Hempel carried out two sets of observations, separated by a period of two weeks. In both tests 100 cheese pieces were offered within the 20x20m observation area; in the first test these were presented in a clumped distribution, in the second they were presented in a uniform distribution. The trails of foragers were recorded until 85% of the baits had been removed. This revealed that foragers which employed a persistent movement pattern, i.e. low directionality, were more efficient at exploiting food items from the clumped distribution, i.e. they retrieved more items within the same time ($p<0.05$).

The total time required for the colony to remove 85% of the baits was "substantially" shorter, although no significance level is given, for the homogenous distribution (78 minutes) than for the clumped distribution (125 minutes).

Evidently the less directed foragers would be the ones to research the area of previous success most intensively and so would be best at exploiting clumped resources.

Presumably the experience of finding a food item caused many of the foragers to change their movements so that they researched the area of their success more intensively; if the initial success was from a clumped distribution they would be more likely find further items on subsequent forays.

5.3 FORAGING MOVEMENTS OF *MYRMICA RUBRA*.

Little is known of the search pattern used by ***Myrmica rubra***. It is known that foragers search individually for a variety of food types. These food types come from a variety of sources, including the tending of aphids to collect honeydew, active predation on other invertebrates and from scavenging on carcasses. Of these sources only aphids represent a predictable and reliable resource; the other food sources will have unpredictable and unreliable distributions. If the movement pattern displayed by the foragers of a colony has been optimized by natural selection then it should be such that all these food stuffs might be encountered.

6 AIMS AND OBJECTIVES.

This work attempts to add to the body of knowledge on the foraging behaviour of the ant, ***Myrmica rubra***, by investigating four aspects of foraging; the choice of food, the temporal pattern of foraging activity, the spatial distribution of foraging effort and the pattern of foraging movements.

Furthermore I attempt to interpret and understand these aspects of foraging behaviour within the framework of optimal foraging theory and so shed some light on the forces of natural selection which have shaped the foraging behaviour of this organism.

It is anticipated that my observations and experiments on the foraging behaviour of ***M. rubra*** will complimenmt the information which has been gathered in other areas, by Brian, Cammaerts and others, and so contribute to a fuller insight into the biology of this species.

FOOD CHOICE is investigated in order to:-

-determine the diet of ***M. rubra,***

-investigate the food selection processes involved in determining the diet, and,

-explore the optimality of such selection processes and choices.

The **TEMPORAL DISTRIBUTION OF FORAGING ACTIVITY** is investigated in order to:-

-determine how foraging activity is distributed over time in ***M. rubra***,

-investigate the constraints imposed by and the influence of environmental factors on any temporal patterns of foraging activity,

-investigate the role of internal factors on any temporal patterns of foraging activity, and,

-explore the optimality of any temporal activity patterns.

The **SPATIAL DISTRIBUTION OF FORAGING EFFORT** is studied in order to:-

-determine how foraging effort is distributed over the area sourounding the nest **in** ***M. rubra***, and,

-explore how such a spatial distribution pattern might optimize food return.

FORAGING MOVEMENTS are investigated in order to:-

-describe the food searching movements of ***M. rubra*** foragers,

-determine whether there is a common pattern of movement employed by all the forager-force,

-assess whether such movement patterns afford a greater possibility of food encounter, and,

-explore how such movements have been optimized by natural selection.

7. MATERIALS AND METHODS.

7.1 *MYRMICA RUBRA*.

The ant chosen for use in this study of foraging behaviour was ***Myrmica rubra*** (L.). There were several reasons for making this choice.

This species is a common one and is found to be widely distributed throughout the British Isles. It is also found to live in accessible habitats; it is most typically found in grasslands where it would seem to have a preference for nesting under stones (which warm in sunlight quicker than the surrounding soil). The species has adapted to cultivated environments, such as gardens, where the foraging activities of individual workers might be more easily observed than in grassland.

Colonies of ***M. rubra*** are moderately sized, rarely exceeding 3000 workers. Of course only a proportion of these will indulge in foraging activity in any period. Thus the forager population should not be so numerous as to overwhelm the observer. Indeed if only a small number of foragers were to be observed this could represent a sizeable proportion of the total population. Another advantage of modest colony sizes is that that they may be more easily maintained under laboratory conditions than colonies with more numerous populations.

Furthermore individual ***M. rubra*** workers are sufficiently large (7-8mm Dreisig 1988) and slow moving to facilitate detailed observation of their activity.

Several aspects of the biology of ***M. rubra*** have been well researched by other authors, particularily Brian and Cammaerts. Their work, and that of various others, reveal many aspects of this ant's biology which influence foraging behaviour and provide a background and a framework on which the result of these foraging studies can be interpreted.

Thus there are many advantages for using ***M. rubra*** as a study organism. There would seem to be only one disadvantage - as pointed out by Brian - ***Myrmica*** stings effectively and painfully when disturbed!

7.2 FIELD COLONIES AND LABORATORY NESTS.

Observation and experiments on foraging behaviour were carried out both in the field with natural colonies and in the laboratory with maintained colony fragments.

Fieldwork was carried out at Wrotham Field Centre (of Goldsmiths College) on the North Kent Downs. This Centre offered a variety of habitats within a small area. Most of the colonies used for extended observation were located in the rosegarden to the South of the centre buildings (Figure 7.1). The beds in this rosegarden were weeded frequently so that was little vegetation to obscure observation of foraging behaviour.

Laboratory nests were established from populations collected from Wrotham Field Centre and its environs. When nests were excavated care was taken to ensure that the entire population was gathered. These were maintained in a fridge at c.4'C until they were sorted. [Kelly's (1973) observation that colonies of ***Lasius flavus*** were often found in juxtaposition with coloniees of ***M. rubra*** was supported by a few similar observations during excavations at Wrotham].

Three types of nest boxes were used to house colony fragments during observations and experiments, these are shown in Figure 7.2. The first two types of nest boxes were plastic lunch boxes; the larger boxes measured 25x15x5cm and were designated FB (and appropriate number). The smaller boxes measured 20x10x10cm and were designated SB (and appropriate number). These were set up with populations of 1 queen, 120 workers and brood of all stages and with 1 queen, 100 workers and brood of all stages. A sponge was kept moist in each nest box and the queen and most of the workers congregated around this. The rim of these boxes were coated with "FLUON' to prevent ants from escaping when the lid was removed to moisten the sponge.

1985

a Nest One

b Nest Two

1986

No.s Nests One — Seven

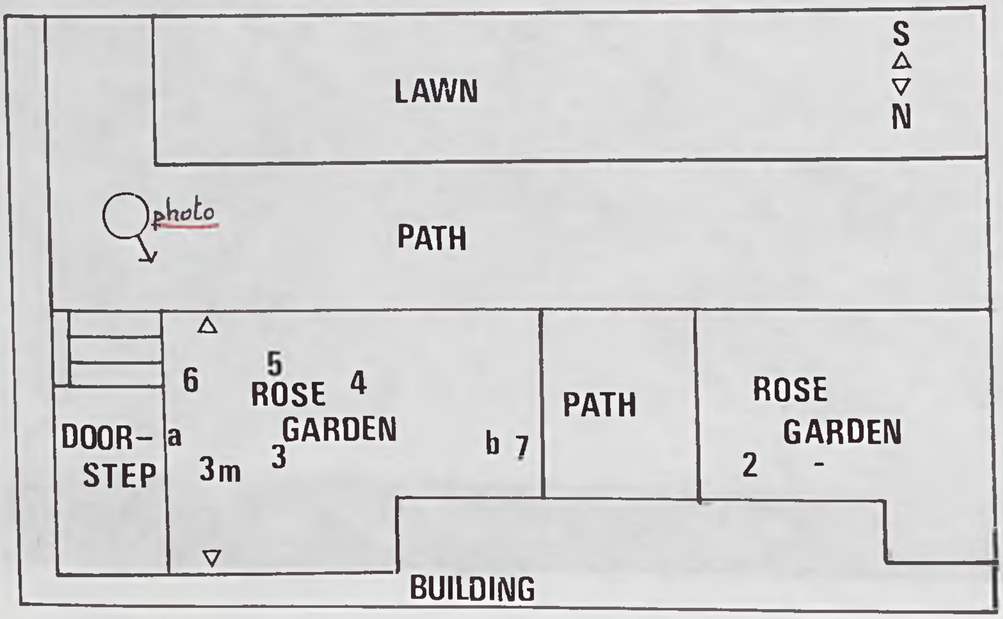


Figure 7.1. Photo and plan of "Doorstep" area at Wrotham Field Centre. Locations of Nests are shown.

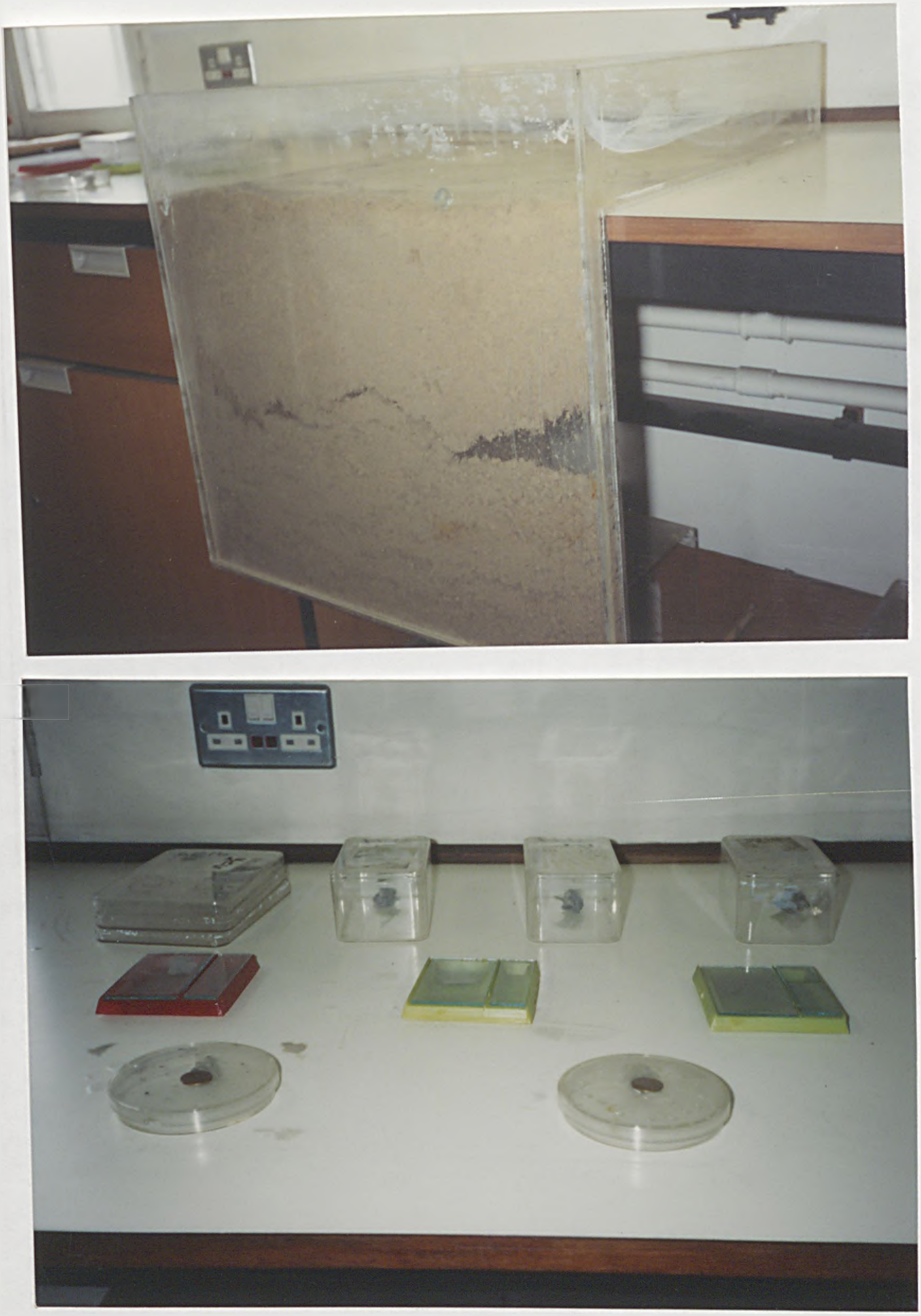


Figure 7.2. Nests used to house colony fragmanmts in the laboratory.

The largest nest box was a large perspex nest with a horizontal foraging arena measuring 50x50 cm attached to a vertical nesting space measuring 50x30x5cm. This nest was be designated LLN.

This nest was placed between two South-facing windows so that the natural light was available. In addition to this artifical light from an overhead source was used between 9.00 and 18.00 hours. Ambient temperature varied in the range 18-25'C over the course ofthe study but was very constant on any particular date. The nesting area was soil filled, this was watered at 9.00 and 17.00hrs on weekdays. Food (dead insects, sugar or sugar solutions) was provided approximately twice a week. The foraging area was divided into a grid of 2x2 cm squares. The foraging area was surrounded by a 10cm high vertical sheet of Perspex topped with "FLUON' repellant.

The nest was founded in October 1984 to contain a population of 6 queens and 1200 workers; subsequent population estimates were made by removing and counting the number of dead ants. All the brood excavated from that colony were left with the residue of the colony for seven days until galleries had been excavated in the soil. Thereafter they were placed in the large laboratory nest. Figure 7.3 shows how the population of this laboratory colony fragment changed over time. This method of estimation may be slightly erroneous toward the end of the period because new young workers were being produced. Another error might arise if all the dead ants were not brought to the surface.

Populations reserves were maintained in petri dishes and two- chambered nests with removable glass roof slides (see Figure 7.2). These reserves were used to replenish the populations in FB and SB nests.

7.3 FOOD CHOICE.

7.3.1 CHOICE OF LIQUID FOODS.

A number of experiments were performed in the laboratory with colony fragments (maintained in FB and SB picnic box nests) to investigate the ants' choice of different

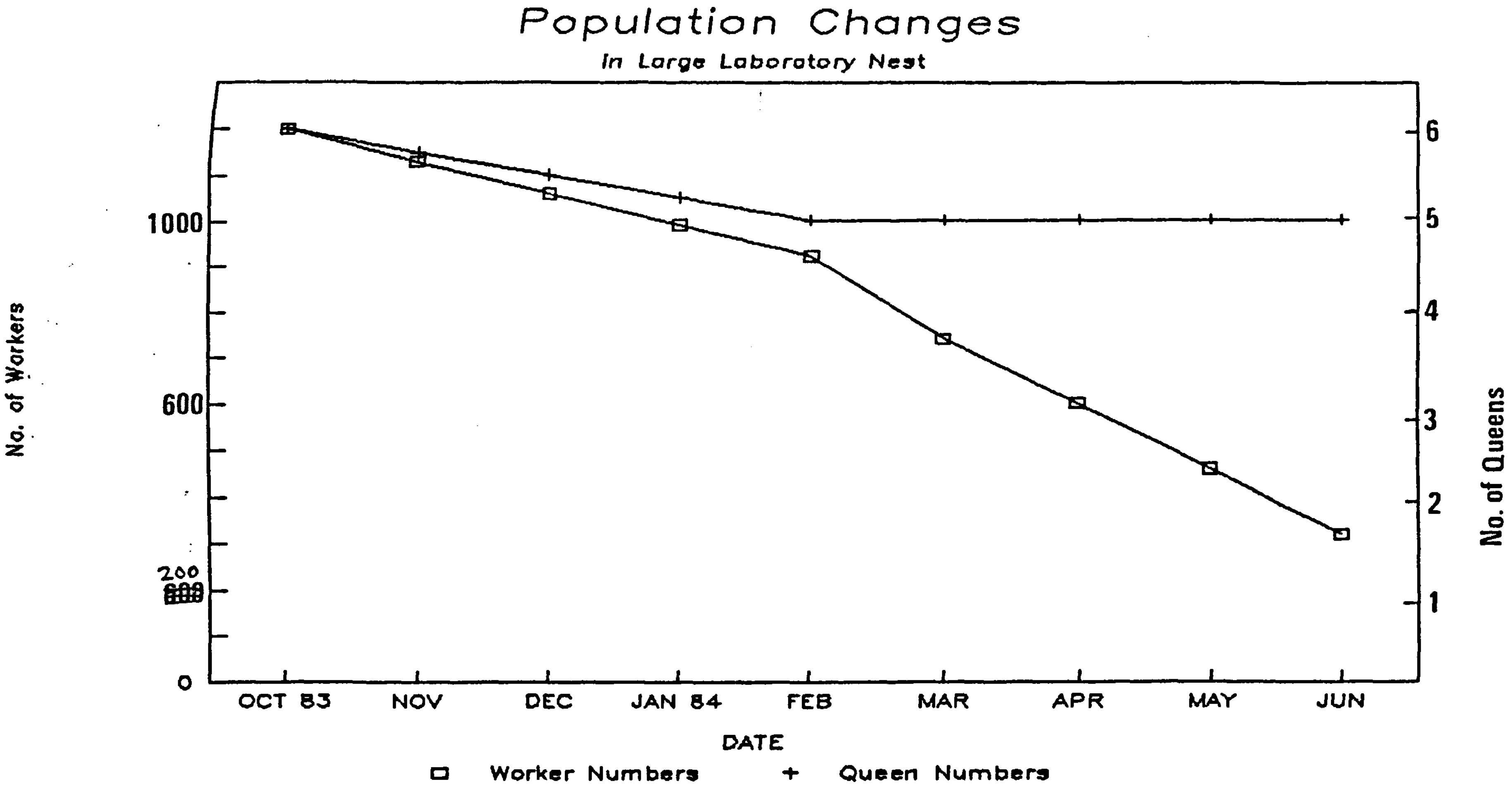


Figure 7.3. Population changes in the Large Laboratory Nest.

liquid foods. In these tests two droplets of the test solutions were placed side by side on coverslips in the nest boxes at the opposite end from the sponges. The response to each solution was assessed as the sum of the number of ants drinking from each droplet at fixed time intervals of five minutes for a period of up to an hour to give an estimate of the number of "ant-minutes" spent drinking. Many individuals remained drinking for several counts.

In the course of the study solutions of three sugars, glucose, fructose and sucrose, at concentrations ranging from 0.001M to 0.1M were used. One amino acid, leucine, was used at concentrations ranging from O.001M to 0.04M. These were chosen because of their ready availability and the fact that they are found in honeydew and extrafloral nectars (#2 above).

There were four groups of experiments where there was a choice between two liquids; between sugar solutions and water, between two sugar solutions, between the amino acid leucine and water, and between leucine and sucrose solutions. Control tests with two drops of pure water were also performed. Such experiments were performed in November 1984, October and November 1986 and February and March 1987. Exact details of the choices available in each particular trial are given where appropiate in the "RESULTS" section below (#8.1.1).

Statistical comparison of the drinking response to each solution in the food choice experiments was performed using a binomial test (Siegel 1956), which compared the null hypothesis that approximately equal numbers of "ant-minutes" should be spent drinking from each solution with the proportions actually observed.

7.3.2 CHOICE OF SOLID FOODS.

Another series of experiments were performed to investigate the selection of solid foods. In these tests baits of different sizes were placed on a glass slide and this was presented to either a colony fragment or placed in the vicinity of a field nest. The time elapsed before each bait was removed was recorded.

In most instances the food used as bait was cheese, although ham and boiled egg white were also used. Cheese was used because it was attractive to the ants, readily cut up into the appropiate sizes. The baits were cut by hand so that the sizes given are approximate but there was always a marked difference between the size classes offered. Different varieties of cheese (cheddar and red leicester) were used so that different sizes might be readily distinguished (care was taken to randomize the baits so that any size preference would not be compromized by a taste preference.

Usually the choice was between two sizes of baits only but in some cases the choice was between three and even four sizes. Exact details of the choices available are given in the "RESULTS" section (#7.1.2).

These tests were performed in the large laboratory nest LLN between April and June 1985 and in August and September 1986. In these tests the majority of baits were removed within 60 minutes. A practical problem encountered was that so many foragers would accumulate around the baits that it was difficult to see exactly when a bait was being removed.

Experiments were also performed in the rosebeds at Wrotham with natural colonies. In these field trials cheese baits were placed on glass slides which were placed on the ground close to nest entrances. The removal times for these baits were recorded. If baits were removed during gaps in observation the removal time was considered to be the mid-point time between the observations. Observations were continued for up to 160 minutes but not all the baits were removed in this period.

Kolomogorov-Smirnov tests (Sokal and Rohlf 1969) were used to determine whether one type of bait was removed significantly quicker than another.

7.3.3 PREY RETURNED TO THE NEST.

In the period of August to September 1985 a collection was made of the solid preys being returned to Nest One (the Doorstep nest) at Wrotham (see below). Collections were made on eleven dates. The time spent making the collection varied with the demands of other activities. The collection was made by pooting up a number of returning foragers which had been observed to be carrying prey, shaking until the ant dropped the prey, and then returning the ant to the nest area. Some ants dropped the prey readily, but most required several vigorous shakes, sometimes they needed to be confined for up to ten minutes and shaken repeatedly. There was a bias in this sampling method towards larger more visible prey.

7.4 TRAFFIC AT DOORSTEP NEST.

Counts were made of the number of ants entering and leaving one particular nest in the rosebeds at Wrotham Field Centre. The nest used, "Nest One" or the "Doorstep Nest", had a very conspicuous entrance located on the face of a West-facing brick doorstep (Figure 7.4). A circle of approximately 10cm diameter was chalked around the nest entrance and this reference line was used to determine the amount of traffic passing out of and into the nest. Counts were made every minute for a number of ten minute observations periods throughout the day. These counts were made from June to October in 1985 and again in 1986.

This was not the only entrance used by this particular colony, nor indeed was it in use all the time but it did appear to be the main entrance.

In the observations of 1986, recordings were also made of the soil surface temperature and light intensity at six sites around this nest (all these recording sites were within the normal foraging range of foragers from this nest). The positions of the recording sites are also shown in Figure 7.4. The temperature was recorded every minute for the entire ten minute period; light intensity was recorded as an average for the ten minute period. The thermometer was manufactured by Grant Instruments (Cambridge) Ltd. and could record

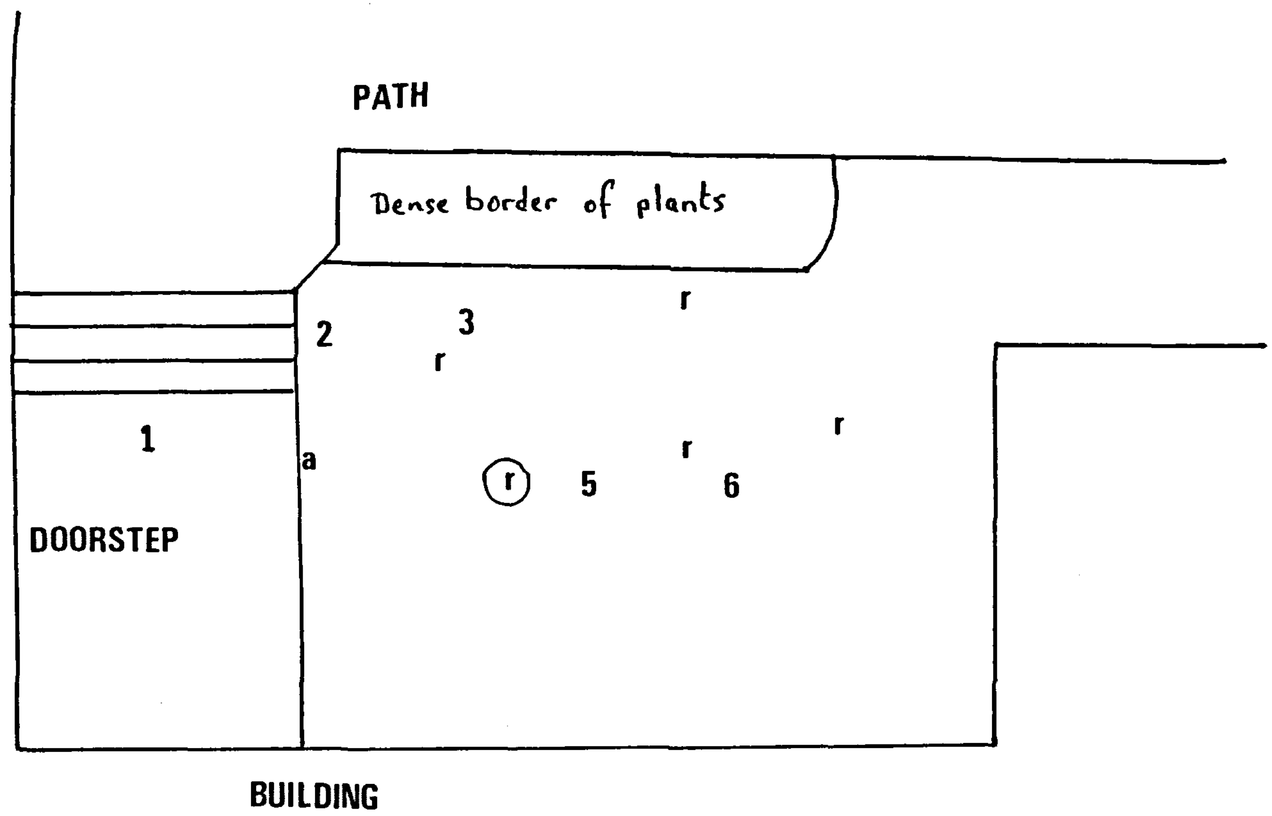


Figure 7.4. Location of Doorstep Nest and sites where temperature and light intensity were recorded during obserbvations of traffic at this entrance in 1986.

ⓡ = rose with tended aphids
a = Nest One

on two scales (0-25'C or -10-40'C) from six channels. The lightmeter was a multipoint mV recorder (Delta-T Devices, Burwell, Cambridge) which could record from six channels onto a scale from 0 to 25 mV.

7.5 FOLLOWING INDIVIDUALS' FORAGING TRIPS.

Foraging movements were investigated by following individuals throughout their foraging trips. Three series of observations were made in the laboratory. In the first two movements were video-recorded and analysed for small scale detail. Larger scale details were obtained in the third series as foragers positions were only recorded at 10 second intervals.

In fieldwork, the level of detail was reduced further, as 30 second fixes were taken, but information was captured covering much longer time periods (up to and including complete round trips). In addition to giving movement pattern information these field observations also provided information on the spatial distribution of foraging effort around field nests.

7.5.1 MOVEMENT IN THE LABORATORY - ONE.

The first set of observations were of ants moving over unfamiliar terrain in April 1984. A colony fragment, maintained in a petri dish, was placed onto the floor of the laboratory. When the lid of the petri dish was removed the ants climbed over the lip of the dish and began to move over the surrounding terrain. These movements were video-recorded. The camera was held in a fixed position so that an area of 20x20cm was in view. Ants wandered into and out of the camera's field of view so it was not possible to determine the "ownership" of all the paths. The video- recordings were replayed frame by frame to retrace the movements of each ant.

Each trail was divided into 10cm segments and for each segment the following parameters were calculated:-

1- the "straightness index", i.e. the ratio between the net distance and the gross distance (10 cm) moved (cf. "meander" ratio of Williamson and Gray, 1975,

2- the "number of changes of direction" in 10 cm (changes judged by eye), and,

3- the "magnitude of these changes of direction", regardless of whether they are clockwise or anticlockwise (small changes would be overlooked).

There were two pre-treatments for the colony fragments prior to the observation period; either the sponge in the nest had been watered or it had not. Thus movements were recorded as those of "Watered" or "Dry" ants. Two sources of sugar solution were available within the 20x20cm area. Thus the ants' paths could be further divided on the consequences of their movements, whether or not they successfully located the sugar solution.

7.5.2 MOVEMENT IN LABORATORY - TWO.

In the second series of laboratory observations foraging ants were video-recorded as they moved over the foraging area of the large laboratory nest, LLN, in December 1984. The video camera was hand-held in these observations so it was possible to follow selected individual ants for extended periods, in some cases from the begining to the end of their foraging trips, as they moved over the total foraging arena of this nest (50x50cm).

When the video-recordings were replayed the position of the ants was fixed every few frames, at approximately 0.5 to 1 second intervals. From these simplified paths the following parameters were calculated:-

1- the "speed" of the ant (cm/sec),

2- the "direction" in which the ant moved (between fixes), 3- the "frequency of changes in direction" (judged by eye; if an ant moved straight ahead no change was recorded), and,

4- the "magnitude" of these changes of direction, regardless of whether turns were clockwise or anticlockwise.

These parameters were calculated for the entire path of each ant. They were also calculated for various subsections of the total path; for each 10 second period, for each 10cm stretch of path andforeach composite of 180 degrees of direction changes.

The second parameter, the direction in which the ant was travelling is a "circular" variable and as such merits special treatment. Details of the use and analysis of circular variables are given in Appendix 1.

The trails of seven ants were used in analysis; four of these were considered to be foragers, the other three carried dead nestmates. The parameters were analysed to look for differences between all seven individuals, between the two groups, "foragers" v "carriers", within the "foragers" group and within the "carriers" group. Although food was available, at two locations within the 50x50cm area, none of the ants was successful in finding it. Therefore a comparison between successful and unsuccessful foragers could not be made.

An analysis was performed to compare between movements made at different times of the same foraging runs. This was done by pooling the information from every ant at each time interval and then comparing the pools at each interval compared (as in Gordon, 1982).

7.5.3 MOVEMENT IN THE LABORATORY - THREE.

Another set of observations were made of ants travelling in the large laboratory nest, LLN, in July 1985. These trails were followed by eye and each ant's position was recorded at 10 second intervals. Thus these paths were recorded in less detail than the previous trails.

Twelve ants were followed for variable lengths of time from leaving the nest area until they returned to it. The following parameters were calculated for each ant using the straight line intercepts joining the 10 second fixes:-

1- the "net distance" moved in 10 seconds.

2- the "direction" in which the ant travelled between fixes (another circular variable see Appendix 1), and,

3- the "size of the direction" changes between 10 second segments.

These parameters were analysed to look for differences between the individual ants and to see if there were any differences between movements made at different stages of the foraging runs.

7.5.4 FORAGING MOVEMENTS IN THE FIELD.

The main set of observations of foraging movements were made by following ants foraging from field nests located at Wrotham Field Centre between June and October 1985 and 1986. These observations were also used to illucidate the spatial distribution of foraging effort around these nests and to give information on the duration of forays.

These nests were situated in rosebeds, where a fairly open ground vegetation was maintained by frequent weeding. Thus individual foragers could be observed on the soil surface as they moved about on their foraging trips. Of the vegetation that did remain several plants (including the roses and groundsel, Senecio bicolor) carried aphid clusters; thus it was possible to pinpoint some permanent food sources.

The paths of individual foragers were followed by eye from the moment the ant left its nest for as much of the foraging trip as possible. Between June and October 1985 a total of 103 ants were followed from two nests (65 and 38 respectively). Over the same period in 1986 146 ants were followed from seven nests (37, 47, 25, 19, 5, 8 and 5 respectively). In 1985 the two nest openings were from separate colonies. In 1986 some of the seven nest openings were just different subnests or different exits from the same colony. Nest One, "Doorstep nest", occupied the same position in both years.

Many foragers were followed for a complete round trip, apparently without finding any reward, until they returned to the nest again (15% of total followed in 1985, 12% in 1986). Others were followed to aphid clusters on one or other of the plants (25% in 1985, 31% in 1986). Yet others were lost (to the observer) after some time (57% in 1985, 56% in 1986).

There were a number of reasons why foragers were lost by the observer before their trail reached a definite conclusion. These included the difficulties which arose in following individuals when different foragers met, when foragers moved behind plants or into holes in the clay, or if the observer was distracted. It was not possible to video-record the paths of the ants because of the uneven nature of the terrain and the long distances over which the ants would travel.

The forager`s paths were recorded by sticking numbered wires into the ground to mark each ants position at thirty second intervals. Shorter intervals were impractical because of the extra workload involved. If the numbered wires were inserted a few seconds after the ant had moved on they seemed not to disrupt the ant. The locations of the numbered wires were recorded and the paths were simplified to a series of straight line segments joining these thirty second fixes.

The positions of the fixes were analysed to determine a "mean movement vector" and a "mean positionvector" for each path. Both the "mean movement vector" and the "mean position vector" contain circular variables and so require special statistical methods for their calculation and analysis - these are detailed in Appendix 1. This Appendix also outlines how the conventional "linear" variables in these vectors are calculated and analysed.

Briefly the "mean movement vector" summarizes an ant`s movements between 30 second fixes and gives six pieces of information. These are the mean and the standard deviation of the movelengths between fixes, the mean movedirection between fixes, two measures of the sample deviation about this mean movelength. The "mean position vector" summarizes the various locations visited by an ant during its foraging trip. It contains six pieces of information; the mean distance (of fixes from the nest) and its standard deviation (linear variables), the mean bearing of fixes from the nest (a circular variable) and two measures of the sample deviation about this mean bearing (the "angular devaition" and the "clumping index"), and a statistical measure of whether the sample of bearings (of the fixes from the nest) are clumped or randomly distributed.

8. RESULTS.

8.1 FOOD CHOICE.

8.1.1 CHOICE OF LIQUID FOODS.

The results of the choice trials where colony fragments were offered two drops of test solutions are summarized in Tables 8.1 to 8.12. The measure of "ant-minutes" spent drinking is the sum of the number drinking at each count (every five minutes for an hour). Some individuals may have been counted several times if they drank for extended periods.

In some of the trials where there was a large response to the test solutions there were obvious differences between individuals as some drank to repletion while others did not.

8.1.1.1 RESPONSE TO PURE WATER.

The control trials where two drops of pure water were available (Table 8.1) showed that some drinking of water, albeit at very low levels, is liable to occur even when the sponges in the nests were kept well moistened. There was no bias towards one or other drop (on the one occasion when the response was sufficient to allow analysis) or when all the data was pooled (Binomial tests).

8.1.1.2 SUGAR v. WATER.

a/ 0.001M sugar solutions.

There was no evidence that the ants responded to 0.001M sugar solutions any differently than they did to water (Table 8.2). Very few ants drank either water or 0.001M sugar. The magnitude of the responses in these trials are about the same as the responses in the trials when only water was available. An average of 3.25 ant-minutes were spent drinking in each trial when only water was available against an average of 2 minutes when 0.001M sugar and water are available; (analysis of variance F=0.5947, df=1,9; n.s.).

DATE	NEST	POPN.	CHOICE 1			CHOICE 2	SIGN.
21/11/84	SB2	1q 100w	Water	0	0	Water	n.t.
21/11/84	SB2	1q 100w	Water	1	1	Water	n.t.
22/11/84	SB2	1q 96w	Water	1	1	Water	n.t.
29/11/84	SB2	1q 47w	Water	4	5	Water	n.s.
SUM of 4 control trials			Water	6	7	Water	n.s.

Table 8.1. Sum of "ant-minutes" spent drinking from droplets in one hour after liquids were placed in nest; control tests with two droplets of water. Significance refers to binomial tests.

DATE	NEST	POPN.	CHOICE 1			CHOICE 2	SIGN.
			0.001M				
21/11/84	SB5	1q 100w	Sucrose	1	3	Water	n.t.
21/11/84	SB5	1q 100w	Sucrose	3	0	Water	n.t.
SUM of 2 trials			Sucrose	4	3	Water	n.s.
21/11/84	SB7	1q 100w	Fructose	1	1	Water	n.t.
21/11/84	SB9	1q 100w	Fructose	0	2	Water	n.t.
SUM of 2 trials			Fructose	1	3	Water	n.t.
21/11/84	SB3	1q 100w	Glucose	1	0	Water	n.t.
21/11/84	SB4	1q 100w	Glucose	0	0	Water	n.t.
SUM of 2 trials			Glucose	1	0	Water	n.t.
SUM of 6 trials			Sugar	6	6	Water	n.s.

Table 8.2. Sum of "ant-minutes" spent drinking from droplets in one hour after liquids were placed in nest; choice tests with 0.001M sugarsand water. Significance refers to binomial tests.

DATE	NEST	POPN.	CHOICE 1			CHOICE 2	SIGN.
			0.01M				
21/11/84	SB7	1q 100w	Sucrose	3	0	Water	n.t.
21/11/84	SB9	1q 100w	Sucrose	4	1	Water	n.s.
SUM of 2 trials			Sucrose	7	1	Water	p<0.05
21/11/84	SB3	1q 100w	Fructose	1	0	Water	n.t.
21/11/84	SB4	1q 100w	Fructose	0	0	Water	n.t.
03/11/86	SB12	22q 9w	Fructose	3	2	Water	n.s.
03/11/86	SB18	2q 200w+	Fructose	7	1	Water	p<0.05
03/11/86	SB20	2q 10w	Fructose	1	1	Water	n.t.
05/11/86	SB12	22q 9w	Fructose	8	2	Water	p<0.05
05/11/86	SB18	2q 200w+	Fructose	1	1	Water	n.t.
05/11/86	SB20	2q 10w	Fructose	0	0	Water	n.t.
SUM 21/11/84 2 trials			Fructose	1	0	Water	n.t.
SUM 03/11/86 3 trials			Fructose	11	4	Water	p<0.05
SUM 15/11/86 3 trials			Fructose	9	3	Water	p<0.05
SUM of 8 trials			Fructose	21	7	Water	p<0.05
21/11/84	SB5	1q 100w	Glucose	1	6	Water	p<0.1
21/11/84	SB6	1q 100w	Glucose	1	0	Water	n.t.
SUM of 2 trials			Glucose	2	6	Water	n.s.
SUM of 12 trials			Sugar	30	14	Water	p<0.1

Table 8.3. Sum of "ant-minutes" spent drinking from droplets in one hour after liquids were placed in nest; choice tests with 0.01M sugars and water. Significance refers to binomial tests.

DATE	NEST	POPN.	CHOICE 1			CHOICE 2	SIGN.
			0.05M				
28/10/86	SB12	22q 18w	Fructose	27	1	Water	p<0.001
28/10/86	SB18	2q 200w+	Fructose	22	0	Water	p<0.001
28/10/86	SB20	2q 28w	Fructose	19	0	Water	p<0.001
30/10/86	SB12	22q 18w	Fructose	44	0	Water	p<0.001
30/10/86	SB18	2q 200w+	Fructose	22	0	Water	p<0.001
30/10/86	SB20	2q 28w	Fructose	11	0	Water	p<0.001
SUM of 6 trials			Fructose	145	1	Water	p<0.0001

Table 8.4. Sum of "ant-minutes" spent drinking from droplets in one hour after liquids were placed in nest; choice tests with 0.05M fructose and water. Significance refers to binomial tests.

DATE	NEST	POPN.	CHOICE 1			CHOICE 2	SIGN.
			0.1M				
22/11/84	SB3	1q 98w	SUCROSE	49	2	Water	p<0.001
22/11/84	SB4	1q 100w	SUCROSE	39	4	Water	p<0.001
24/10/86	SB12	22q 18w	SUCROSE	30	0	Water	p<0.001
24/10/86	SB16a	52w	SUCROSE	96	0	Water	p<0.001
04/03/87	SB23	4q 58w	SUCROSE	159	0	Water	p<0.001
04/03/87	SB26	2q 45w	SUCROSE	92	0	Water	p<0.001
04/03/87	SB24	28w	SUCROSE	30	0	Water	p<0.001
22/11/84	SB5	1q 95w	FRUCTOSE	20	5	Water	p<0.05
22/11/84	SB6	1q 100w	FRUCTOSE	15	1	Water	p<0.05
24/10/86	SB16b	52w	FRUCTOSE	83	0	Water	p<0.001
31/10/86	SB12	22q 15w	FRUCTOSE	84	0	Water	p<0.001
31/10/86	SB18	2q 200w+	FRUCTOSE	80	1	Water	p<0.001
31/10/86	SB20	2q 17w	FRUCTOSE	25	0	Water	p<0.001
06/11/86	SB12	21q 2w	FRUCTOSE	88	0	Water	p<0.001
06/11/86	SB18	2q 200w+	FRUCTOSE	35	0	Water	p<0.001
06/11/86	SB20	1q 8w	FRUCTOSE	7	0	Water	p<0.01
22/11/84	SB7	1q 99w	GLUCOSE	36	1	Water	p<0.001
22/11/84	SB9	1q 100w	GLUCOSE	30	1	Water	p<0.001
24/10/86	SB18	2q 200w+	GLUCOSE	158	2	Water	p<0.0001
24/10/86	SB19	1q 146w	GLUCOSE	147	1	Water	p<0.0001

Table 8.5. Sum of "ant-minutes" spent drinking from droplets in one hour after liquids were placed in nest; choice tests with 0.1M sugars and water. Significance refers to binomial tests.

DATE	NEST	POPN.	CHOICE 1			CHOICE 2	SIGN.
			0.1M			0.1M	
23/10/86	SB12	2q 18w	SUCROSE	40	3	Fructose	p<0.001
23/11/86	SB16a	38w	SUCROSE	92	16	Fructose	p<0.001
23/10/86	SB16b	71w	SUCROSE	99	24	Fructose	p<0.001
23/10/86	SB18	2q 200w+	SUCROSE	228	51	Fructose	p<0.001
23/10/86	SB19	1q 146w	SUCROSE	190	61	Fructose	p<0.001

Table 8.6. Sum of "ant-minutes" spent drinking from droplets in one hour after liquids were placed in nest; choice tests with 0.1M sucrose and fructose. Significance refers to binomial tests.

DATE	NEST	POPN.		CHOICE 1			CHOICE 2	SIGN.
				0.1M			0.1M	
23/11/84	SB2	1q	96w	SUCROSE	23	8	Glucose	p<0.05
23/11/84	SB3	1q	96w	SUCROSE	12	0	Glucose	p<0.002
23/11/84	SB4	1q	96w	SUCROSE	14	3	Glucose	p<0.05
23/11/84	SB6	1q	96w	SUCROSE	42	2	Glucose	p<0.001
23/11/84	SB7	1q	96w	SUCROSE	88	29	Glucose	p<0.001
23/11/84	SB9	1q	96w	SUCROSE	84	26	Glucose	p<0.001
21/10/86	SB18	1q	96w	Sucrose	104	134	Glucose	n.s.
21/10/86	SB19	1q	96w	SUCROSE	175	24	Glucose	p<0.001

Table 8.7. Sum of "ant-minutes" spent drinking from droplets in one hour after liquids were placed in nest; choice tests with 0.1M sucrose and glucose. Significance refers to binomial tests.

DATE	NEST	POPN.		CHOICE 1			CHOICE 2	SIGN.
				0.1M			0.1M	
23/10/86	SB16a		33w	FRUCTOSE	37	4	Glucose	p<0.001
23/10/86	SB16b		71w	FRUCTOSE	70	24	Glucose	p<0.001
22/10/86	SB18	2q	200w+	Fructose	97	82	Glucose	n.s.
22/10/86	SB19	1q	146w	FRUCTOSE	122	58	Glucose	p<0.001

Table 8.8. Sum of "ant-minutes" spent drinking from droplets in one hour after liquids were placed in nest; choice tests with 0.1M fructose and glucose. Significance refers to binomial tests.

DATE	NEST	POPN.		CHOICE 1			CHOICE 2	SIGN.
				0.001M				
23/02/87	SB26	2q	80w	Leucine	2	0	Water	n.t.
23/02/87	SB27	1q	99w	Leucine	10	4	Water	n.s.
23/02/87	SB28	5q	77w	Leucine	2	1	Water	n.t.
23/02/87	SB29		156w	Leucine	1	1	Water	n.t.
27/02/87	SB21		52w	Leucine	1	0	Water	n.t.
27/02/87	SB22		26w	Leucine	0	0	Water	n.t.
27/02/87	SB23	4q	84w	Leucine	2	0	Water	n.t.
27/02/87	SB24	21q	77w	Leucine	4	1	Water	n.s.
27/02/87	SB25	9q	77w	Leucine	6	1	Water	p<0.1
SUM 23/02/87 4 trials				LEUCINE	15	6	Water	p<0.05
SUM 27/02/87 5 trials				LEUCINE	13	2	Water	p<0.05
SUM of all 9 trials				LEUCINE	28	8	Water	p<0.05

Table 8.9. Sum of "ant-minutes" spent drinking from droplets in one hour after liquids were placed in nest; choice tests with 0.001M leucine and water. Significance refers to binomial tests.

DATE	NEST	POPN.	CHOICE 1			CHOICE 2	SIGN.
			0.004M				
27/02/87	SB26	2q 58w	Leucine	4	1	Water	n.s.
27/02/87	SB27	1q 93w	LEUCINE	13	2	Water	p<0.005
27/02/87	SB28	5q 55w	LEUCINE	22	4	Water	p<0.001
27/02/87	SB29	71w	Leucine	3	2	Water	n.s.
02/03/87	SB26	2q 45w	LEUCINE	12	0	Water	p<0.001
02/03/87	SB27	1q 50w	LEUCINE	12	1	Water	p<0.001
02/03/87	SB28	5q 31w	LEUCINE	8	0	Water	p<0.001
02/03/87	SB29	71w	Leucine	2	0	Water	n.t.
SUM 23/02/87 4 trials			LEUCINE	42	9	Water	p<0.005
SUM 27/02/87 4 trials			LEUCINE	34	1	Water	p<0.001
SUM of all 8 trials			LEUCINE	76	10	Water	p<0.005

Table 8.10. Sum of "ant-minutes" spent drinking from droplets in one hour after liquids were placed in nest; choice tests with 0.004M leucine and water. Significance refers to binomial tests.

DATE	NEST	POPN.	CHOICE 1			CHOICE 2	SIGN.
			0.01M				
23/02/87	SB21	66w	LEUCINE	15	0	Water	p<0.001
23/02/87	SB22	67w	Leucine	0	0	Water	n.t.
23/02/87	SB23	4q 107w	LEUCINE	34	0	Water	p<0.001
23/02/87	SB24	22q102w	LEUCINE	42	1	Water	p<0.001
23/02/87	SB25	9q 105w	LEUCINE	44	3	Water	p<0.001
02/03/87	SB21	30w	LEUCINE	13	0	Water	p<0.001
02/03/87	SB22	24w	LEUCINE	17	0	Water	p<0.001
02/03/87	SB23	4q 58w	LEUCINE	55	0	Water	p<0.001
02/03/87	SB24	20q 57w	LEUCINE	46	3	Water	p<0.001
02/03/87	SB25	8q 57w	LEUCINE	52	0	Water	p<0.001
04/03/87	SB23	8q 57w	LEUCINE	63	0	Water	p<0.001
04/03/87	SB24	1q 50w	LEUCINE	14	0	Water	p<0.001
04/03/87	SB25	5q 31w	LEUCINE	7	0	Water	p<0.01

Table 8.11. Sum of "ant-minutes" spent drinking from droplets in one hour after liquids were placed in nest; choice tests with 0.01M leucine and water. Significance refers to binomial tests.

DATE	NEST	POPN.	CHOICE 1			CHOICE 2	SIGN.
			0.1M			0.01M	
04/03/87	SB21	30w	SUCROSE	52	6	Leucine	p<0.001
04/03/87	SB22	24w	SUCROSE	33	3	Leucine	p<0.001
04/03/87	SB24	57w	SUCROSE	142	7	Leucine	p<0.001

Table 8.12. Sum of "ant-minutes" spent drinking from droplets in one hour after liquids were placed in nest; choice test with 0.1M sucrose and 0.01M leucine. Significance refers to binomial tests.

When all the data on 0.001M sugars was pooled, disregarding the nature of the sugar, it was seen that equal number ofant-minutes were spent drinking sugar solution and water.

b/ 0.01M sugar solutions.

There is evidence that both sucrose and fructose are prefered to water, at this concentration, but there is no evidence that glucose is prefered (Table 8.3). The sucrose preference was found when the data from two trials was pooled. Fructose preferences were found when data was pooled on two out of three days and for two out of eight individual trials. In one trial with glucose it seemed that more ants drank water than the sugar solution, but the difference was not significant ($p=0.0547$).

The total response, in terms of the amount of drinking from both droplets was approximately the same as when only water was available ($F=0.0682$, $df=1,15$; n.s.).

c/ 0.05M fructose solution.

Fructose was the only sugar to be tested at a concentration of 0.05M. In all six trials there was a very marked preference for the fructose solution over the water ($p<0.001$ in each case, Table 8.4). With this 0.05M solution the total response is much greater than was the case in the trials with only water, with 0.001M solutions or 0.01M solutions ($F=23.8808$, $df=1,9$; $p<O.001$).

d/ 0.1M sugar solutions.

All three sugars were clearly favoured at 0.1M concentration (Table 8.5). This preference was clearly seen in all 19 trials. The response of ants to 0.1M sugars is seen in more detail in Figure 8.1 which shows how the number of ants drinking at each sugar solution changed over the course of the hours observation. At the begining of the trials the sucrose solution produces the greatest response but this declines in the second half hour. The response to fructose seems to mirror the sucrose response although it doesn't quite attain

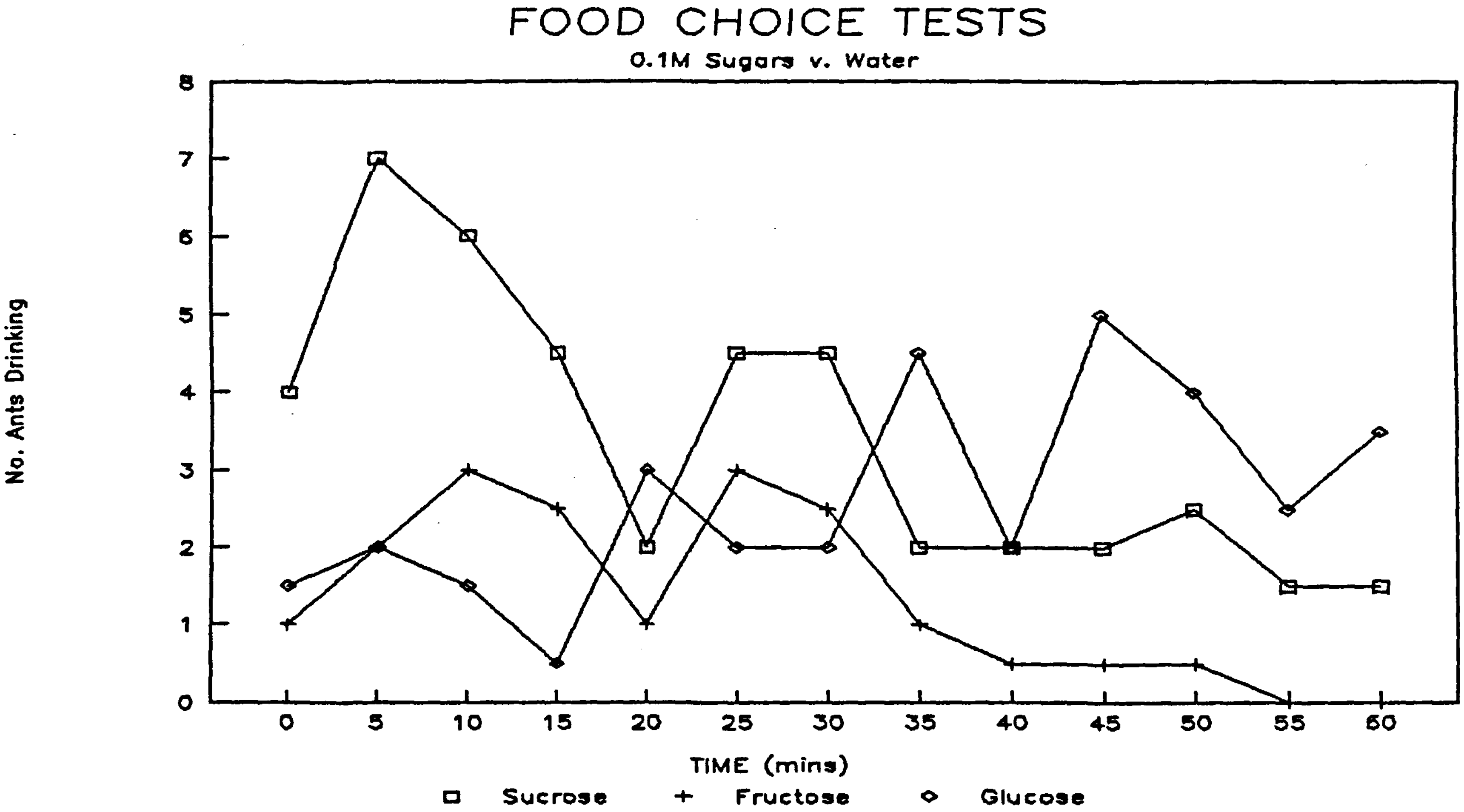


Figure 8.1. Number of ants drinking from 0.1M sugar solutions (sucrose, fructose, glucose) when presented in competition to water over a period of one hour.

the proportions of the sucrose response; it is at its highest in the first half hour but then declines. By contrast the response induced by glucose is relatively small initially but increases as time progresses.

8.1.1.3 SUGAR v. SUGAR.

a/ 0.1M sucrose v. fructose.

Sucrose was preferred to fructose in all five trials (Table8.6). The pattern of response over time, as seen in Figure 8.2, is much as it was when these solutions were trialed against water; the greatest number of ants were drinking at both solutions in the first fifteen minutes but then both tail off as time progresses. Again the fructose response does not attain the same levels as the sucrose response at any time during the hours observation.

b/ 0.1M sucrose v. glucose.

Sucrose was prefered to glucose in seven out of eight trials (Table 8.7). In the eigthth test no preference was observed as over one hundred ant-minutes were spent at each droplet. In this case it was observed that the sucrose droplet was showing signs of being exhausted after 35 minutes. In the first half hour of the trial sucrose was prefered to glucose, with 106 ant-minutes drinking sucrose but only 32 ant-minutes spent drinking glucose.

The pattern of response over time is presented in Figure 8.3. Again the same pattern is seen for sucrose; initially high, then tailing off. The pattern for glucose is like that for sucrose in this instance (unlike the glucose pattern when glucose and water were available) for the trials where the sucrose preference was established.

c/ 0.1M fructose v. glucose.

Fructose was clearly prefered to glucose in three out of four trials (Table 8.8). In the fourth (SB18) both solutions received a lot of attention. In the first half hour of this trial fructose was prefered to glucose (54 ant-minutes against 13) while in the second half hour

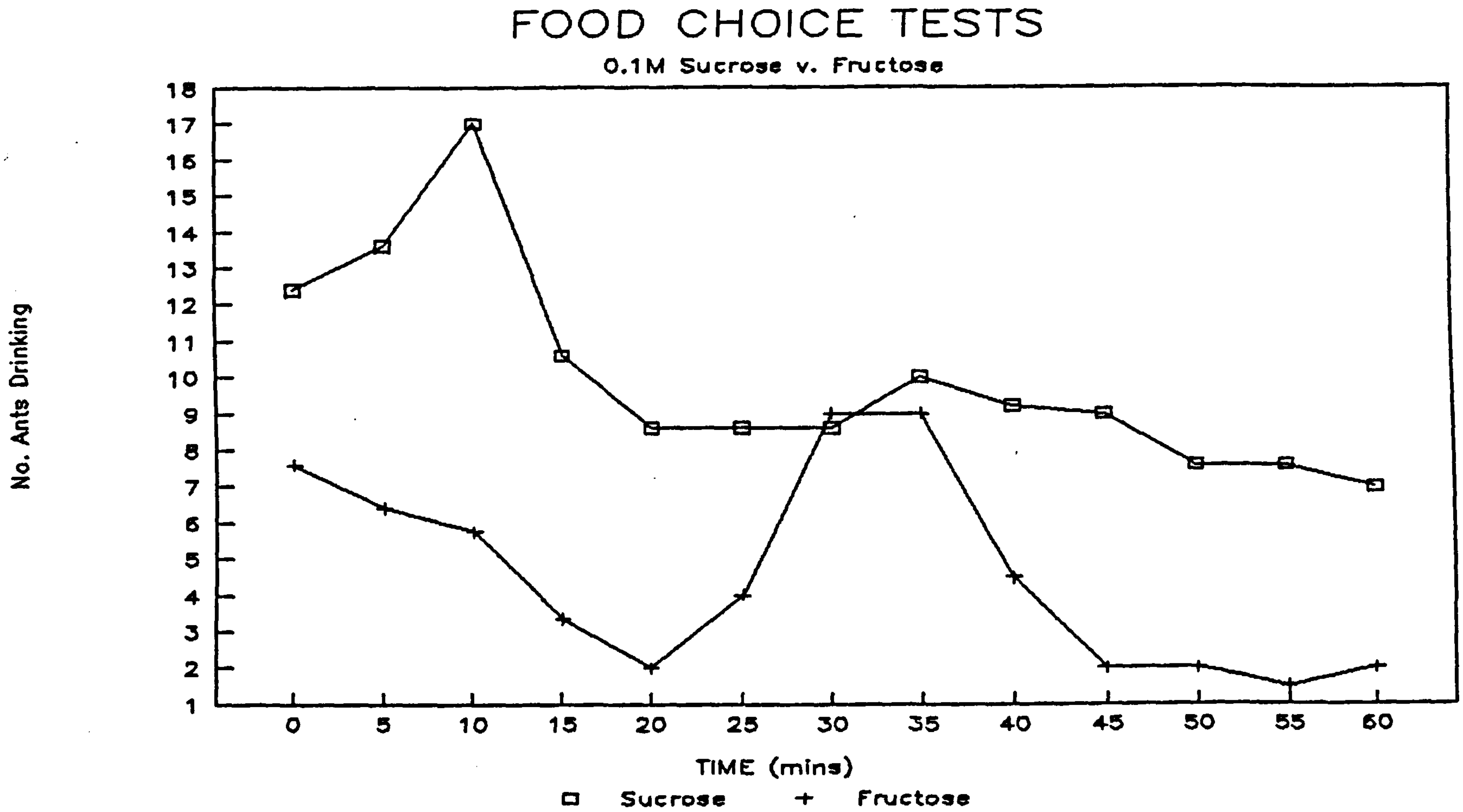


Figure 8.2. Number of ants drinking from 0.1M sucrose and fructose solutions when presented in competition to each other over a period of one hour.

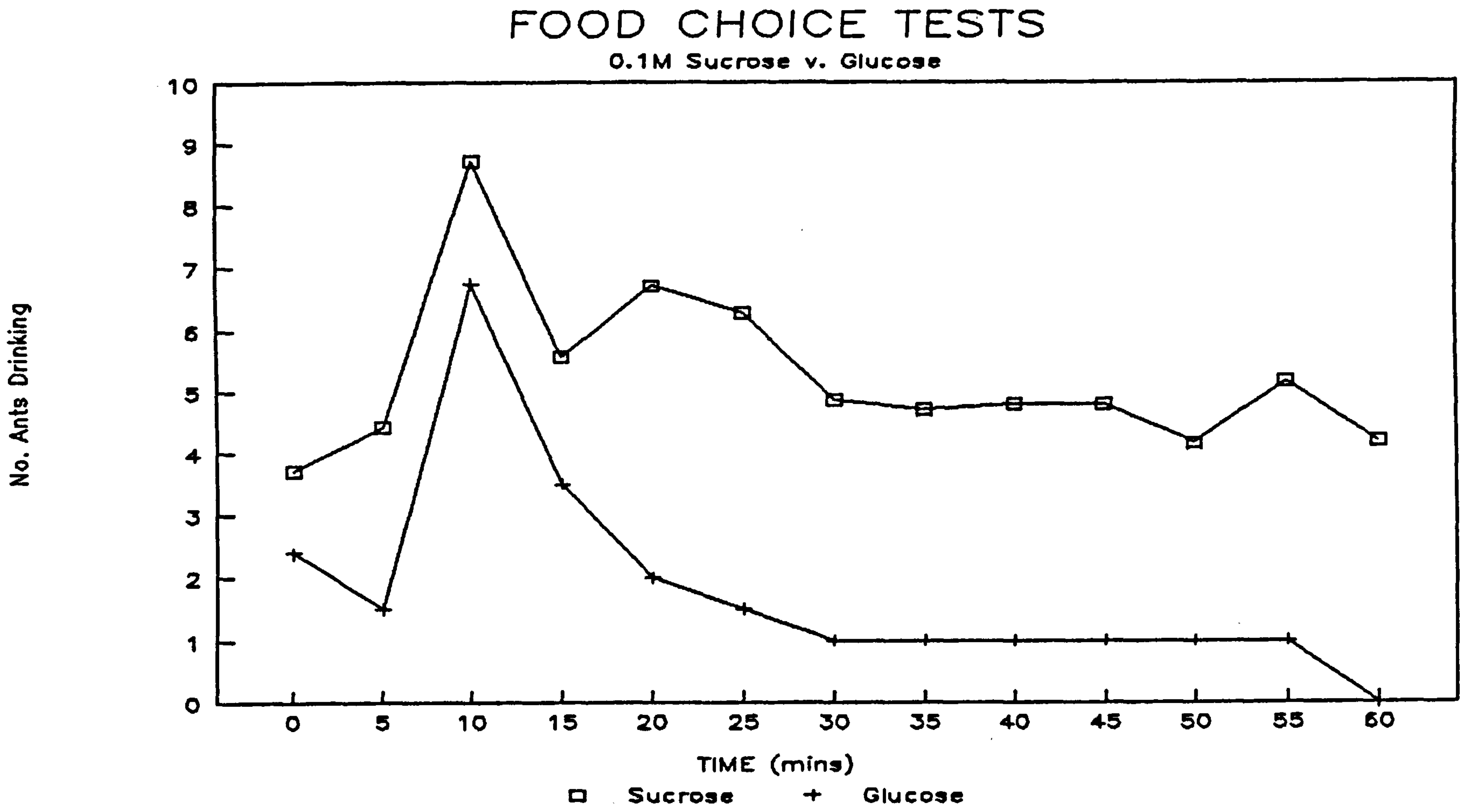


Figure 8.3. Number of ants drinking from 0.1M sucrose and glucose solutions when presented in competition to each other over a period of one hour.

glucose is prefered (33 fructose v. 69 glucose). (I did not record that the fructose droplet was drying up.)

The pattern of response over time is shown in Figure 8.4. Again fructose follows the same pattern as before; initially high, then tailing off. However the glucose pattern is different again; it is high both at the begining and the end of the observation with a trough of response in between.

The second increase in response to glucose comes almost exclusively from the one trial where there was a great response to both sugars.

8.1.1.4 LEUCINE v. WATER.

a/ 0.001M leucine.

The total number of ant-minutes spent drinking (from both droplets) when 0.001M leucine and water were available was quite low in all trials (Table 8.9). Indeed the number drinking in each trial did not differ from the number drinking when only water was available (F=0.098, df=1,12; n.s.).

In only three of the nine trials, performed over two days, was there sufficient drinking to allow statistical comparison of the responses to the two types of droplet but in no instance was one prefered to the other (although in one case p=0.0547). However, pooling the data for each day revealed that significantly more ant-minutes were spent drinking leucine.

b/ 0.004M leucine.

0.004M leucine was clearly prefered to water in five of the eight trials (Table 8.10) and this preference is also seen when the data is pooled for each date. Moreover, when the data from the three trials which did not reveal a preference are pooled a preference for leucine was found (9v2 $p<0.05$).

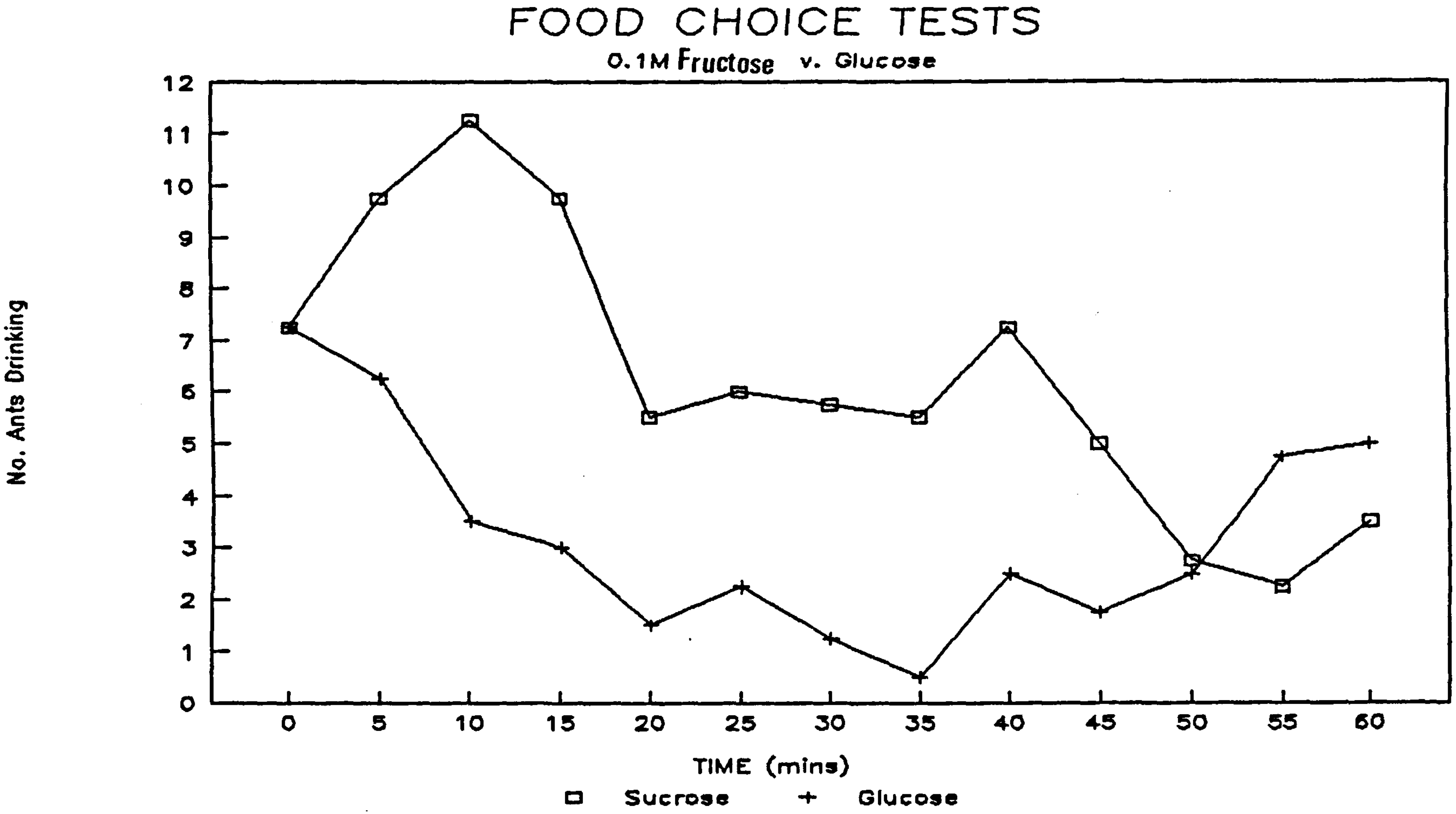


Figure 8.4. Number of ants drinking from 0.1M fructose and glucose solutions when presented in competition with each other over a period of one hour.

It might appear that there are more ants drinking in these trials than when only water was available but this difference is not significant (F=3.63, df=1,11; p<0.2).

The pattern of response in these leucine:water trials over time can be seen in Figure 8.5. Peaks in the number of ants drinking both leucine solution and water occur at the same time (10 minutes). Thereafter both go into decline; the number drinking leucine remains in the range of 2 to 6 ants at any time in the second half hour while water drinking ceases within the first half hour.

c/ 0.01M leucine.

There was a pronounced preference for leucine over water in 13 of the 14 trials (Table 8.11). The colony fragment in the one case which did not show a preference had a sharply declining population; 23/2/87 67 workers, 27/2/87 26 workers, 2/3/87 24 workers, 4/3/87 24 workers. It displayed no prefernces on the former two dates (for 0.01M and 0.004M leucine respectively) but was able to demonstrate a preference (for 0.01M leucine) on the third date [and for sucrose over leucine on the fourth].

The total response is much greater than when only water was available (F=5.5499, df=1,18, p<0.05).

8.1.1.5 SUCROSE v. LEUCINE.

Sucrose solutions were clearly prefered to leucine solutions in all three trials (Table 8.12). However, the amount of ant-minutes spent drinking leucine, when sucrose was the other choice, was not significantly less than the time spent when water was the alternative (F=3.5059, df=1,17, p<0.2).

When trialled alongside water, both 0.1M sucrose and 0.001M leucine solutions were clearly prefered to the water, but the total response was greater for 0.1M sucrose and water than for 0.01M leucine and water (F=5.1527, df=1,19, p<0.05).

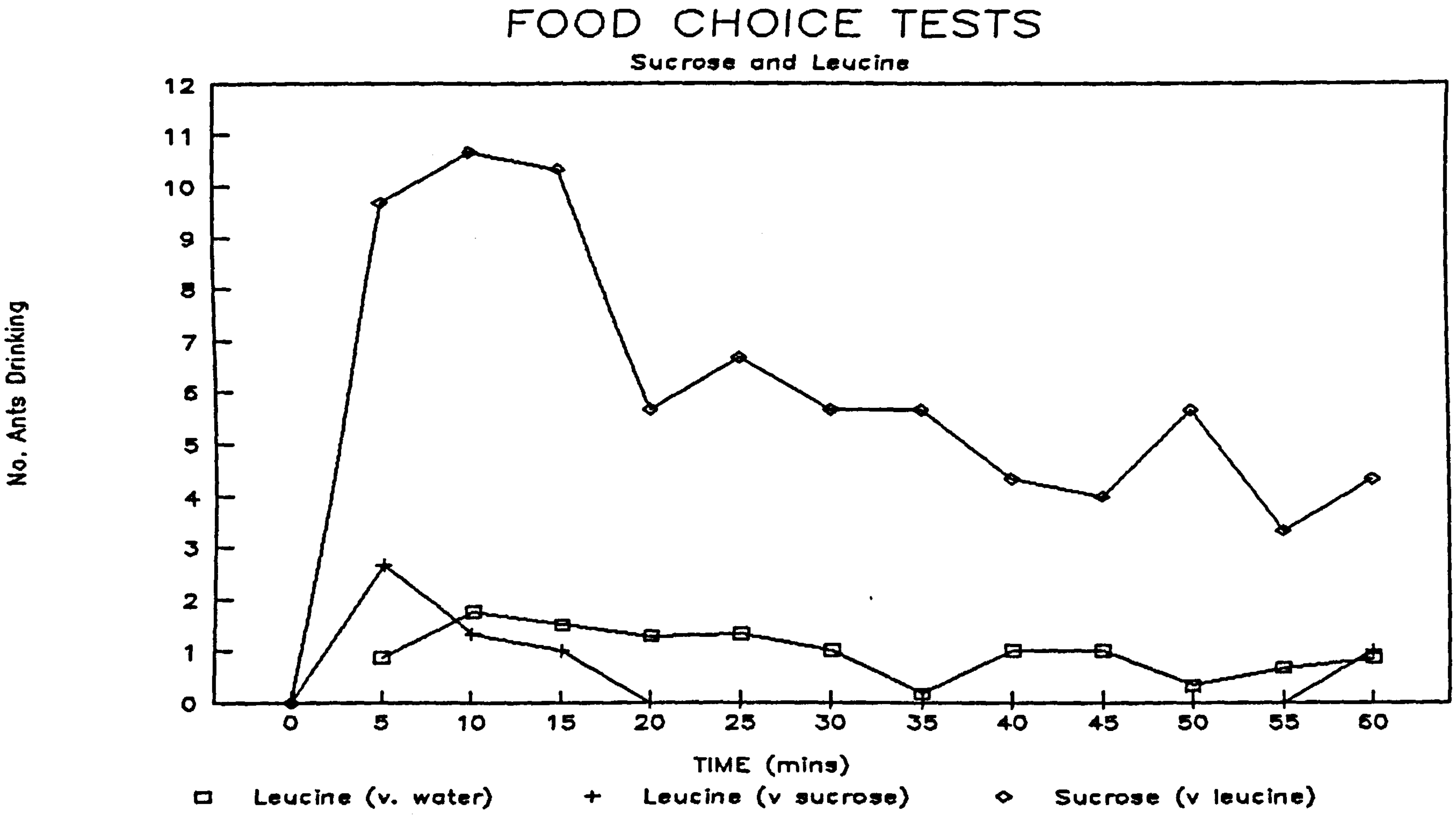


Figure 8.5. Number of ants drinking from 0.004M leucine solution when presented in competition to water over a period of one hour and numbers of ants drinking from 0.1M sucrose and 0.01M leucine solutions when presented in competition with each other.

The changing responses over time are presented in Figure 8.5. As before the number drinking from the sucrose droplets was greatest early on in the trial but them began to tail off. The response to leucine was confined to the early period; after a peak of drinking the number of ants choosing to drink at the leucine droplets quickly fell to zero.

8.1.2 CHOICE OF SOLID FOODS.

8.1.2.1 CHOICE BY SIZE.

a/ two sizes available.

In the first three trials (in the large laboratory nest, LLN) all the baits were removed within 30 minutes of the start of the trial (Table 8.13). Only in the first of these trials was there a significant difference in the rates of removal for different sized baits. A greater proportion of the smaller baits (0.5mm3) were taken earlier in the trial than the larger (1mm3) baits (Kolomogorov-Smirnov, $p<0.05$).

In the second trial it appeared that 1mm3 baits were taken more quickly than 4mm3 baits but this difference was not significant. In the third trial there was no difference in the rates at which 3mm3 and 1mm3 baits were taken.

In the fourth trial (carried out with a colony fragments of 9 queens and 200 workers maintained in a lunch box nest) nine of the ten 1mm3 baits were removed in two hours whilst only three of ten 8mm3 baits were removed. However this difference was not significant.

b/ three sizes available.

Two trials were carried out, in LLN in May and June 1985, where three sizes of baits were available (Table 8.14). In the first trial a Kruskall Wallis test (Sokal and Rohlf, 1969) revealed that the smaller baits were taken significantly quicker than largest ones ($p<0.05$) from the range available (32mm3, 4mm3 and 1mm3).

Date	No.	Size(mm)	Removal times (mins)
a 30/4/85	5	1x1x1	13, 15, 17, 18, 20:
bait=edam	10	1x1x0.5	8, 10, 10, 10, 10, 12, 14, 16, 18, 20:
b 30/4/85	4	4x1x1	22, 24, 24, 27:
bait=edam	4	1x1x1	11, 16, 17, 26:
c 7/5/85	4	3x1x1	11, 12, 16, 19:
egg white	8	1x1x1	7, 8, 10, 13, 14, 17, 17
d 11/9/86	10	2x2x2	60, 100, 100
red leic.	10	1x1x1	10, 15, 20, 30, 30, 40, 40, 60, 80

Table 8.13. Bait removal times in trials where two different sized baits were available. The first three trials were perforemed in LLN, the other was performed in a picnic box nest with a colony fragments of 9 queens and 200 workers.

Date	No.	Size(mm)	Removal times (mins)
a 7/5/85	4	8x2x2	50, 74, 79, 86;
bait=	4	2x2x1	50, 50, 51
cheddar	4	1x1x1	50, 50, 50
b 13/6/85	2	4x1x1	NO BAITS TAKEN
bait=edam	8	1x1x1	68
	16	1x.5x.5	33, 55, 63, 88

Table 8.14. Bait removal times in trials where three different sized baits were available. Both trials were perforemed in LLN.

In the second trial none of the largest baits were removed, one of the eight medium baits was removed and five of the sixteen smallest baits were removed within 2 hours. Thus it would seem that the smallest baits are prefered but there was insufficient data for a significance test to be carried out.

c/ four sizes available.

One trial was carried out, in the field at Wrothan Field Centre, where four sizes of baits were available; the removal times are presented in Table 8.15; 28% of the smallest, and 12.5% of the next smallest, were removed within an hour whilst none of the larger baits were removed. Again this indicates a preference for the smaller baits but there was insufficient data for analyses.

8.1.2.2 CHOICE BY TASTE.

Two trials were performed in September 1986 with colony fragments maintained in picnic boxes (8 queens, 46 workers and 3 queens, 28 workers respectively) to investigate whether the ants discriminated between red leicester and cheddar baits. Bait removal times are presented in Table 8.16.

Fifteen of the twenty smaller baits were removed with two hours at approximately the same rate. Indeed a Kolomogorov-Smirnov test showed that there was no difference in the removal rates for the two types of baits. Only three of the larger baits were removed; insufficient for analysis.

It is notable again that if the two trials are compared a much greater proportion of the smaller baits were removed.

A third trial was performed at Wrotham near the Doorstep Nest (Nest One) to compare the removal rates of 1mm3 baits of cheddar and red leicester. The removal times are also presented in Table 8.16. Although more of the red leciester baits were taken this difference

Date	No.Baits	Size(mm)	No. Removed
30/5/85	4	18.0x1.5x1.5	0
bait=	4	9.0x1.5x1.5	0
cheddar	8	4.5x1.5x1.5	1
	16	2.0x1.5x1.5	9

Table 8.15. Number of baits removed within one hour in a food choice trial with four sizes of cheddar cheese baits in field at Wrotham Field Centre.

	Date	Bait	Size(mm)	No.	Removal times (mins)
a	11/8/86	rl	2x2x2	10	50, 100
		ch	2x2x2	10	25
b	11/9/86	rl	1x1x1	10	25, 30, 50, 90, 90, 100, 140
		ch	1x1x1	10	25, 30, 50, 80, 80, 140
c	5/9/86	rl	1x1x1	10	60, 70, 100, 105, 110, 120, 120
		ch	1x1x1	10	110, 120, 130, 140

Table 8.16. Bait removal times in food choice trials where two types of bait were available; rl = red leicester, ch = cheddar. The first two trials were performed in laboratory with colony fragments of 5 queen, 46 workers and 3 queens, 28 workers maintained in picnic box nests. The third trial was performed in field at Wrotham Field Centre.

is not significant (binomial test, 7 v 4, p=0.15). The red leicester baits also seemed to be removed quicker but this difference was not significant either.

8.1.2.3 CHOICE BY SIZE AND TASTE.

Three trials were carried out where both the size and the type of the bait varied; one with a colony fragment in the laboratory, the other two at Wrotham. The bait removal times in these trials are presented in Table 8.17.

In the laboratory trial all the baits were removed within 70 minutes but there were no significant differences in the removal rates between large and small baits or between the two types of bait.

In the first field trial only six out of 80 baits were removed, and although the three red leicester baits which were removed were taken away before any of the three cheddar baits were removed there was insufficient data for analysis. In the second trial only four out of forty baits were removed within two hours; two each of red leicester and cheddar, and three of the smaller size. Again the data was insufficient for analysis.

8.1.3 PREY RETURNED TO THE NEST.

The items of prey which were collected from foragers returning to Nest One in 1985 summarized in Table 8.18 (a fuller list of the items collected is presented in Appendix 2. There were 115 prey items collected on 11 days of sampling; the variation between days in the number collected (from 2 to 25) just reflects the differences in the time allocated to collection on each day.

Many of the items could not be identified but their general appearance, and the state of the intact preys, suggested that they were dead on discovery rather than having been freshly killed. The only freshly captured items were caterpillars and beetles, these were not killed at all but brought back to the nest still alive. The caterpillars would still be struggling but the beetles would be perfectly still. It was observed that if an ant were to put down a

	Date	Bait	Size(mm)	No.	Removal times (mins)
a	13/5/85	ham	6x1x1	2	23, 29:
		ch	5x1x1	2	22, 68:
		ham	1x1x1	4	12, 21, 23, 51:
		ch	1x1x1	4	14, 25, 39, 40:
b	5/9/86	rl	2x2x2	20	70, 110
		ch	2x2x2	20	150
		rl	1x1x1	20	110
		ch	1x1x1	20	130, 140
c	8/9/86	rl	2x2x2	10	NO BAITS REMOVED
		ch	2x2x2	10	110
		rl	1x1x1	10	42, 62
		ch	1x1x1	10	110

Table 8.17. Bait removal times in food choice trial where both size and taste choices were available. Trial a was carried out in LLN, trial b *was carried out near Nest One at Wrotham Field* Centre and trial c was performed near Nest Two at Wrotham.

PREY	AUGUST						SEPTEMBER					TOTAL
TYPE	12	14	15	21	28	30	4	9	12	16	17	
Entire	1	6	1	8	12	3	5	3	0	1	4	44
Part	2	0	0	1	2	2	1	0	1	2	3	13
Identifable	1	5	1	7	5	2	2	5	1	2	3	34
Amorphous	0	3	1	2	6	4	0	6	0	1	1	24
Flies	1	0	0	2	0	1	2	2	0	0	1	9
Aphids	1	0	0	1	2	0	0	1	0	1	1	7
Hoverflies	0	0	0	2	0	0	1	0	0	0	0	3
Beetles	0	0	0	0	2	0	0	0	0	0	0	2
Bugs	0	0	0	0	0	1	0	0	0	0	0	1
Caterpillars	0	0	1	0	1	1	1	0	0	0	1	5
Pupae	0	3	0	1	0	0	0	0	0	0	0	4
Woodlice	1	0	0	1	3	0	0	0	0	0	0	5
Seedheads	0	1	0	1	0	0	0	0	0	1	0	3
Worms	0	1	0	0	2	0	0	0	0	0	0	3
Centipedes	0	0	0	0	0	0	0	0	0	0	1	1
Spiders	0	0	0	0	1	0	0	0	0	0	0	1
Other	1	8	2	10	13	8	3	11	0	4	6	66
TOTAL	4	14	3	18	25	11	8	14	2	6	10	115

Table 8.18. Prey items taken from foragers returning to Nest One at Wrotham Field Centre in 1985.

beetle, perhaps to change its grip, the beetle would right itself and begin to walk away. It would be recaptured though.

There was no relationship between time of year and the percentage of intact prey returned on any date (r=-0.3182, df=10, n.s.).

8.2 TRAFFIC AT DOORSTEP NEST ENTRANCE.

Activity at this Doorstep Nest entrance was first observed on 14 June 1985 during a feeding test as food baits were returned to this nest entrance. This nest entrance remained in use until September 20 that year at least. On the next visit on October 2 there was no activity at this entrance although it was noted that activity continued at other entrances in the vicinity (considered to be subsidiary entrances for the same colony). On the first two recording visits in 1985 (August 12 and 21) only the number of exits were recorded. Thereafter both exits and entrances were recorded.

On one particular occassion unusually high counts were made of the number of ants entering and leaving the nest. This was the third count made on 12 September 1985, at 16.20h, when 97 ants left the nest and 100 entered during a ten minute observation period. Some sexuals were seen in this area later that afternoon so it is might be suggested that this high turnover of ants owed more to the release of sexuals than to foraging activity. Nonetheless, many of the ants emerging from the nest continued onto the foraging area whilst many of the ants entering the nest were returning from the foraging area.

In 1986 activity was observed on June 6 (the first visit that year) but was not recorded. On June 13 the number of exits and entrances were recorded for 100 minutes. From June 13 onwards there was no activity at this entrance until September, i.e. for a period of almost two months the colony did not appear to use this entrance. Activity was recorded on every field visit from September 8 to October 3, for at least 40 minutes through the day on each occasion. Activity had ceased again on October 7 - on this visit however there was very little activity at any of the nest entrances in the vicinity and foraging activity was considered to have terminated for that year.

8.2.1 SAMPLE DISTRIBUTION.

The numbers of ants leaving and entering the Doorstep Nest during these periods of observation are presented in Figure 8.6. In 1985 the rate of exits varied from none to 19

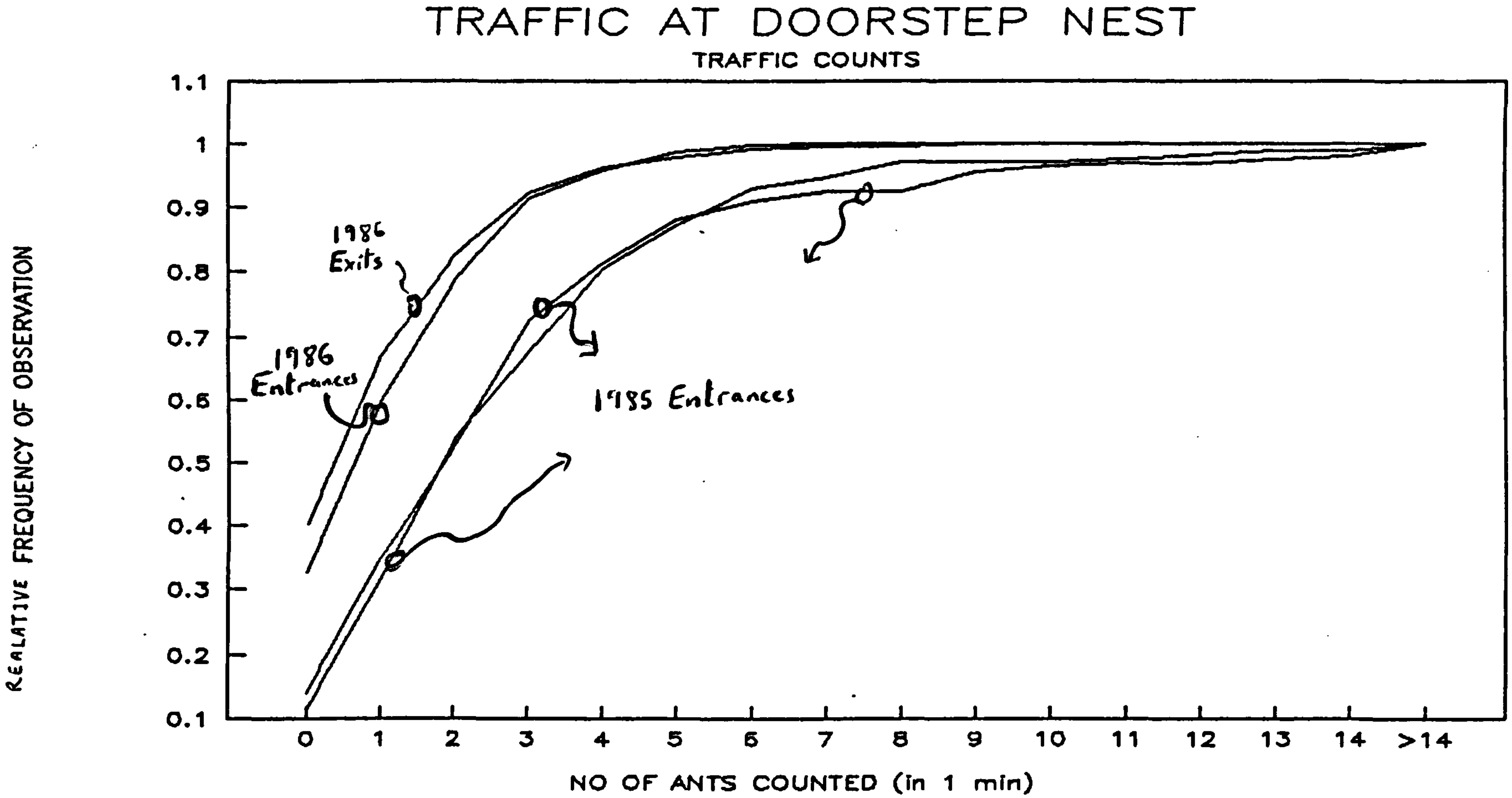


Figure 8.6. Counts of traffic of ants entering and leaving the Doorstep Nest

per minute with a mean of 3.01 ants per minute (s.d. 3.12, n=200 minutes), while entrances varied from none to 22 per minute around a mean of 3 ants per minute (s.d. 2.91, n=170). In 1986 the corresponding rates varied less; exits varied from none to nine per minute (mean 1.257, s.d. 1.504, n=630 minutes) and entrances ranged from none to seven (mean 1.43, s.d. 1.436, n=630).

However, these samples did not have random distributions, as is indicated by their relatively large variances. Indeed when these sample distributions were compared to Poisson distributions with the same means, as seen in Table 8.19, it was found that they were significantly different. In 1985 there were more occassions of low activity (0 or 1 ant leaving or entering the nest) and more occasions of very high activity (6 or more ants entering or leaving) than would be predicted. Similarly in 1986 there were more occassion of low activity (0 ants exiting and entering) and moreoccassions of very high activity (more than 5 ants exiting and entering) than would be predicted.

The number of exits and entrances in each ten minute observation block also differed from a random Poisson distribution. In 1985 the number of exits per 10 minute block ranged from 12 to 97 (mean 30.1, s.d. 18.9, n=20 ten minute blocks) while the number of entrances varied from 10 to 100 (mean 30, s.d. 20, n=17 ten minute blocks). These samples were too small to compare to Poisson distributions.

In 1986 there was enough data to compare the observed distributions of exits and entrances with Poisson distributions by means of chi-squared tests. Such comparisons are seen in Table 8.20 which revealed significasnt differences. There were more occassions of low activity and of very high activity than predicted. In 1986 the number of exits ranged from 1 to 37 (mean 12.57, s.d. 9.08, n=63 ten minute blocks) while entrances ranged from 0 to 33 (mean 14.3, s.d. 8.26, n=63). On some individual dates (or combinations of adjacent dates) the distributions also varied from random distributions (Table 8.21).

8.2.2 RELATIONSHIP BETWEEN EXITS AND ENTRANCES.

No. Ants	85				86			
	EXITS		ENTRANCES		EXITS		ENTRANCES	
per minute	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.
0	28	9.9	19	8.5	253	178.7	206	150.7
1	42	29.7	35	25.4	170	225.2	172	215.6
2	36	44.7	38	38.1	97	141.8	119	154.2
3	39	44.8	23	38.1	61	59.6	78	73.5
4	18	33.7	22	28.6	25	18.8	28	26.3
5 (1986 <4)	13	20.3	11	17.1	24	5.9	27	9.8
6	6	10.2	10	8.6				150.7
>6	18	6.8	12	5.6				150.7
TOTAL	200	200	170	170	630	630	630	630
X-sq	71.29		33.83		115.59		37.53	
df=	6		6		4		4	
Sign.	p<0.001		p<0.001		p<0.001		p<0.001	

Table 8.19. Comparisons of observed distributions of number of ants per minute with Poisson distribution with the same mean value (x).

No. Ants	1986 EXITS		No. Ants	1986 ENTRANCES	
in 10 mins	Obs.	Exp.	per minute	Obs.	Exp.
0-8	25	8	0-9	18	6.0
9-10	6	10.7	10-11	4	13.8
11	3	6.7	12	5	5.9
12	3	7.1	13	3	6.5
13	1	6.9	14	3	6.7
14	2	6.2	15	3	6.4
15	3	5.2	16	5	5.7
16-17	1	7.1	17-18	5	8.6
>17	16	5.5	>18	17	8.5
TOTAL	63	63	TOTAL	63	63
X-sq	77.99			45.23	
df=	7			7	
Sign.	p<0.001			p<0.001	

Table 8.20. Comparisons of observed distributions of numbers of ants leaving and entering in ten minute observation blocks with Poisson distributions with the same mean (x).

DATE	NO. MINS	EXITS	ENTRANCES
21/8/85	20	n.s.	----
28/8/85	20	n.s.	----
30/8/85	30	n.s.	n.s.
12/9/85	20	$p<0.05$	n.s.
16/9/85	20	$p<0.1$	n.s.
17/9/85	20	$p<0.1$	n.s.
+ 5 days	50	$p<0.01$	n.s.
13/6/86	100	$p<0.1$	$p<0.1$
08/9/86	50	n.s.	n.s.
09+12/9	110	$p<0.05$	n.s.
16+18/9	120	$p<0.1$	n.s.
19/9/86	50	$p<0.01$	n.s.
29+30/9 +3/10/86	180	$p<0.01$	n.s.

Table 8.21. Summary of comparisons of observed distributions of numbers of ants leaving and entering per minute with Poisson distributions with the same mean (x) on individual dates.

DATE	NO. COUNTS	EXITS	SIGN.	ENTRANCES	SIGN.
1985 TOTAL	19,17	r=+0.334	n.s.	r=+0.3232	n.s.
1986 TOTAL	58	+0.1849	n.s.	+0.2446	$p<0.1$
13/6/86	10	+0.2454	n.s.	+0.6788	$p<0.05$
08/9/86	5	-0.06	n.s.	-0.675	n.s.
09/9/86	5	+0.8	n.s.	+0.9	$P<0.05$
12/9/86	6	+0.257	n.s.	-0.1857	n.s.
16/9/86	6	+0.6714	n.s.	+0.4571	n.s.
18/9/86	8	+0.6131	n.s.	+0.8512	$p<0.01$
19/9/86	5	+0.8	n.s.	+0.9	$p<0.01$
29/9/86	7	-0.723	$p<0.1$	-0.6696	$p<0.1$
3/10/86	7	-0.482	n.s.	-0.5357	n.s.

Table 8.22. Summary of correlations analyses (by ranks) between time of day and the numbers of ants counted exiting from and entering into Nest One at Wrotham in 10 minute observation periods. For the 1985 totals the third count made on 12 September (97 exits, 100 entrances) is excluced, thus leaving 19 counts of exits and 16 counts of entrances. There was insufficient data to perform correlation analyses for any individual day in 1985.

The relationship between the numbers of exits and entrances is displayed in Figures 8.7, which shows how the number of exits in 10 minutes observation blocks varied with the number of entrances in 1985 and 1986 respectively. The relationship for the numbers per minute were not presented because there are so many data points (n=170 and n=630).

There was a significant positive correlation between these two measures of activity. This significance was found both when the exits and entrances per minutes were compared and also when the numbers in 10 minute observation blocks were analysed (1985 $r=0.30995$, $n=160$ minutes, $p<0.01$; 1986 $r=0.3279$, $n=630$ minutes, $p<0.001$; 1985 $r=0.7626$, $n=16$, $p<0.001$; 1986 $r=0.8294$, $n=63$, $p<0.001$). The third set of observations made on 12 September 1985 were excluded from these analyses because they were abnormally high (in preparation for sexual swarming).

Correlation analyses were also performed on the data from each date separately. In 1985 two of the nine dates showed significant positive correlation between the numbers of exits and entrances per minute (30 August: $r=+0.5044$, $n=30$ minutes, $p<0.01$; 6 September: $r=+0.7372$, $n=10$ minutes, $p<0.01$). In 1986 two of the ten dates showed significant positive correlation between the numbers of exits and entrances per minute (13 June: $r=+0.2623$, $n=100$ minutes, $p<0.01$; 12 September: $r=+0.3192$, $n=60$ minutes, $p<0.01$).

On four of the ten days in 1986 significant positive correlation were found between the numbers of exits and entrances in 10 minute observation blocks (13 June: $r=+0.7752$, $n=10$ ten minute blocks, $p<0.01$; 8 September: $r=+0.9308$, $n=5$, $p<0.01$; 16 Sept.: $r=+0.9048$, $n=6$, $p<0.01$; 19 Sept.: $r=+0.8527$, $n=5$, $p<0.02$). Only on 13 June was significant correlation found for numbers per minute and numbers per 10 minute observation blocks. There was insufficient data for any individual date in 1985 to do correlation analyses for 10 minute blocks.

8.2.3 VARIATION BETWEEN YEARS.

Both measures of activity were higher in 1985; 3.01 (+/-3.1) exits per minute against 1.257 (+/-1.5) and 3 (+/-2.9) entrances per minute versus 1.43 (+/-1.44). When these were

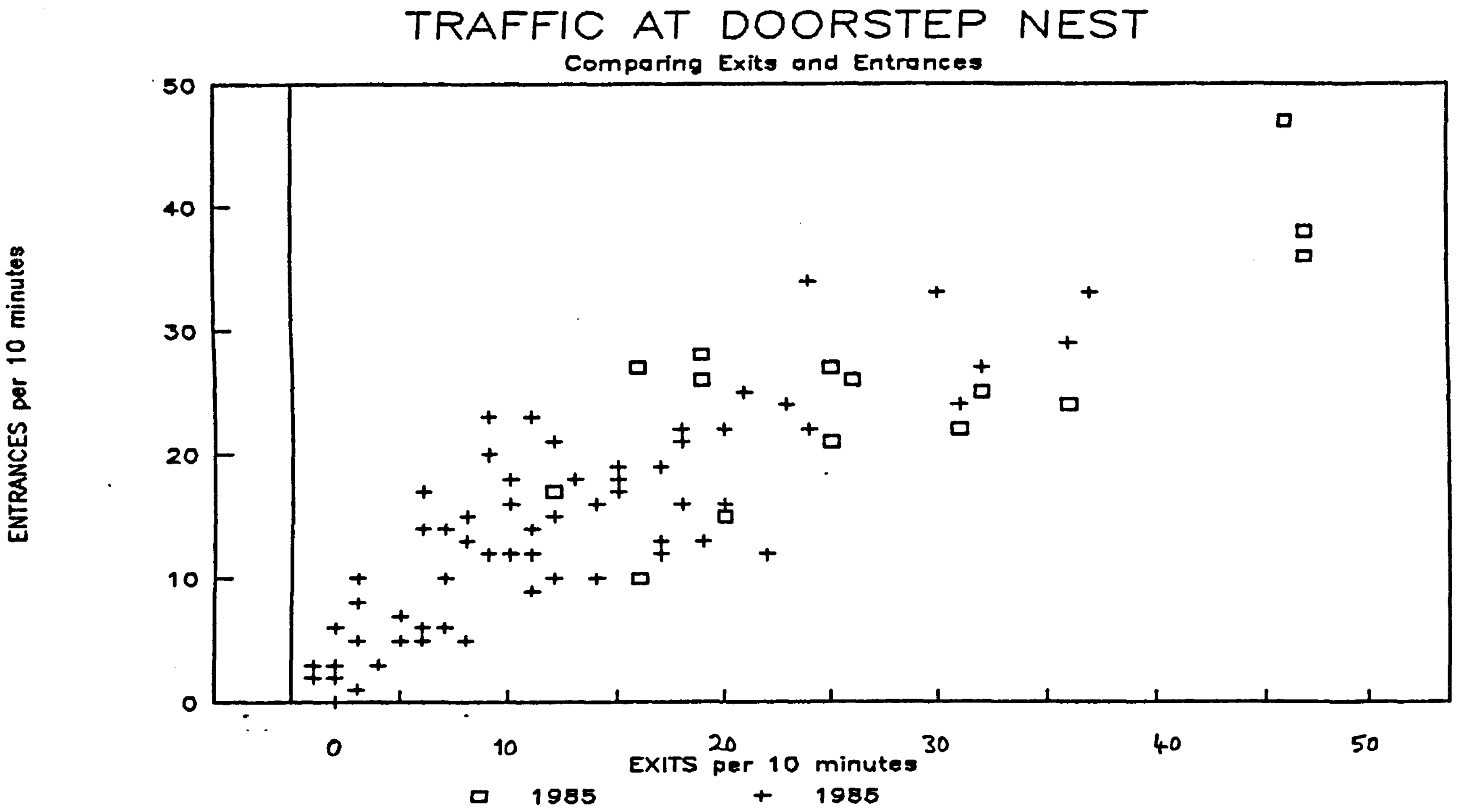


Figure 8.7 Relationship between numbers of exits and entrances at the Doorstep Nest.

compared by means of analyses of variance tests (because the samples had the same non-random distribution straight analyses of variance was used) it was found that these differences were indeed significant (Exits: F=98.14, df=1,818, $p<0.001$; Entrances: F=69.9, df=1,788, $p<0.001$).

8.2.4 VARIATION WITH TIME OF YEAR.

Figure 8.8 shows how the number of exits and entrances (per 10 minute period) varied with time of year. Correlation by ranks (because the samples did not have random distributions) revealed that there was no significant relationship between date and either measure of activity in 1985 (Exits: r=+0.1391, n=18 ten minute blocks, n.s.; Entrances: r=0.3765, n=16, n.s.). A closer inspection of activity changes over time suggests that the number of exits may have increased somewhat in the period up to 12 September (r=+0.467, n=14, $p<0.1$) and declined over the period from 6 September onwards (r=-0.6083, n=9, $p<0.1$).

In 1986 there were clearly significant correlations between both the numbers of exits and entrances and date (Exits: r=-0.6651, n=58, $p<0.001$; Entrances: r=-0.6508, n=58, $p<0.001$). Of course there was no activity at this entrance through July and August 1986. Yet even if the data is restricted to the period at the end of the season significant correlations are still found (Exits: r=-0.6457, n=53, $p<0.001$; Entrances: r=-0.7297, n=53, $p<0.001$).

If the data were restricted further, so that only the period when counts were made in both years was included (from 4 to 20 September) the same significant negative correlations are found for the 1986 data (Exits: r=-0.6531, n=35, $p<0.001$; Entrances: r=-0.6929, n35, $p<0.001$) but there was again no correlation for the 1985 data (Exits r=-0.1606, n=10, n.s.; Entrances: r=-0.1667, n=10, n.s.).

Correlation analyses were not performed with the numbers of exits and entrances per minute. This was because of the high frequencies of observations of 0, 1, 2, or 3 ants per

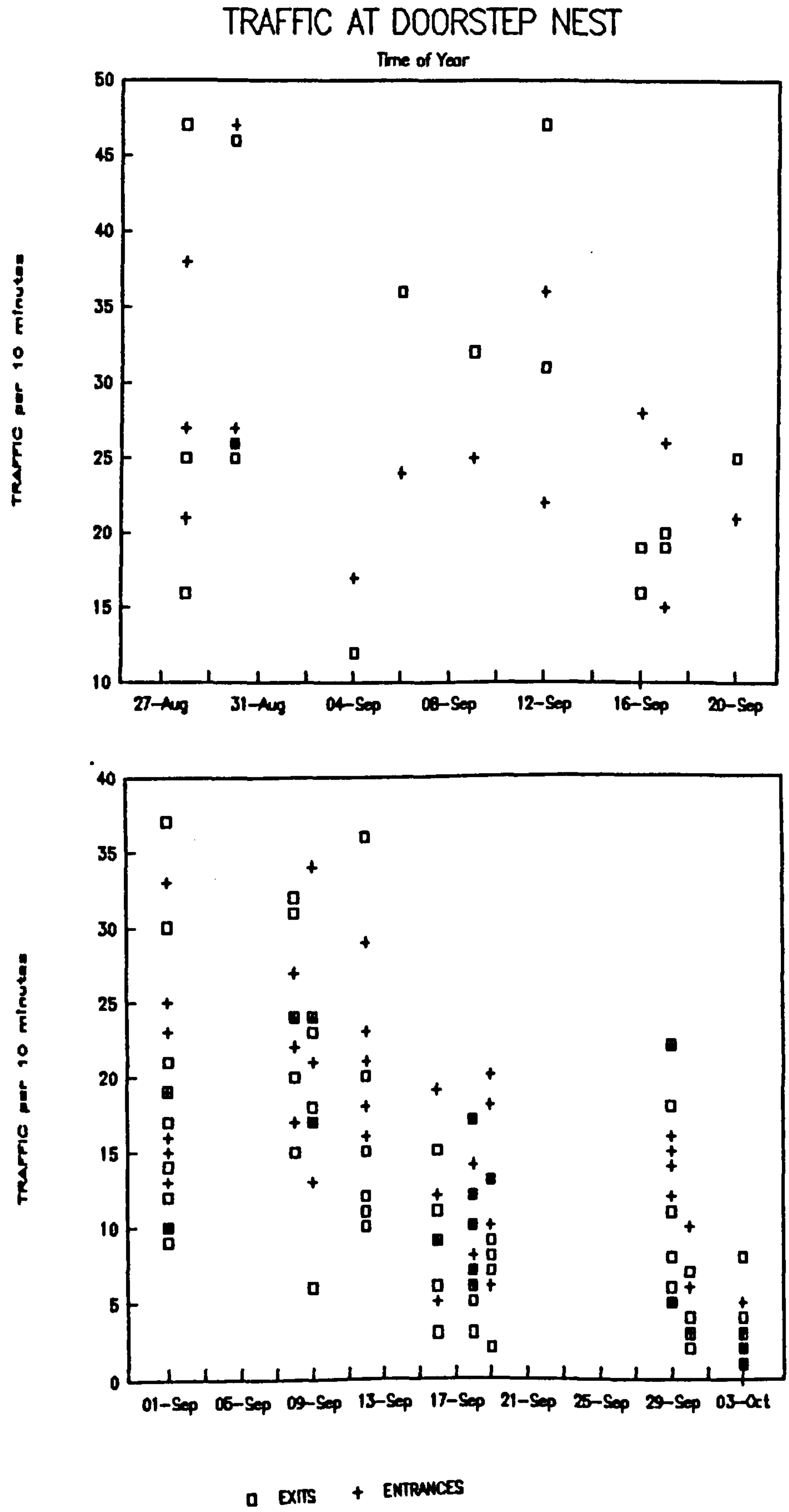


Figure 8.8. Relationship between traffic at Doorstep Nest entrance and date.

minute. There would have been so many ties when the data were ranked as to render the correlation meaningless.

8.2.5 VARIATION WITH TIME OF DAY.

The relationships between the numbers of exits and entrances and time of day is presented in Figure 8.9. There were no significant correlations between time of day and either measure of activity in either year (correlation analyses summarized in Table 8.22) although there was some indication of a positive connection between entrances and time of day ($p<0.1$).

Further correlation analyses were performed using the data from each date separately, except for the data from 1985 when there were too few counts made on any particular day to allow this. Analyses were possible for all ten dates in 1986 when activity data was collected. The results of these analyses are also presented in Table 8.22.

There were no occassions when the number of exits were correlated to time of day. However there were four days when there were positive correlations between time of day and the number of ants returning to the nest; 13 June when activity was recorded every half hour from 11.30h to 16.30h, 9 Sept. activity recorded every hour from 12.00h to 16.00h, 19 Sept. every hour 11.00h to 17.40h, and 19 Sept. every hour 11.00h to 15.00h. On 29 Sept. activity was recorded every hour between 11.00h and 17.00h it appeared that both exits and entrances were negatively associated with time of day (both $p<0.1$).

8.2.6 INFLUENCE OF TEMPERATURE.

The temperatures recorded around Nest One are contained in Appendix 3. Temperature varied significantly between the four dates on which it was recorded ($F=124.1484$, $df=2,147$, $p<0.001$). On June 13 the mean temperature was 31.33'C (+-2.12'), on September 18 it was 17.04'C (+-3.16'), on September 19 it was 17.08'C (+-4.37') and on October 3 it was 25.02'C +-6.64'.

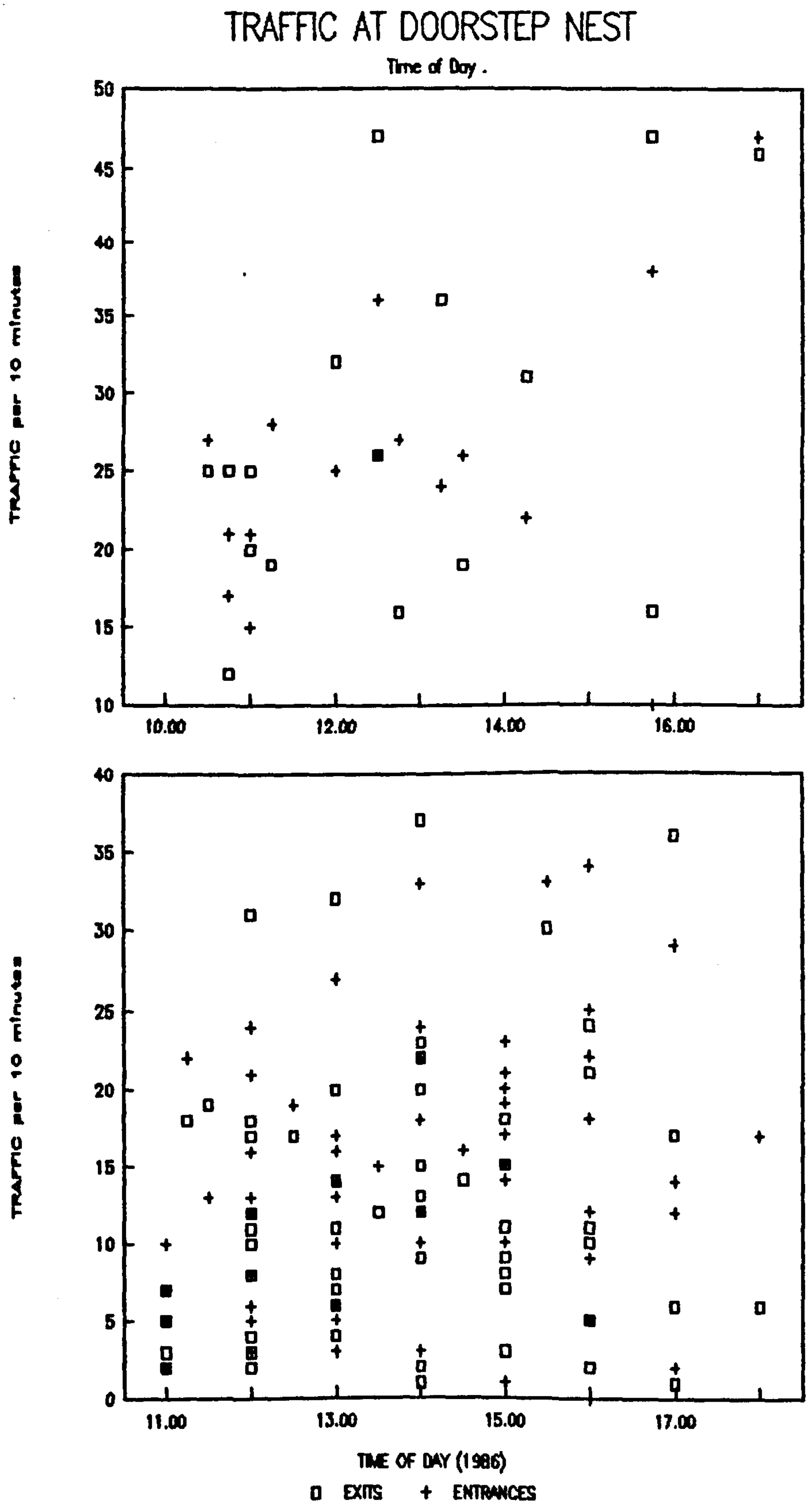


Figure 8.9. Relationship between traffic at Doorstep Nest entrance and time of day.

The relationships between temperature and the number of exits and entrances in 10 minute observation periods are shown in Figure 8.10. There was a significant positive correlation between temperature and number of exits ($p<0.05$) and although the number of entrances seemed to increase with temperature this relationship was not significant ($p<0.1$). These correlation analyses (by ranks) are summarized in Table 8.23.

Similar correlation analyses were performed using the data from each date separately. These analyses are also summarized in Table 8.23. There was only one individual date when a significant correlation between activity and temperature was found; September 19 when the number of exits rose significantly as the temperature increased. On that date the number of entrances also seemed to rise with temperature, but this relationship was not significant. On the previous day the number of entrances seemed to decrease as temperature increases but this relationship was not successful either.

Ranked correlations analyses were not carried out to investigate the relationship between temperature and activity for each minute because there were so many values which shared the same rank (e.g. on October 3 there were 45 minutes when no ants left the nest and 49 minutes when no ants entered the nest out of a total of 60 minutes observation).

8.2.7 INFLUENCE OF LIGHT INTENSITY.

Light intensity (Appendix 4) varied significantly between the four days on which it was recorded ($F=30.57$, $df= 3,133$, $p<0.001$). On June 13 the mean light intensity was 11.28 +/-3.14 (arbitary units), on September 18 it was 5.79 +/-3.59, on September 19 it was 5.87 +/-3.13 and on October 3 it was 5.25 +/-1.55.

Figure 8.11 displays the relationship between light intensity and the numbers of exits and entrances. Correlation analyses (by ranks) reveal that the number of exits increases significantly as light intensity increases but there is no relationship with the numbers of entrances. These analyses are summarized in Table 8.24.

DATE	NO. COUNTS	EXITS	SIGN.	ENTRANCES	SIGN.
TOTAL	26	r=+0.3807	p<0.05	r=+0.326	p<0.1
13/6/86	9	+0.4042	n.s.	+0.4347	n.s.
18/9/86	8	-0.5298	n.s.	-0.6607	p<0.1
19/9/86	5	+0.9	p<0.05	+0.8	p<0.1
3/10/86	4	+0.1	n.s.	+0.325	n.s.

Table 8.23. Summary of correlation analyses (by ranks) to investigate the relationship between temperature and numbers of ants exiting from and entering into Nest One during 10 minute observation periods.

DATE	NO. COUNTS	EXITS	SIGN.	ENTRANCES	SIGN.
TOTAL	26	r=+0.5091	p<0.01	r=+0.3132	n.s.
13/6/86	9	+0.025	n.s.	-0.3709	n.s.
18/9/86	8	+0.131	n.s.	-0.0536	n.s.
19/9/86	5	+0.4	n.s.	-0.125	n.s.
3/10/86	4	-0.7	n.s.	-0.55	n.s.

Table 8.24. Summary of correlation analyses (by ranks) between light intensity and the number of ants exiting from and entering into Nest One in 10 minute observation periods.

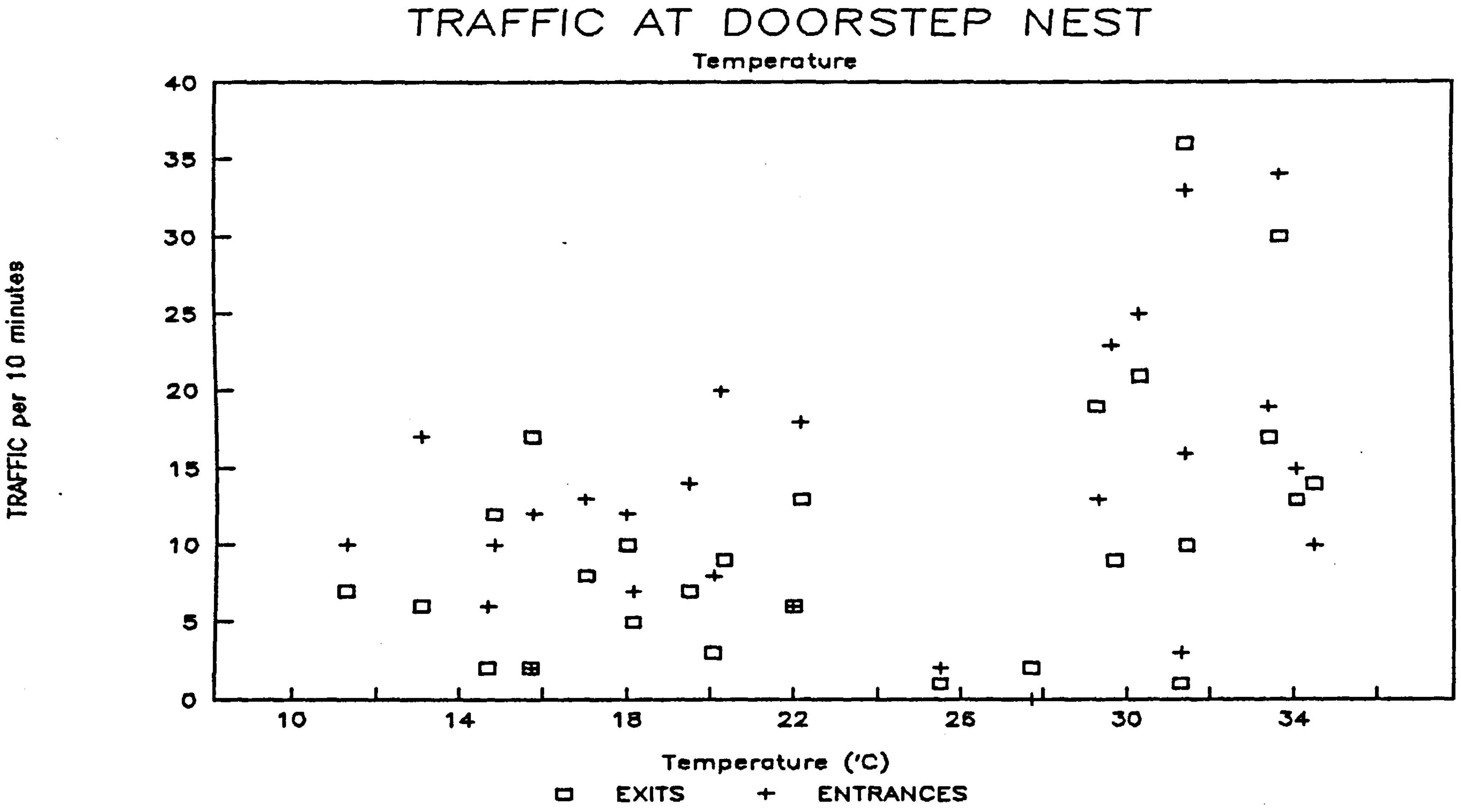


Figure 8.10. Relationship between traffic at Doorstep Nest entrance and temperature.

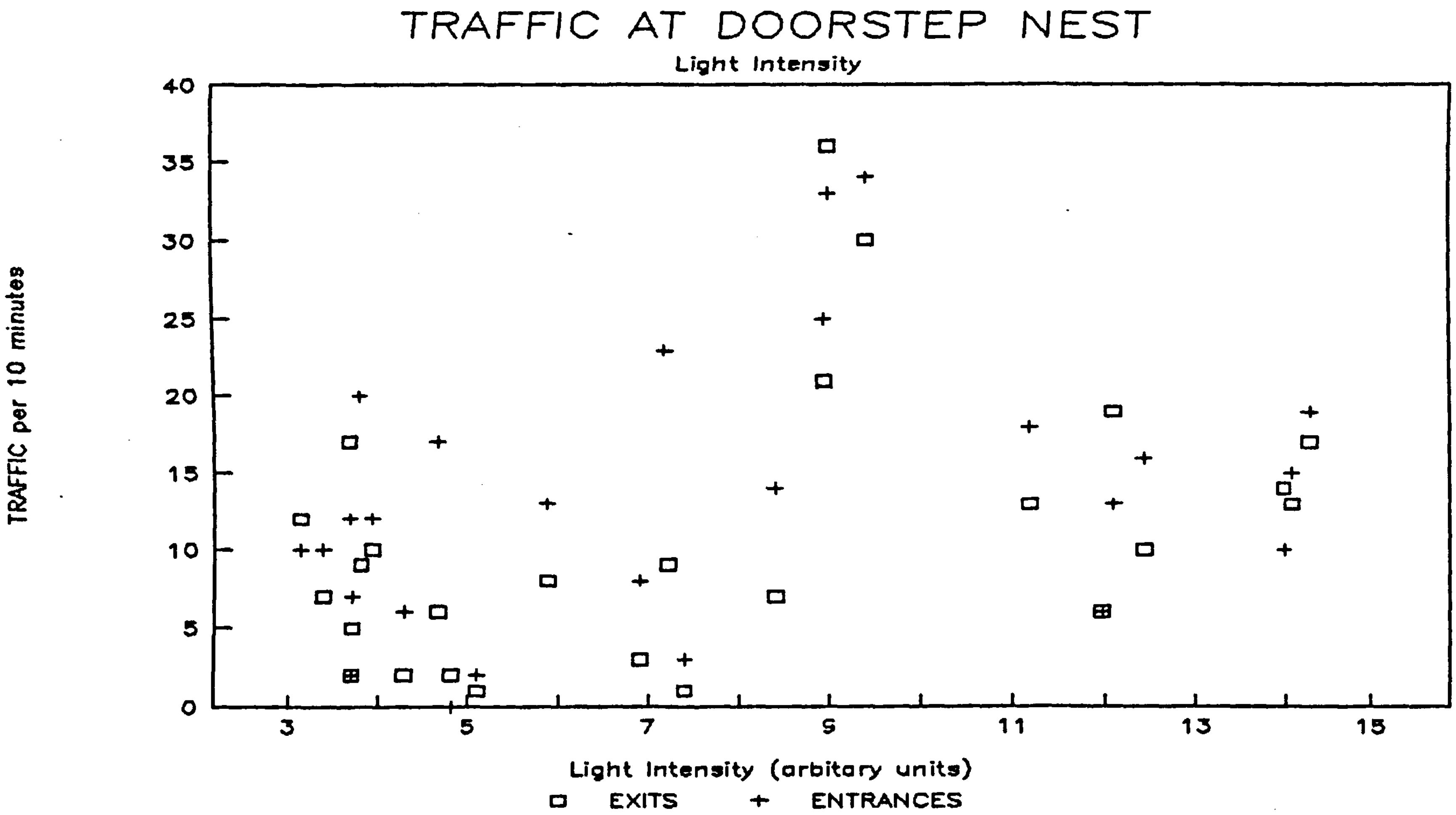


Figure 8.11. Relationship between traffic at Doorstep Nest entrance and light intensity

Similar analyses were also performed using the data from each date separately. The results of these analyses are also presented in Table 8.24. There were no dates when either numbers of exits or entrances were correlated to light intensity.

8.3 MOVEMENTS OF INDIVIDUAL FORAGERS IN THE LABORATORY.

8.3.1 FIRST SERIES.

One and one quarter hours of video recording was made of ants moving on the laboratory floor in the first series of observations. The trails recorded could immediately be divided into two categories when replayed from video-recordings. In the first category the trails either formed tight concentric circles or followed the edges of the petri dish nests. These trails did not appear to be similar to foraging movements as seen in the field, or indeed in larger, more established, laboratory nests. These very intricate trails were not analysed further. The second set of trails formed the majority; they were more like typical foraging movements. These trails were subjected to further analysis. Examples of some of the paths traced from these video- recordings are presented in Figure 8.12.

Fifty 10cm stretches of path were traced from ants moving out from watered nests; of these eleven 10cm stretches were seen to lead the ant to one or other of the available food sources. Eleven 10cm stretches of path were traced from ants moving from unwatered nests; of these five stretches led to a food source. Thus the paths traced could be divided into 39 "watered" and "unsuccessful" segments, 11 "watered" and "successful" segments, 6 "unwatered :unsuccessful" segments and 5 "unwatered : successful" segments.

a/ Straightness index.

The straightness indices of each group of trails are presented in Table 8.25 and are displayed in Figure 8.13. The average straightness index, for the total of 61 segments was 7.72 (+/- 1.93). The variance to mean ratio shows that the sample has a random distribution. The means for each of the four groups all fell within one standard deviation of the grand mean suggesting that there was very little variation between the groups. This suggestion is borne out by a series of analyses of variance tests, sumnarized in Table 8.26, which showed that there were indeed no significant differences between any of the groups. Nor were there any significant differences between any of the sub- totals.

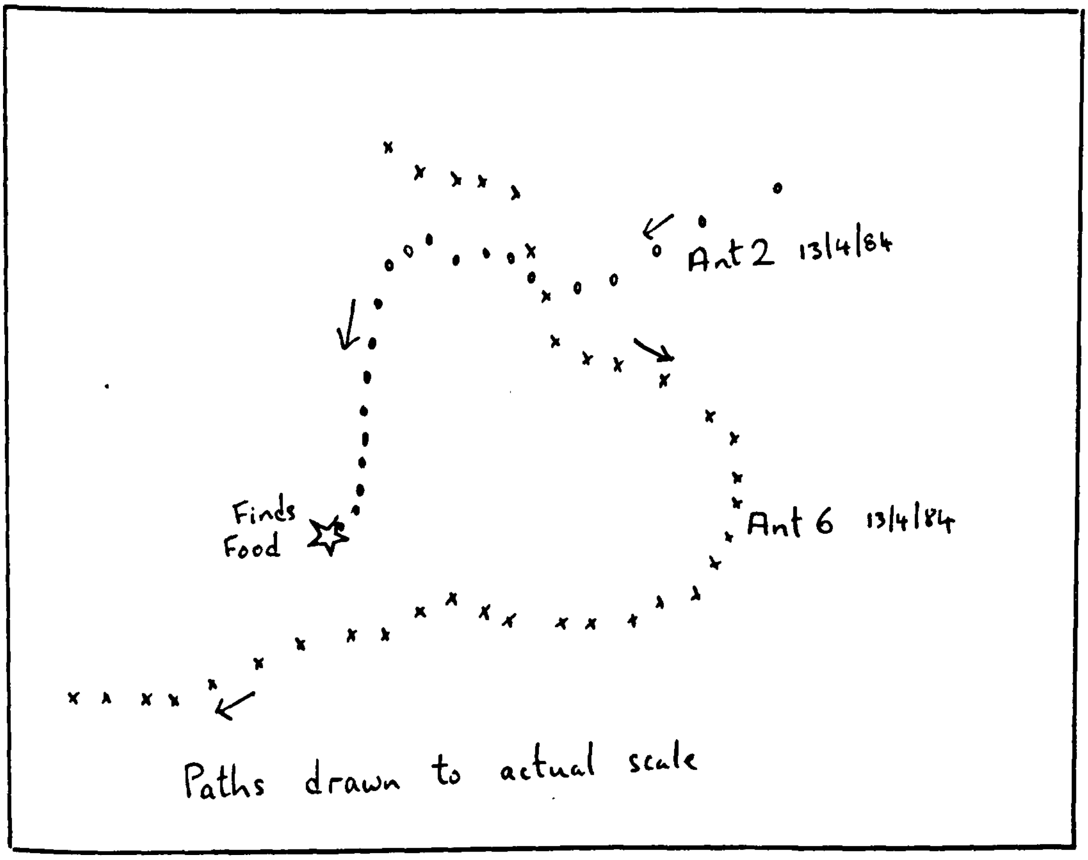


Figure 8.12. Example of movements made by ants in first laboratory observations.

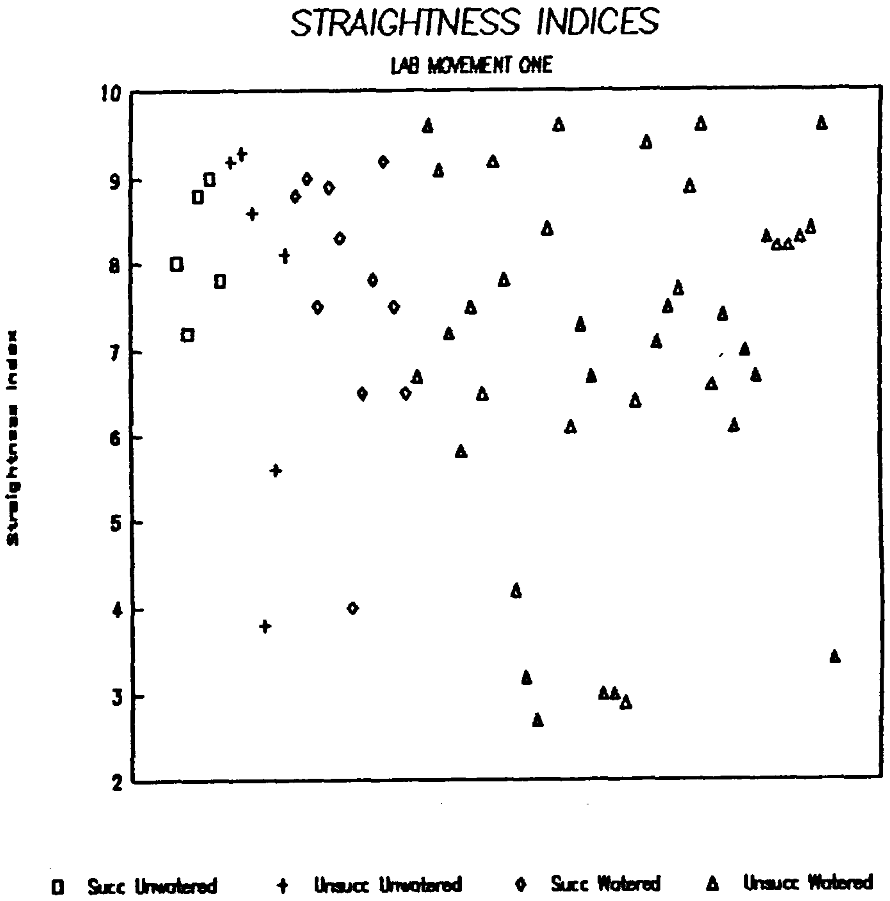


Figure 8.13. Straightness indices of ants followed in first series of laboratory observations.

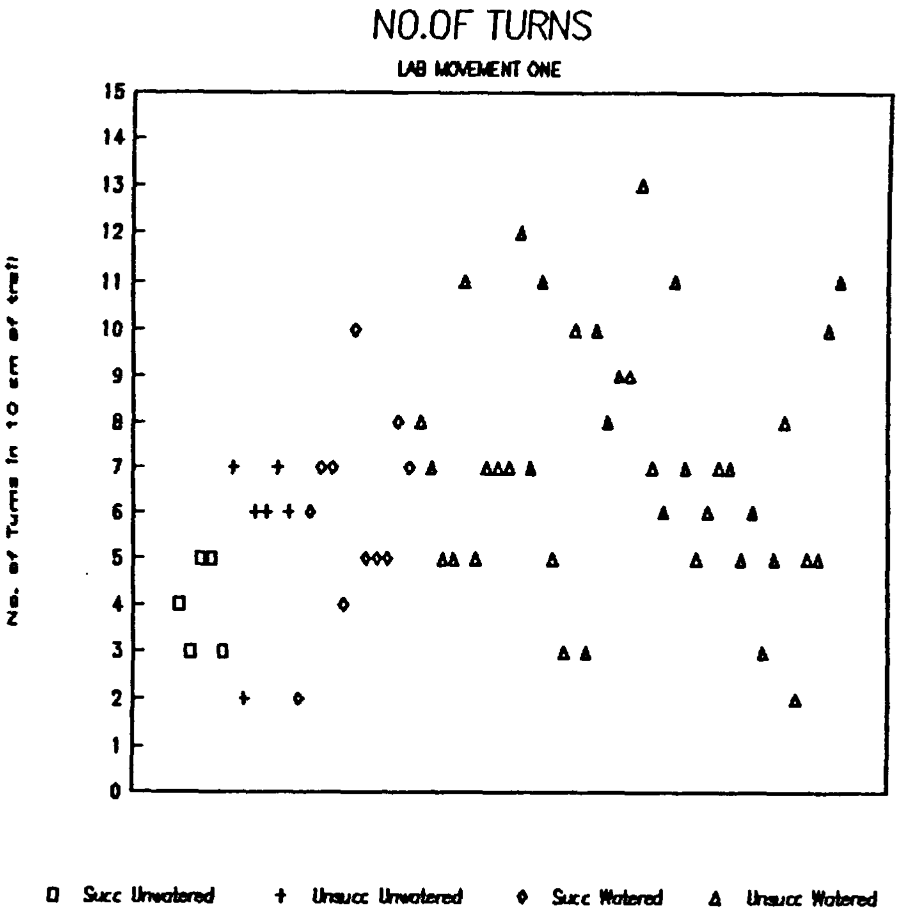


Figure 8.14. Number of turns of ants followed in first series of laboratory observations.

GROUP	SUCCESSFUL			UNSUCCESSFUL			SUBTOTAL		
	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n
WATERED	7.64	1.54	11	6.96	2.08	39	7.11	1.98	50
UNWATERED	8.16	0.74	5	7.43	2.24	6	7.76	1.69	11
SUBTOTAL	7.8	4.81	16	7.02	2.08	45	7.72	1.93	61

Table 8.25. Straightness indices of ants followed in small scale laboratory study. Data presented are mean, standard deviation and number of 10cm trail segments.

ANALYSES OF VARIANCE	F	df	prob.
BETWEEN FOUR GROUPS	0.8223	3,57	n.s.
WATERED v UNWATERED	1.07	1,59	n.s.
SUCCESSFUL v UNSUCCESSFUL	1.95	1,59	p<0.2
ONE v TWO	1.01	1,48	n.s.
THREE v FOUR	0.43	1, 9	n.s.
ONE v THREE	0.51	1,14	n.s.
TWO v FOUR	0.27	1,43	n.s.

Table 8.26. Summary of analyses of variances tests of straightness indices between various groupings of 10cm segments of ants' trails. GROUPS: ONE - watered:successful; TWO - watered:unsuccessful; THREE - unwatered:successful; FOUR - unwatered:unsuccessful.

b/ Number of Turns (in 10cm).

The number of turns which the ants made in each 10cm segment of trail are summarized in Table 8.27 and are presented in Figure 8.14. The overall average number of turns in 10cm was 6.52 (+/- 2.57). The variance to mean ratio shows that the sample has a random distribution. Again the means of each individual group of segments falls with one standard deviation of the grand mean. However an analysis of variance tests revealed there were significant differences in number of turns between all four groups. Further analyses revealed that unwatered ants made significantly fewer turns in 10cm segments than did watered ants and similarily that the trail segments which were ultimately successful contained fewer turns than did those which were unsuccessful. These analyses of variance tests are summarized in Table 8.28.

c/ Size of Turns.

The magnitude of the turns made by the ants in the 10cm trail segments are summarized in Figure 8.15. Note that in this case the sample number represents the total number of turns rather than the number of 10 cm sections of trail. Binomial tests revealed that ants were equally likely to turn clockwise or anticlockwise as there was no bias for right or left turns in any group of trails.

As can be seen from the figure the standard deviations represent a very large proportion of the means. Indeed the variance:mean ratios show that sample probably does not have a random distribution. Inspection of Figure 8.15 shows that in all cases the median value falls to the left of the mean value (i.e. the median is smaller). As the sample is not randomly distributed it is not appropriate to use analyses of variance tests to compare groups. Instead chi-squared tests are used to compare the sample distributions. The results of such chi-squared tests are summarized in Table 8.29.

Significanct differences are found between the distributions of all four groups. The trails of watered ants contained significantly more smaller turns than did the trails of ants from

GROUP	SUCCESSFUL			UNSUCCESSFUL			SUBTOTAL		
	Mean	s.d.	n	Mean	s.d.	n	Mean	s.d.	n
WATERED	6.00	2.14	11	7.13	2.69	39	6.88	2.60	50
UNWATERED	4.00	1.00	5	5.67	1.86	6	4.91	1.70	11
SUBTOTAL	5.38	2.99	16	6.93	2.62	45	6.52	2.57	61

Table 8.27. Frequency of turning of ants followed in small scale laboratory study. Data presented is mean number of turns per 10 cm, standard deviation and number of 10 cm trail segments.

ANALYSES OF VARIANCE	F	df	prob.
BETWEEN FOUR GROUPS	2.98	3,57	p<0.05
WATERED v UNWATERED	5.7527	1,59	p<0.05
SUCCESSFUL v UNSUCCESSFUL	4.6288	1,59	p<0.05
ONE v TWO	1.6362	1,48	n.s.
THREE v FOUR	3.1926	1, 9	p<0.2
ONE v THREE	3.85	1,14	p<0.2
TWO v FOUR	1.636	1,43	n.s.

Table 8.28. Summary of analyses of variance tests of the number of turns in 10cm segments between various groupings of ants' trails. Groups are numbered as in Table 8.26.

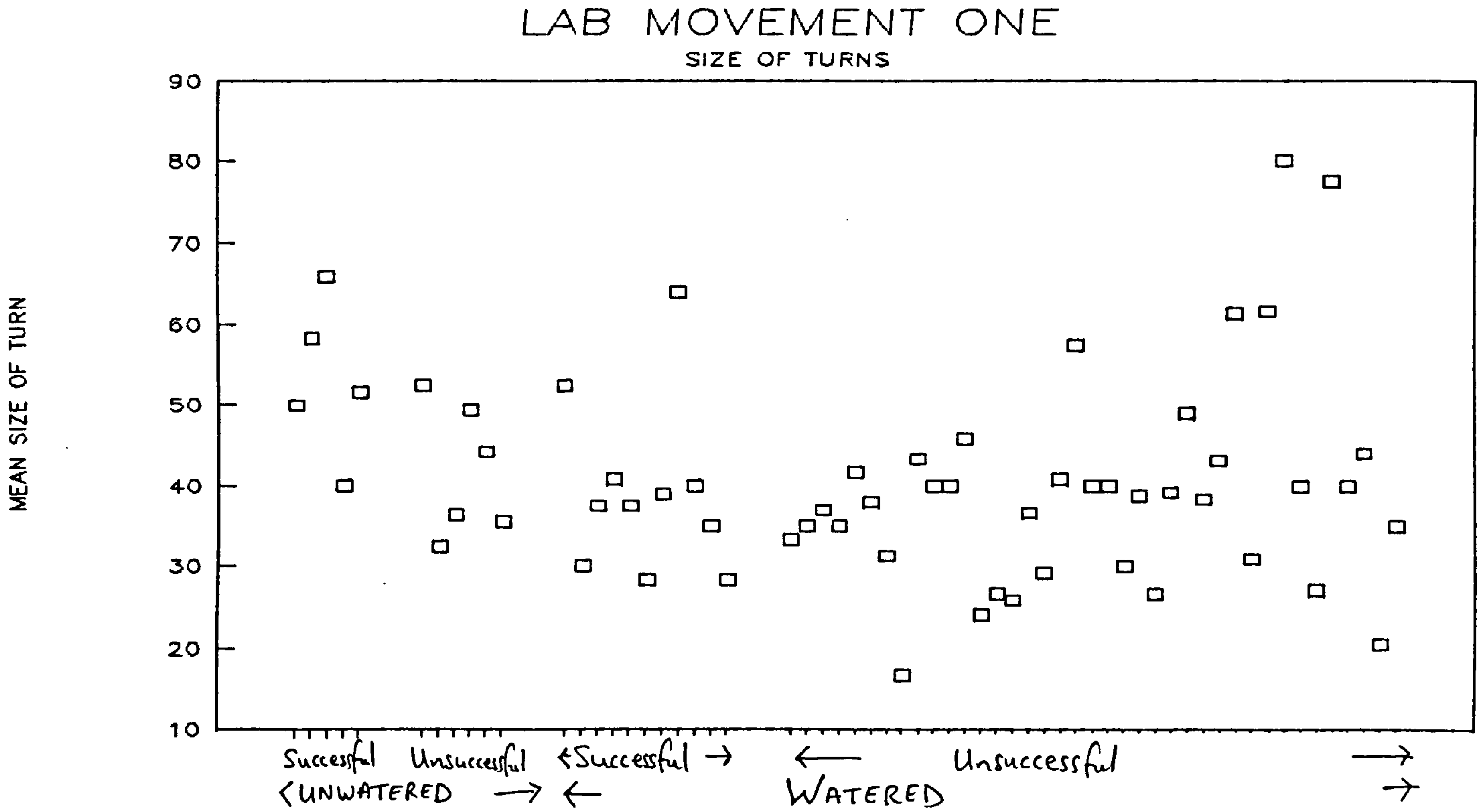


Figure 8.15. Size of turns of ants followed in first series of laboratory observations.

CHI-SQUARE TESTS	X-sq.	df	prob.
BTW FOUR GROUPS	35.187	6	p<0.001
WATERED v UNWATERED	17.998	5	p<0.01
SUCCESSFUL v UNSUCCESSFUL	8.68	7	n.s.
ONE v TWO	3.53	5	n.s.
THREEvFOUR	2.07	2	n.s.
ONEvTHREE	9.28	1	p<0.01
TWOvFOUR	10.92	3	p<0.02

Table 8.29. Summary of chi-squared tests to compare the distribution of sizes of turn between various groups of ants' trails. Groups are numbered as in Table 12.26.

GROUP	CORRELATIONS						
	r1		r2	r3		n
TOTAL	-0.5117	****	-0.1117	-0.2710	**	61
WATERED	+0.525	****	-0.156	+0.2455	*	50
UNWATERED	+0.2795		+0.0466	+0.0712		11
SUCCESSFUL	+0.5380	**	+0.1759	+0.4877	**	16
UNSUCCESSFUL	+0.5342	****	-0.1478	+0.1188		45
ONE	+0.6500	**	+0.0737	+0.3739		11
TWO	+0.4916	***	-0.1955	+0.226		39
THREE	-0.9456	***	+0.2370	+0.1044		5
FOUR	+0.3621		-0.3144	+0.6897	*	6

Table 8.30. Correlation between movement parameters of ants followed in small scale laboratory nest study. r1 is correlation of straightness index and frequency of turns, r2 is correlation of straightness index and magnitude of turns, r3 is correlation of frequency of turns and their magnitude. N refers to the number of 10 cm segments involved. Groups are numbered as in Table 8.26.

nests which had not been watered. This difference was evident when the all the watered trails were compared with all the unwatered trails. The same difference was also evident when the comparison was restricted to the trails which were successful or to the trails which were unsuccessful.

d/ Correlation between parameters.

A series of correlation analyses were performed to see how the three movement parameters were related to each other. These results of these analyses are summarized in Table 8.30.

There was a very strong negative correlation between the first two parameters, straightness index and number of turns. Such significant correlations were found when all the data was considered, for three of the four subtotals (the unwatered subtotal was the exception) and for three of the four groups (the unsuccessful:unwatered group was the exception). Thus the more turns an ant makes the smaller will be its straightness index.

There were negative correlations between the number of turns in 10cm segments and the mean size of turns in that segment (the mean turn size per 10cm segment had a random distribution so that straight correlation analyses were permissable). These correlations were seen when all the data was considered and when the successful subtotal was considered. Thus if an ant makes more turns these turns will be of smaller magnitude.

There were no correlations between straightness index and size of turn.

8.2.2 SECOND SERIES.

The foraging paths of several ants were video recorded as they moved over the large laboratory nest (LLN) foraging arena. Most of these were the paths of unladen foragers but some of the workers trailed were carrying dead nestmates. Only those ants which were followed continuously for more than 20 seconds were included in analyses. Thus the paths of four "foragers" and three "carriers" were analysed. Only one type of trail was seen in this stage of the study; an example is presented in Figure 8.16. Details of the seven trails analysed are summarized in Table 8.31.

a/ Speed.

Two measures of the ants' velocity were available; the distance moved in 10 seconds and the time required to move 10cm. These measures should be approximately reciprocal but would only be exact reciprocals if the speed was 1cm/sec, otherwise slightly different stretches of the trail is used for each computation. Both measures of velocity are presented for all seven ants in Figure 8.17.

Analyses of variance tests were used to investigate how both measures of velocity varied between the individual ants and between the "foragers" and "carriers" groups. These analyses are summarized in Table 8.32. There were significant differences in velocity between all the different ants and these differences were also present within both the "foragers" and the "carriers" groups. There were no significant differences between the "foragers" and "carriers" groups.

b/ Frequency of Turns.

There are also two measures of the number of turns; the number of turns in 10 second segments and the number in 10 cm segments. These are presented for each ant in Figure 8.18. (The two measures would only be the same if the ant moved at 1cm/second).

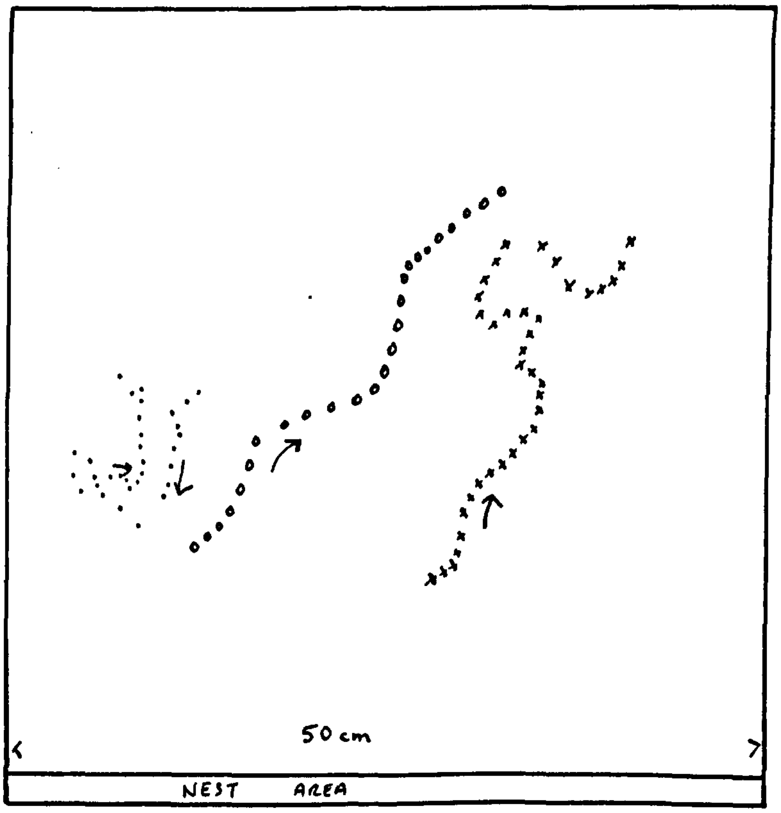


Figure 8.16. Example of movements made by ants in second laboratory observations.

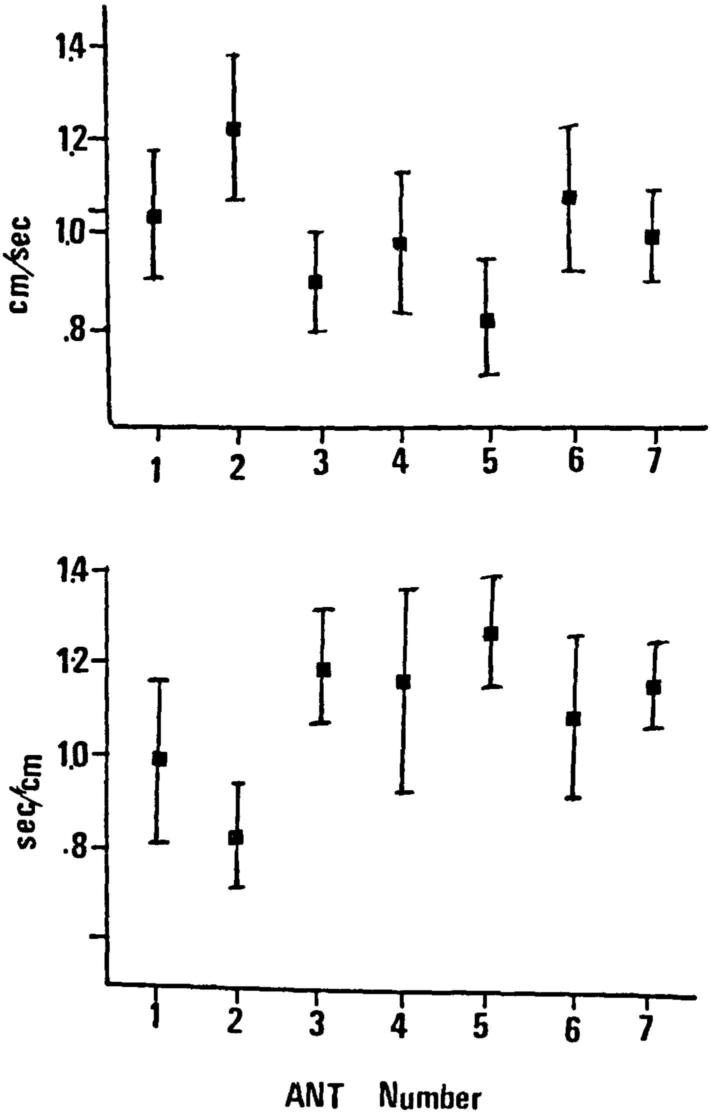


Figure 8.17. Speed of ants followed in second series of laboratory observations.

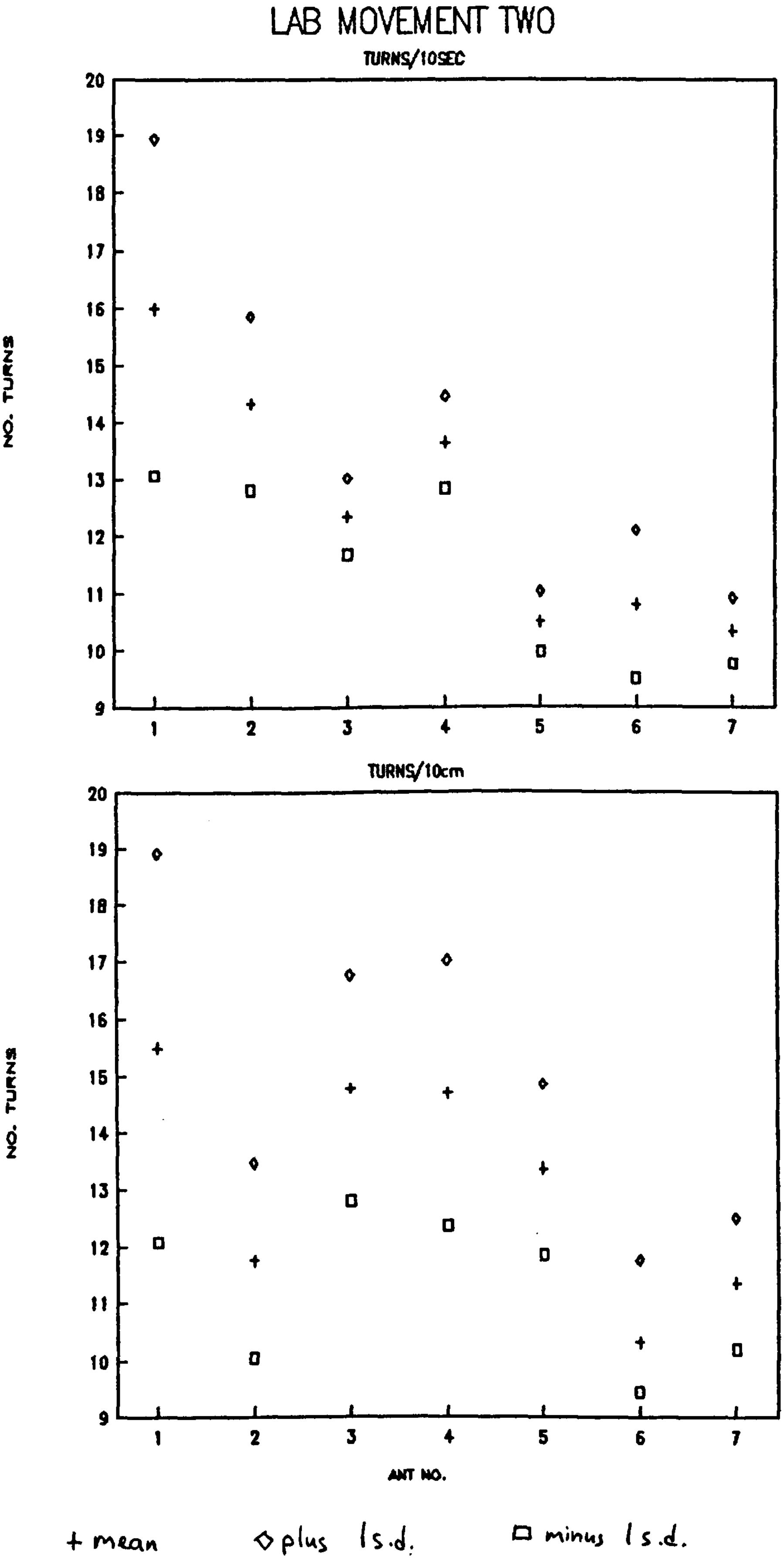


Figure 8.18. Frequency of turns made by ants followed in second series of laboratory observations.

ANT	DURATION (sec)	DISTANCE (cm)	NO. TURNS	SUM TURNS	MEAN TURN	TURN FREQ. (no/cm)
FORAGER 1	44.26	45.51	71	2306	32.48	1.56
FORAGER 2	35.40	45.2	53	1466	27.66	1.17
FORAGER 3	113.19	101.42	140	4195	29.96	1.38
FORAGER 4	72.0	67.65	94	3311	35.22	1.38
CARRIER 5	91.90	73.28	95	2311	24.54	1.3
CARRIER 6	71.09	70.19	75	3041	40.55	1.07
CARRIER 7	37.05	34.28	37	759	20.55	1.08
TOTAL	464.89	511.28	565	17409	30.81	

Table 8.31. Summary of movements of ants followed and analyzed in medium scale laboratory study.

ANALYSES OF VARIANCE	cm/10 sec			sec/10cm		
	F	df	sign.	F	df	sign.
ALL SEVEN ANTS	13.1132	3,32	****	4.0898	6,30	****
FORAGERS v CARRIERS	1.5897	1,39		2.0976	1,35	*
FOUR FORAGERS	5.7905	3,20	***	5.4945	3,19	***
THREE CARRIERS	10.9218	3,12	***	2.3509	2,11	*

Table 8.32. Summary of analyses of variance tests comparing the speeds of ants between and within groups. **** =p<0.001, ***=p<0.01, **- p<0.05, *=p<0.2.

ANALYSES OF VARIANCE	turns/10 sec			turns/10cm		
	F	df	sign.	F	df	sign.
ALL SEVEN ANTS	14.5594	6,33	****	4.4396	6,30	***
FORAGERS v CARRIERS	36.0134	1,38	****	10.0059	1,35	***
FOUR FORAGERS	7.1648	3,20	***	2.1337	3,19	*
THREE CARRIERS	0.3226	2.13		6.2247	2,11	**

Table 8.33. Summary of analyses of variance tests comparing frequency of turning between and within groups of ants.

Analyses of variance tests were used to investigate differences in the amount of turning within and between the groups; the results are summarized in Table 8.33.

There were significant differences in both measures between the seven ants, and in one measure between the ants of both "foragers" and "carriers" groups. Both measures of the amount of turning varied significantly between the two groups with the "foragers" turning more frequently than the "carriers".

c/ Size of Turns.

The turns made by the ants are summarized in Figure 8.19. A series of chi-squared tests were performed to compare the size distributions for the various individuals and groups of ants. These tests, summarized in Table 8.34, show that there were significant differences in the size distributions between the seven ants, between the four "foragers", and between the three "carriers" but not between the "foragers" and "carriers" groups.

The magnitude of the ants' turns was also assessed as the number required to make up 180 degrees. This information is presented in Table 8.35. Analysis of variance of the number of turns required for 180' revealed that there were significant differences between ants when all seven were considered together (F=3.14, df=6,77, p<0.01). Unlike the chi-squared analyses of size distributions this analysis found no significant differences between the ants in either group ("foragers": F=0.96, df=3,52, p<0.2; "carriers": F=2.28, df=2,25, n.s). In agreement with the former analysis this analysis found that there were no significant differencesbetween the foragers and the carriers (F=2.0977, df=1,82, p<0.2).

d/ Directionality.

The direction in which each ant travelled between fixes are summarized in Table 8.36. Circular chi-squared tests showed that for all but one (Ant No.4) the sample distribution of directions between fixes differed significantly from a regular distribution. Therefore each ant travelled consistently in one direction.

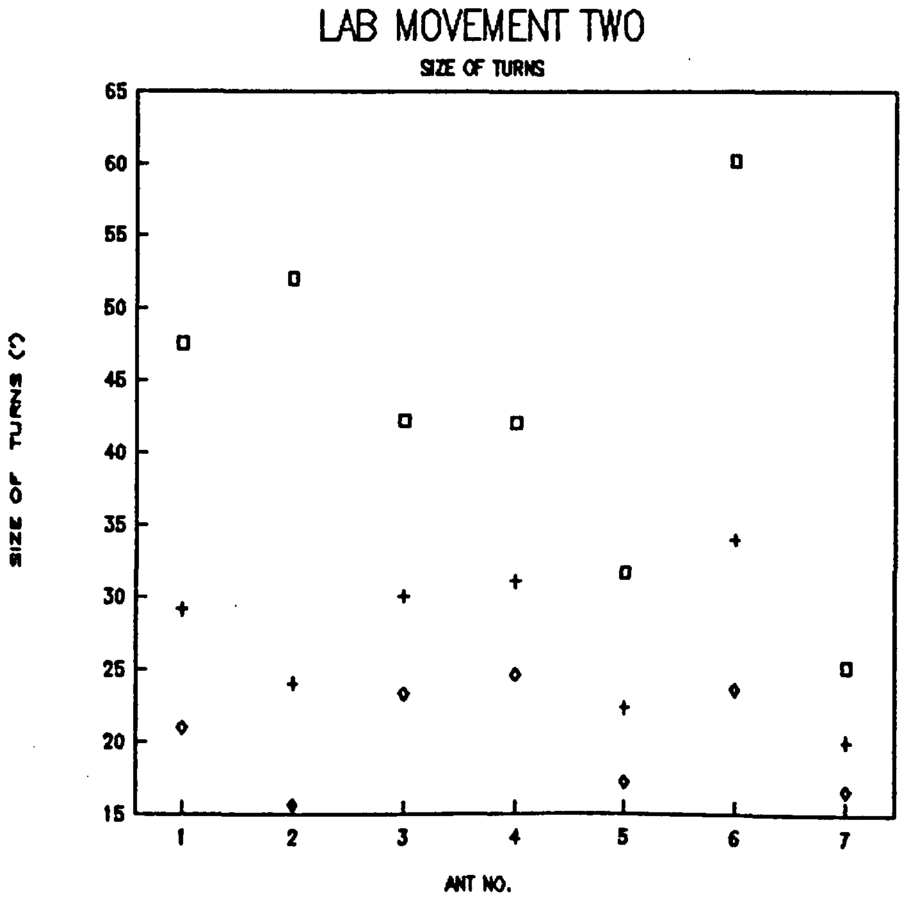


Figure 8.19. Size of turns of ants followed in second series of laboratory observations.

□ mean plus s.d.

+ mean

◇ mean minus s.d.

CHI-SQUARED TESTS	X-sq.	df	sign.
ALL SEVEN ANTS	52.67	24	****
FORAGERS v CARRIERS	5.183	12	
FOUR FORAGERS	23.07	12	**
THREE CARRIERS	23.90	8	***

Table 8.34. Summary of chi-squared tests to compare the size distribution of turns made by individual and groups of ants.

ANT	MEAN	S.D.	No. Segments
FORAGER 1	6.18	2.4	11
FORAGER 2	7.5	4.04	6
FORAGER 3	6.0	1.73	23
FORAGER 4	5.81	1.52	16
CARRIER 5	8.09	2.39	11
CARRIER 6	5.31	2.32	13
CARRIER 7	9.0	1.83	4

Table 8.35. The number of turns required to make up 180' in ants' trails presented as the mean of the number of 180' segments in each ants' trail. The grand mean was 6.4 turns (+/-1.63, n=84 180' segments).

DIRECTION	"FORAGERS"				"CARRIERS"		
DIRECTION	1	2	3	4	5	6	7
341-020'	3	1	6	6	3	9	1
021-060'	4	0	12	9	2	12	3
061-100'	8	0	13	13	12	21	21
101-140'	10	6	18	10	12	9	13
141-180'	19	22	34	17	3	9	1
181-220'	23	18	21	13	2	3	0
221-260'	9	6	20	9	15	1	0
261-300'	1	3	14	8	23	6	0
301-340'	2	3	9	10	19	9	0
NO. STEPS	79	59	147	95	91	79	39
X-sq.	38.7	56.6	33.4	7.8	32.5	19.1	1.6
df	5	3	7	7	5	6	1
Sign.	****	****	****		****	***	****

Table 8.36. Distribution of directions in which ants travelled while their movements were video recorded. 000' is away from the nest towards the wall. Circular chi-squared tests show that for all trails with the exception of Ant #4 there was a significant clumping of move directions, i.e. all but one ant moved consistently in the same direction (df=n-2). ** =p<0.05, *** = p<0.01, **** = p<0.001.

However, this prefered direction differed between ants. Another circular chi-squared test compared the different sample distributions and found that they were significantly different (X-sq=211.24, df=48, p<0.001).

e/ Changes with time.

As the ants were trailed for at least 30 seconds and because the movement parameters were calculated for each consecutive segment of 10 seconds, 10 cm and 180', it was possible to compare the movements early on in a foraging trip with those made later. For instance the parameters for all the "first" segments could be pooled and compared with the parameters pooled for all the "second" segments, and with all the "third" segments and so on.

The speed of the ants changed significantly between consecutive 10 cm segments (sec/10 cm: F=3.19, df=5,28, p<0.025). This variation in the time required for the ants to cover 10 cm did not follow any simple pattern but rather showed itself as an acceleration from 0.806 cm/sec to 1.07 cm/sec followed by a subsequent deceleration to 0.844 cm/sec. The same pattern was seen for the other measure of speed (distance covered in 10 seconds) but this variatiion was not significant (cm/10 sec: F=1.87, df=5,27, p<0.2).

The number of turns did not vary between consecutive 10 second and 10 cm segments (F=0.34, df=5,27, n.s. and F=0.8212, df=5,28, n.s. respectively).

The size of the turns made by the ants also showed an amount of variation although this variation did not quite attain the 5% confidence level (F=2.01, df=10,54, p=0.06). In the first 180' segment there were 8.43 turns while in later segments this had fallen to 6.00 turns.

No analysis was performed to investigate how the parameter directionality might change over time.

8.3.3 THIRD SERIES.

Twelve foragers were selected at random and followed from leaving the nest area until they returned to it. These foraging trips lasted at least 40 seconds though some extended for upwards of five minutes. One ant was trailed for ten minutes before it was lost as it encountered other ants. The ants' positions were recorded every 10 seconds throughout their trail. An example of the trails followed in the LLN by recording the position of foragers every 10 seconds is presented in Figure 8.20.

a/ Movelength.

The movelengths of the ants, i.e. the net distance moved in 10 seconds, are presented in Figure 8.21. Movelength varied greatly between ants, from the extremes of 1.91 cm (+/-1.34) for Ant No. #10 to 12.19 cm (+/-5.53) for Ant No. #1. An analysis of variance test showed that these differences between ants were indeed significant (F=13.028, df=11,244, p<0.001). This significant difference is also seen if the analysis is restricted to the seven ants which travelled for more than 2 minutes (F=18.88, df=6,221, p<0.001).

b/ Directionality.

The direction in which each ant moved between consecutive fixes was summarized as a the mean direction, two measures of the deviation of the sample around this mean movedirection and a test of whether the directions between fixes were statistically clumped. This information is presented in Table 8.37. There was no significant clumping of the movedirections between fixes for any of the twelve ants.

c/ Size of direction changes.

The size distribution of the changes of direction between 10 second segments are presented in Figure 8.22 along with the mean size (and standard devaition). Binomial tests

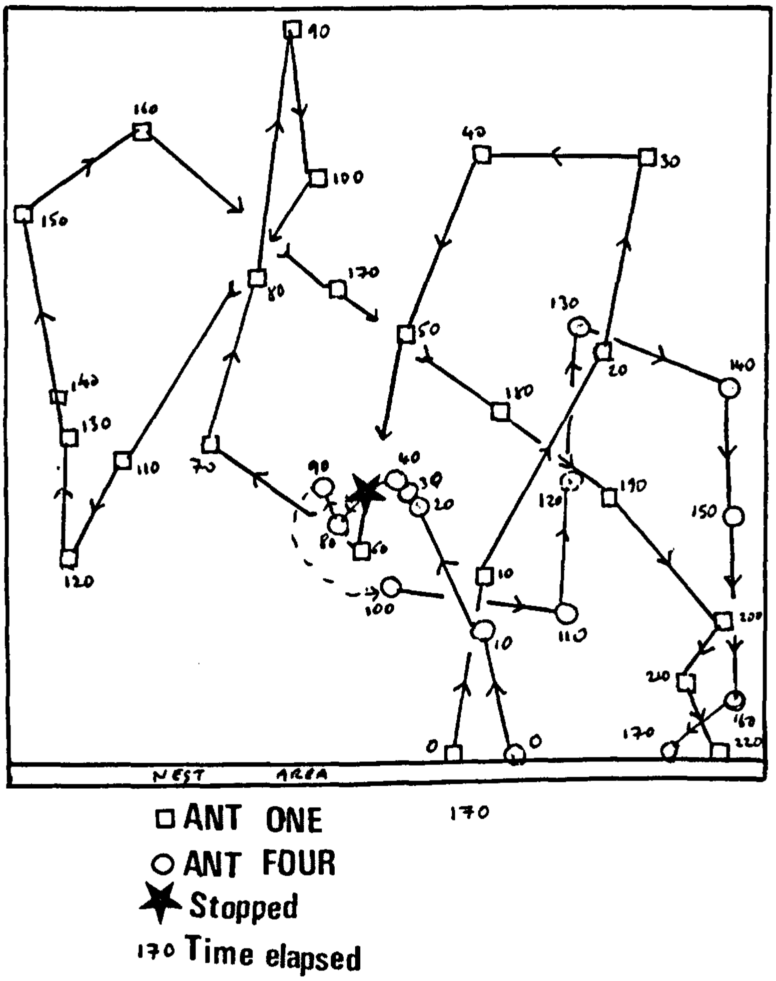


Figure 8.20. Example of movements made by ants in third series of laboratory observations.

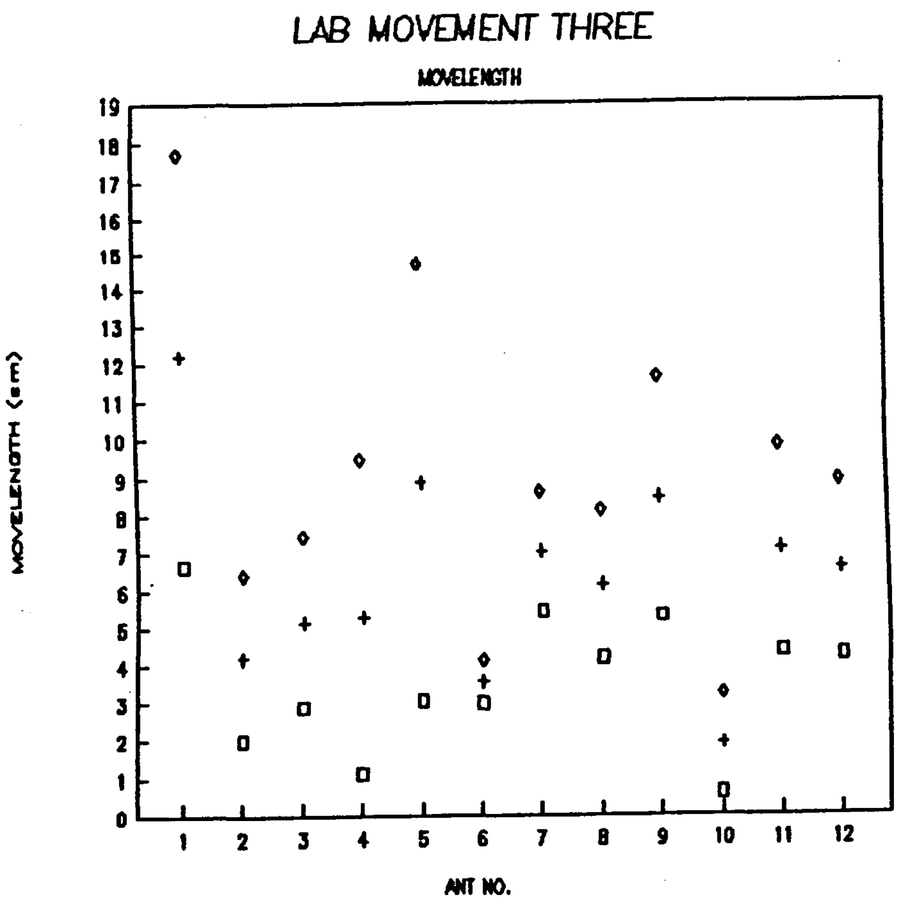


Figure 8.21. Movelengths of ants followed in third series of laboratory observations.

◇ mean + s.d.
+ mean
□ mean − s.d.

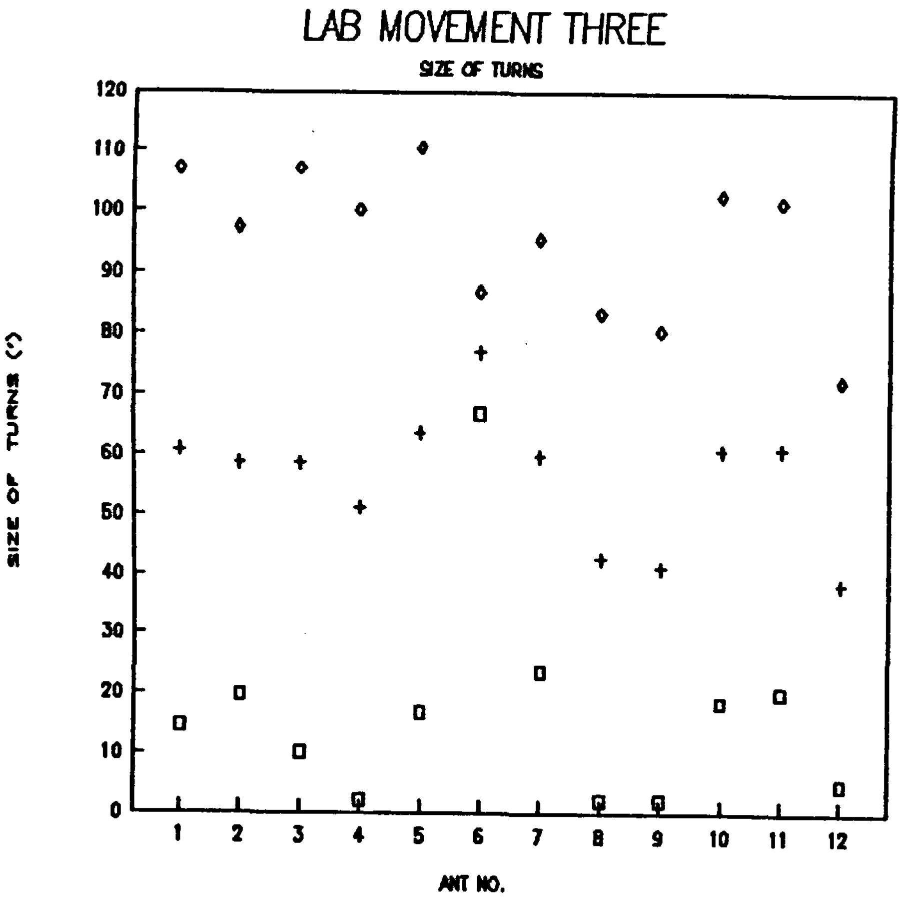


Figure 8.22. Size of turns of ants followed in third series of laboratory observations.

◇ mean + s.d.
+ mean
□ mean − s.d.

ANT	NO. STEPS	MEAN DIRECTION	ANGULAR DEVIATION	CLUMPING INDEX	SIGN.
1	22	256.5	77.3	0.0907	n.s.
2	32	169.18	70.6	0.2379	n.s.
3	31	39.78	78.1	0.0761	n.s.
4	17	90.65	76.4	0.1078	n.s.
5	5	23.21	65.9	0.34	n.s.
6	6	353.01	55.6	0.527	n.s.
7	5	357.6	77.2	0.0819	n.s.
8	35	302.87	80.2	0.0281	n.s.
9	8	8.36	76.0	0.1226	n.s.
10	4	179	49.9	0.6211	no test
11	34	297.77	76.0	0.1223	n.s.
12	57	66.02	74.3	0.1596	n.s.

Table 8.37. Mean movement vectors of twelve ants followed by recording their position every 10 seconds in foraging arena of LLN. Twelve ants followed for a total of 254 steps (= 42.4mins).

revealed that there were no significant differences in the numbers of clockwise and anticlockwise turns.

The standard deviations were very large relative to the mean size of direction change. The variance:mean ratios show that the sample distribution is not random. Therefore analyses of variance were not appropriate to compare the size of direction changes between ants. A Chi-squared test was used to compare the size distributions of the ants which were followed for more than 30 direction changes (No.s #2, #2, #8, #11, #12) showed that there were significant differences in the size distribution between the ants (X-sq=26.15, df=12, $p<0.02$). Ants which were followed for shorter periods were excluded so that the requirement of the chi- squared test that expected frequencies be at least 5 could be met.

d/ Variation of movement parameters with time.

Movements made at different times into the foraging run were compared by pooling the data for each parameter after 2, 4, 7, 10, 13, 16, 19 and 22 steps and then comparing the data between each pool. The data was restricted to each third step so that the workload for computation and analyses was reduced.

i/ variation in movelength with time.

The movelengths at each time interval of the ants followed for the longest periods are summarized in Figure 8.23. They were compared by means of a Friedman analysis of variance by ranks test. For each ant followed for more than two minutes, movelength was ranked at each time interval. Ranking was used because movelength varied between ants. There were no significant differences between the sum of the ranks at each time interval (X-sq=3.7857, df=7, n.s.). Thus movelength did not vary significantly between time intervals.

ii/ variation in directionality with time.

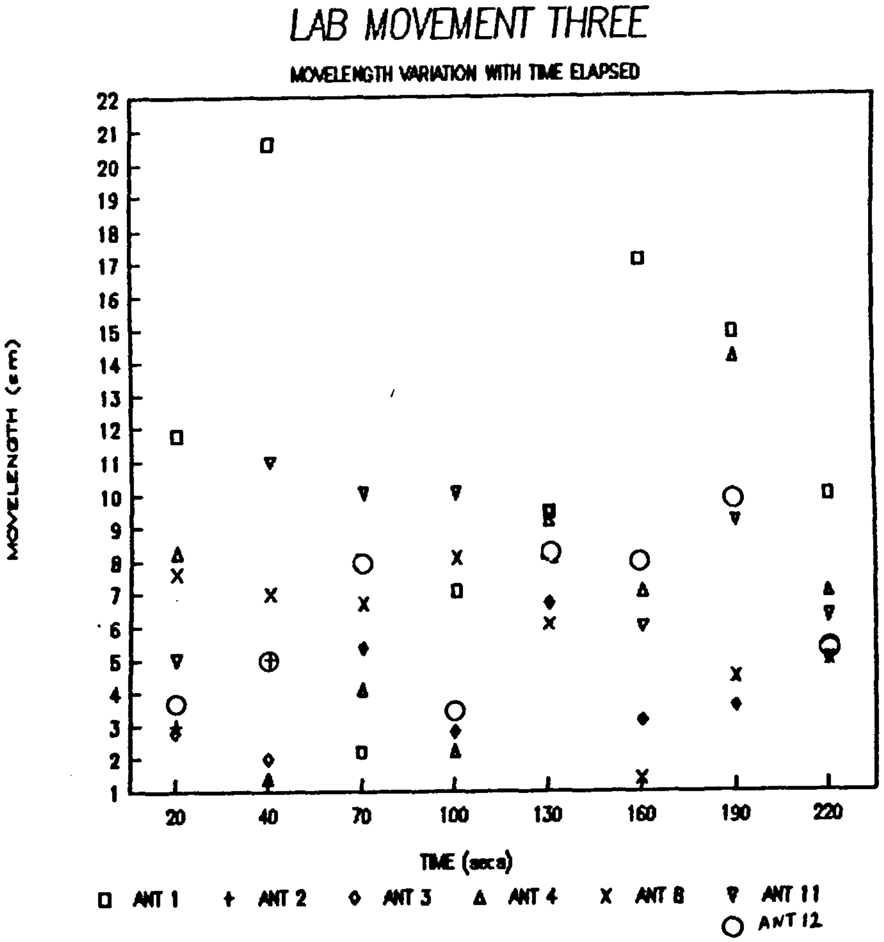


Figure 8.23. Variation in movelength over time of ants followed in third series of laboratory observations.

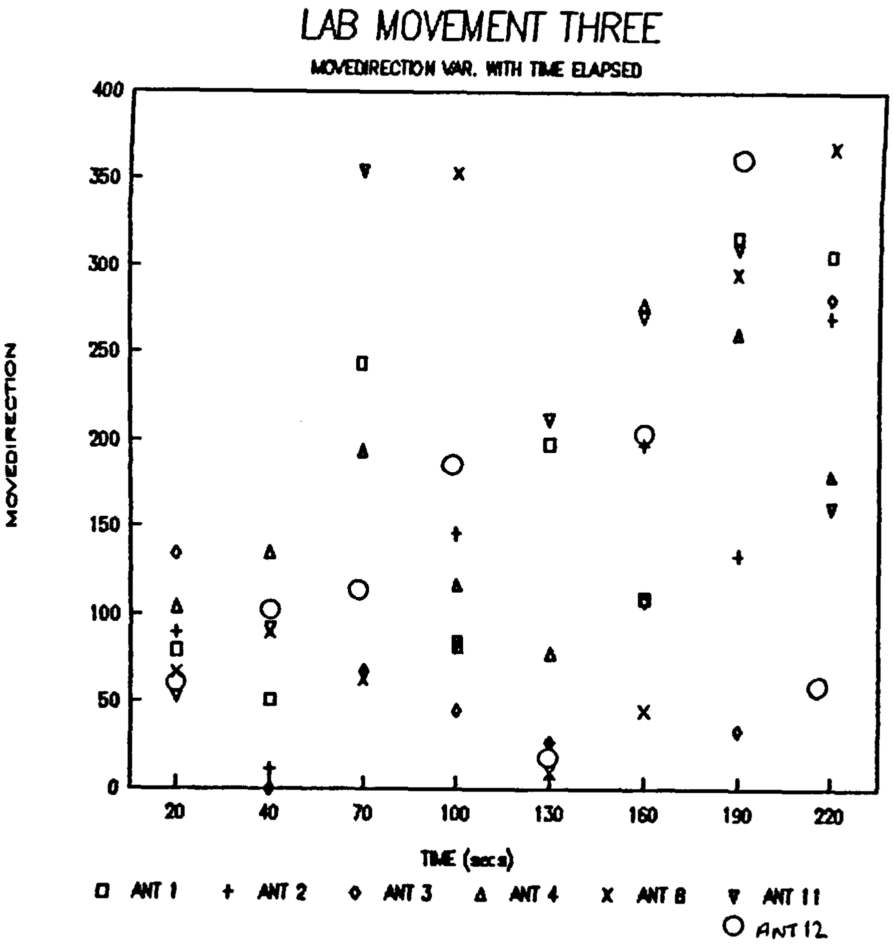


Figure 8.24. Variation in directions of movement of ants followed in third series of laboratory observations with time.

The directions in which each of the seven ants which were followed for longest were travelling at the time intervals stated were used to calculate a "mean movement vector" for each time interval. These vectors are presented in Figure 8.24. There was significant clumping of the directions after 20 seconds and 40 seconds but not at the later time intervals. Thus all the ants travelled in the same direction early in their foraging trips but not later on. A Mardia-Watson-Wheeler test to compare the dispersion of the directions of the ants at each time interval suggested that the directions become more dispersed as the foraging trip progresses (MWW=23.06, df=14, $p<0.07$).

iii/ variation in size of direction changes with time.

A Friedman analysis of variance by ranks comparing the size of direction changes of the same seven ants between the given time intervals found that there was no significant difference in the sizes of the direction changes between different time intervals (X=5.0357, df=7, n.s.).

8.4 FORAGING MOVEMENTS IN THE FIELD.

The movements of many foragers were followed from their nests in the rosebeds at Wrotham. However, some of these ants were followed for less than 2.30 minutes, i.e. for less than five 30 second fixes. Such short paths were not used in further analysis as they did not provide enough data for circular statistics.

In 1985 a total of 103 trails of more than 2.30 minutes were recorded from two nests (65 and 38 respectively); in 1986 146 such trails were recorded from seven nests (37, 47, 25, 19, 5, 8 and 5 respectively).

In some cases the ant`s foraging movements were followed from the moment it left the nest, right through its entire foraging run, until it returned to the nest. In other cases the ants' trails were followed from they left the nest until they reached and began to climb a plant which carried tended aphids. Ihe paths were not followed up the plants although casual observations revealed that the ants did indeed go on to collect honeydew from the aphids. It was observed that most ants would spend upwards of five minutes in and around the aphid cluster. The foraging paths of other ants were followed carefully from the nest but the forager was lost after a period of time. The most common causes of losing ants were if the ant moved into a hole in the soil, moved behind a piece of vegetation, met with other ants, or if the observer was distracted or had to move in order to continue observation or lost concentration. The numbers (and percentages) of trails falling into each of these major categories are given in Table 8.38.

The total duration of these recorded foraging trails was variable as is seen in Table 8.39. The majority of recordings were of five minutes or less although a few did extend for more than ten minutes. One ant was recorded for 53 minutes (from Nest One on September 20, 1985):- it moved for the first 13 minutes but thereafter it remained stationary with its head in a hole in the ground. After 20 minutes observation its position waas checked every few minutes. It did eventually move away again but only after this extended time period had

GROUP	ROUND-TRIPS TOTAL	SUCCESS	APHID-TENDERS	LOST	TOTAL
1985	12 (12%)	1 (1%)	33 (32%)	59 (57%)	103
NEST ONE	9 (14%)		14 (22%)	43 (66%)	65
NEST TWO	3 (8%)		19 (50%)	16 (42%)	38
1986	16 (13%)	3 (2%)	45 (31%)	82 (56%)	146
NEST ONE	4 (11%)	0	12 (32%)	21 (57%)	37
NEST TWO	7 (15%)	0	16 (34%)	24 (51%)	47
NEST THREE	2 (8%)	2 (8%)	6 (24%)	15 (60%)	25
NEST FOUR	1 (11%)	1 (1%)	6 (32%)	10 (53%)	19
NEST FIVE	1 (20%)	1 (20%)	3 (60%)	1 (10%)	5
NEST SIX	0		2 (25%)	6 (75%)	8
NEST SEVEN	0		0	5 (100%)	5

Table 8.38. The numbers and proportions of foraging trails which were followed for complete round trips (total and successful), or until the ant encountered a aphid-bearing plant, or was lost. - the trail of one ant was followed until it met another forager and got involved in a fight with it.

DURATION OF FORAGING TRIPS

MINS	1985 ONE	1985 TWO	1986 ONE	1986 TWO	1986 THREE	1986 FOUR	1986 FIVE	1986 SIX	1986 SEVEN
<2.00			1	1	1			1	1
2.00	1	2			2	3		2	
2.30	1	□□5		□11	3	3		1	1
3.00	□3	2	7	9	□5		1	2	1
3.30	8	11	6	□9	□4	3		1	
4.00	□6	2	5	5	1	□3		1	2
4.30	□6	□5	1	2	1	3	□3		
5.00	□7	1	3	4	2	□2			
5.30	6	□3	7	1		1			
6.00	2	3	2	1	1				
6.30	3	1	4		□1				
7.00	□2				1				
7.30	1	1	□1		1				
8.00	5						1		
8.30	1								
9.00	2	1			1				
9.30	□2			1					
10.00	□1								
>10.00	□8	1		3	1				
TOTAL	65	38	37	47	25	18	5	8	5

Table 8.39. Durations of foraging trips followed in the rosebeds at Wrotham Field Centre. □ round trip

elapsed. The distribution of durations of those foraging trails which were recorded throughout from leaving the nest until the ants return are also displayed in Table 8.39.

8.4.1 INDIVIDUAL TRAILS.

Examples of the trails followed in the field are given in Figure 8.25. The movements of each ant between fixes was characterised by a "mean movement vector" which summarizes the "movelength" (as a mean movelength and its standard deviation) and "directionality" (the mean movedirection, its angular deviation, and a "clumping index" which indicates whether the sample directions are significantly clumped) of each foragers movements. The mean movement vector of each ant is presented in Appendix 5.

a/ mean movelength.

The mean movelengths of all the ants are presented in Figure 8.26(a-g). The mean movelength of the 2271 30 second steps followed from 249 foragers was 14.58cm. No standard deviation was calculated for this sample (as data was analysed by separate computer programs in each year). In 1985 the mean movelength was 15.04cm +/- 7.37 (1067 steps) while in 1986 the mean movelength was 14.18 +/-10.08 (1204 steps). It was noted that in some cases the standard deviation of the movelengths of individual ants was greater than the mean movelength. Such large deviations were found for ants which remained stationary for a large portion of their foraging trip and hence many movelengths of zero were introduced into the sample.

b/ directionality.

The directionality of each of the ants is also presented in Appendix 5 and in Figure 8.27. For 56.2% of the ants the distribution of sample movedirections showed significant clumping (Rayleigh tests, $p<0.05$ at least). That is to say that over half of the ants travelled consistently in the same direction between fixes during its foraging trip.

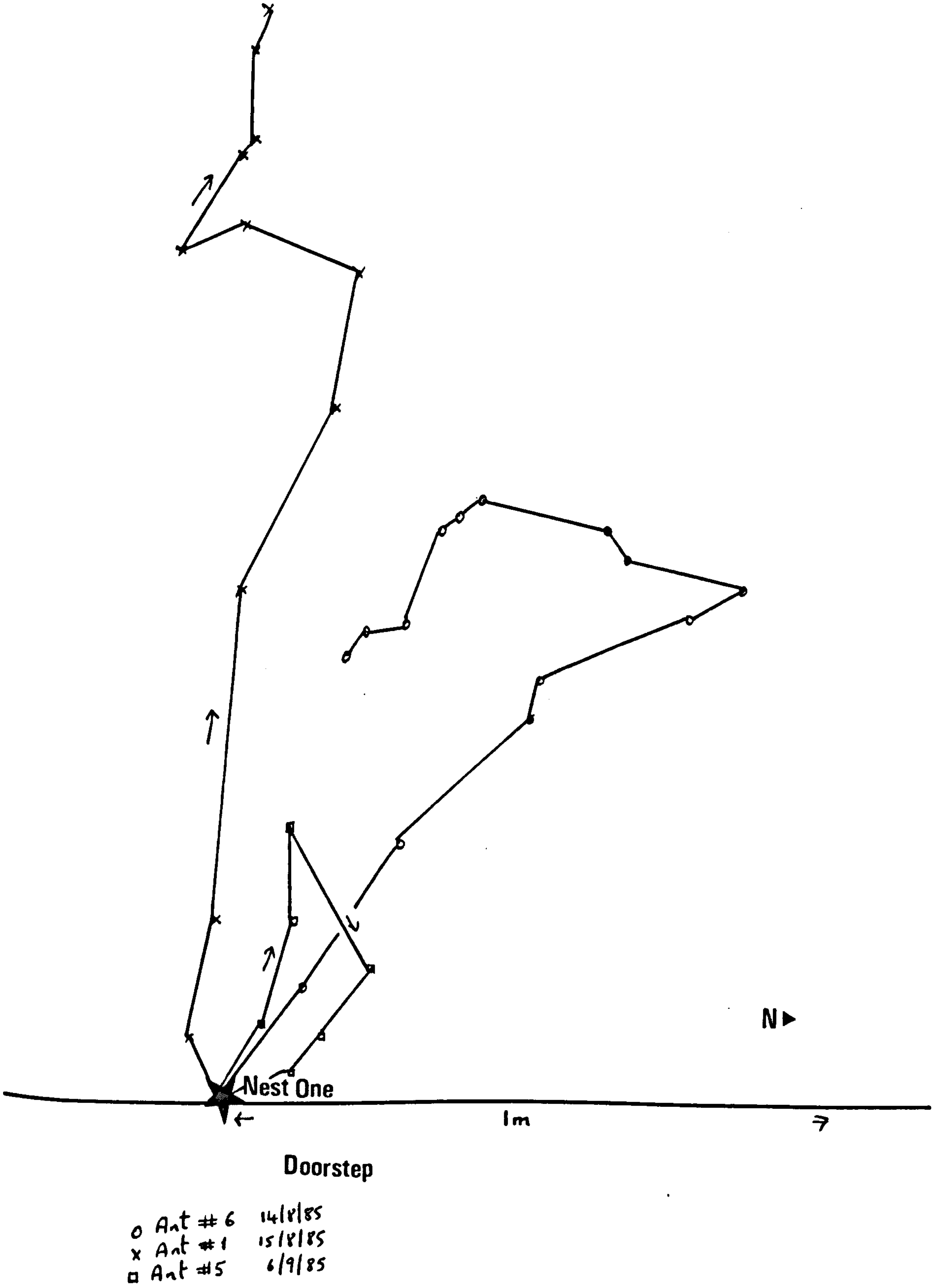


Figure 8.25. Example of path of individual foragers followed in field at Wrotham.

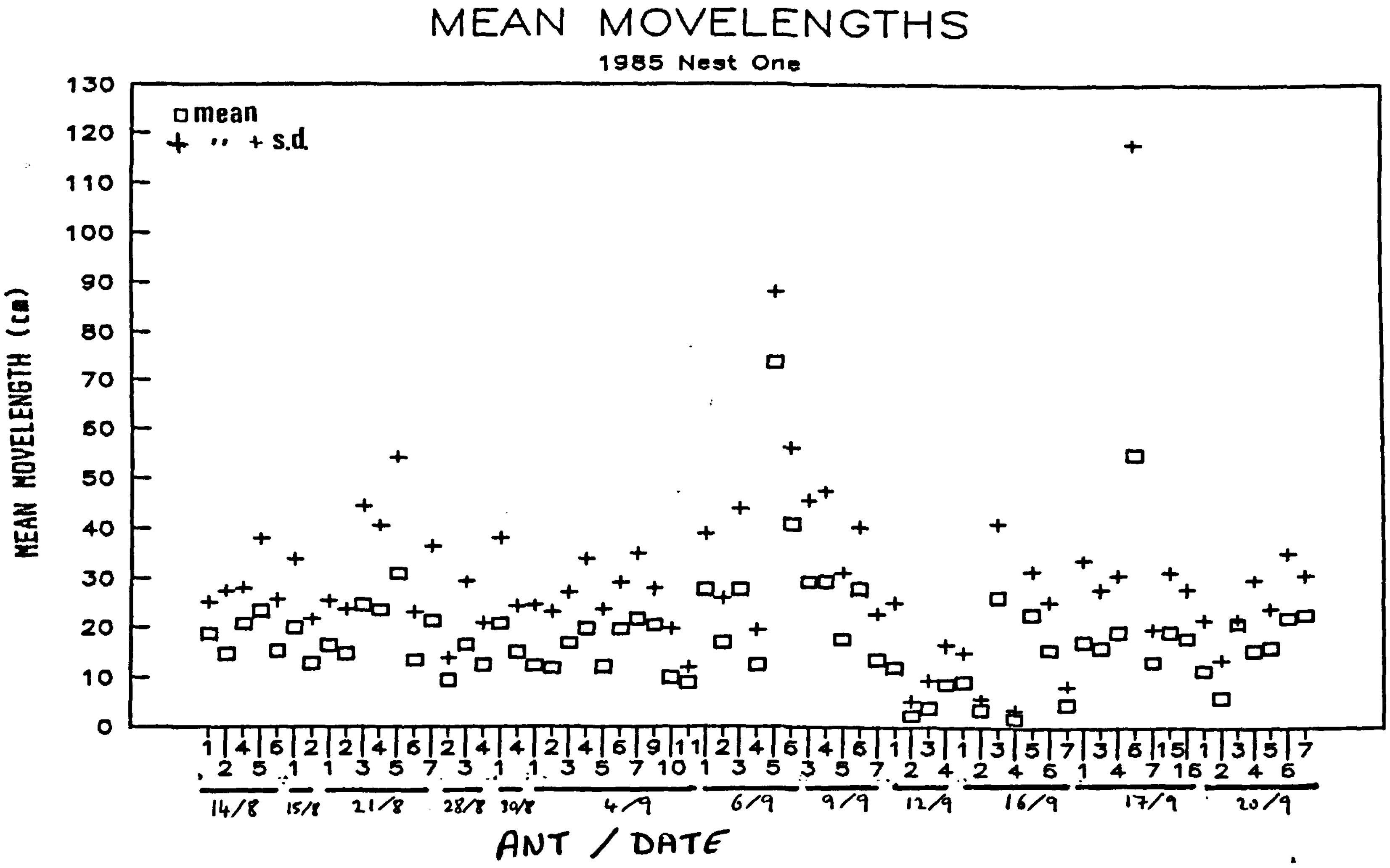


Figure 8.26. Mean movelengths of ants followed in field at Wrotham.

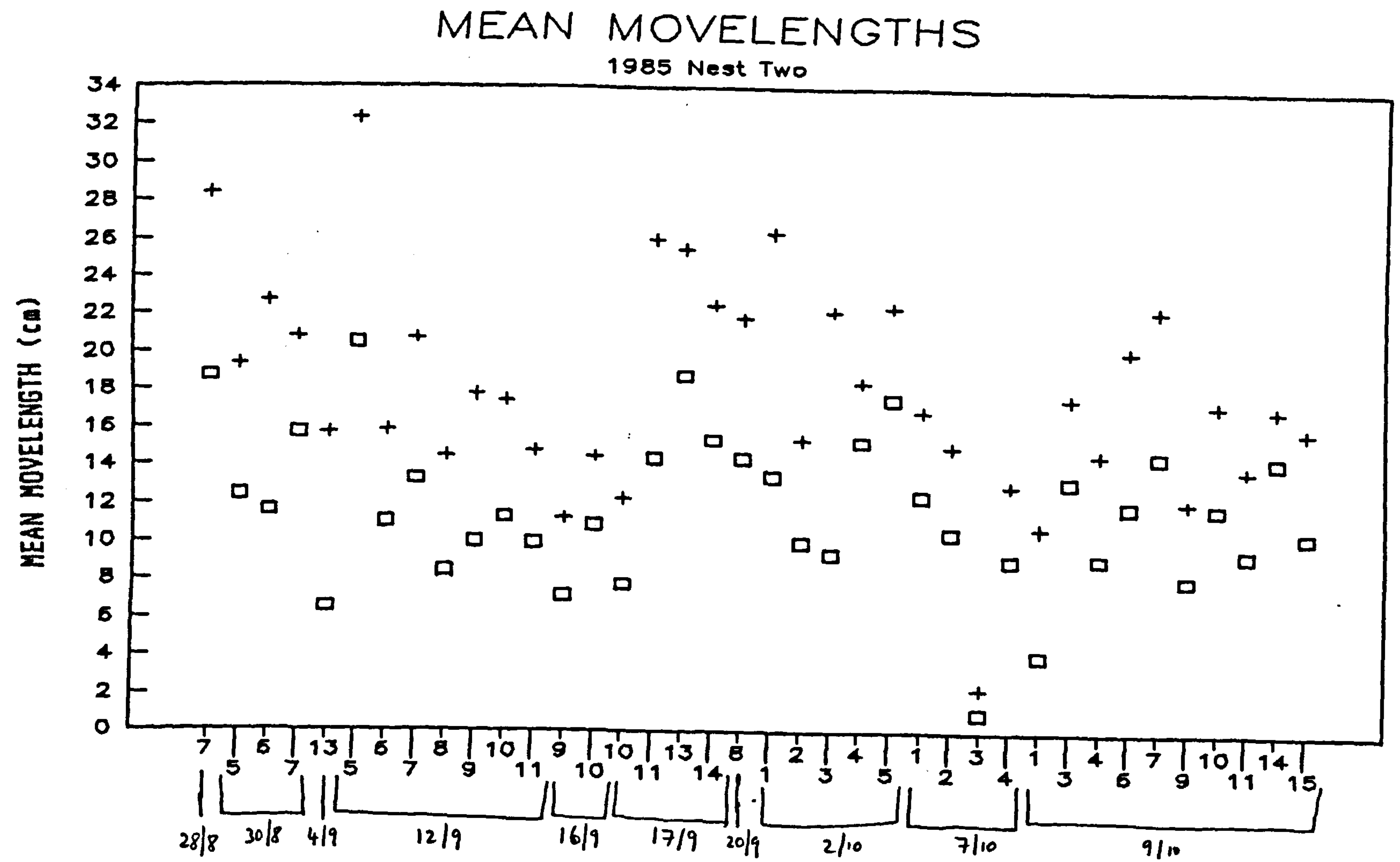
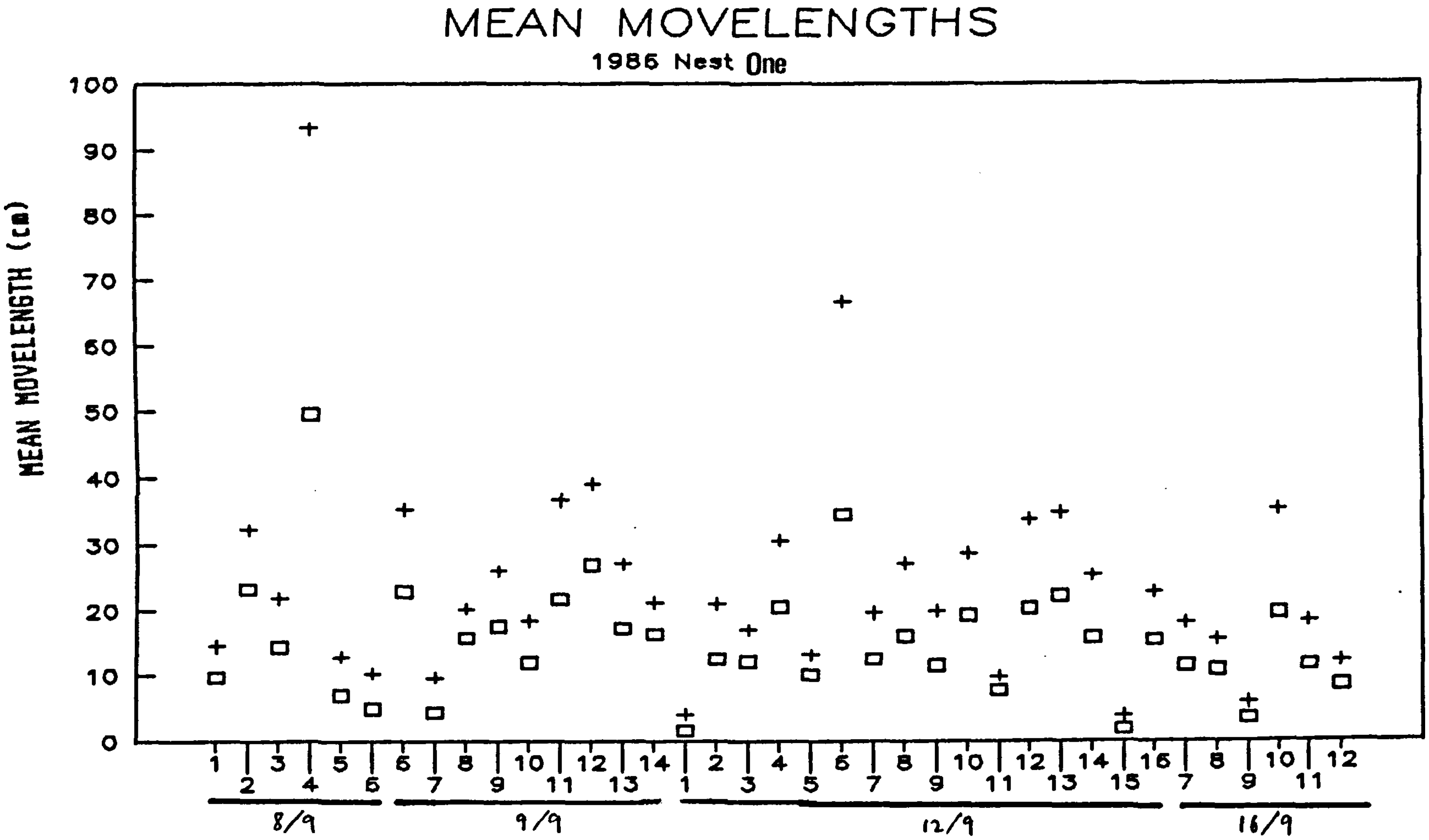


Figure 8.26 (cont.)



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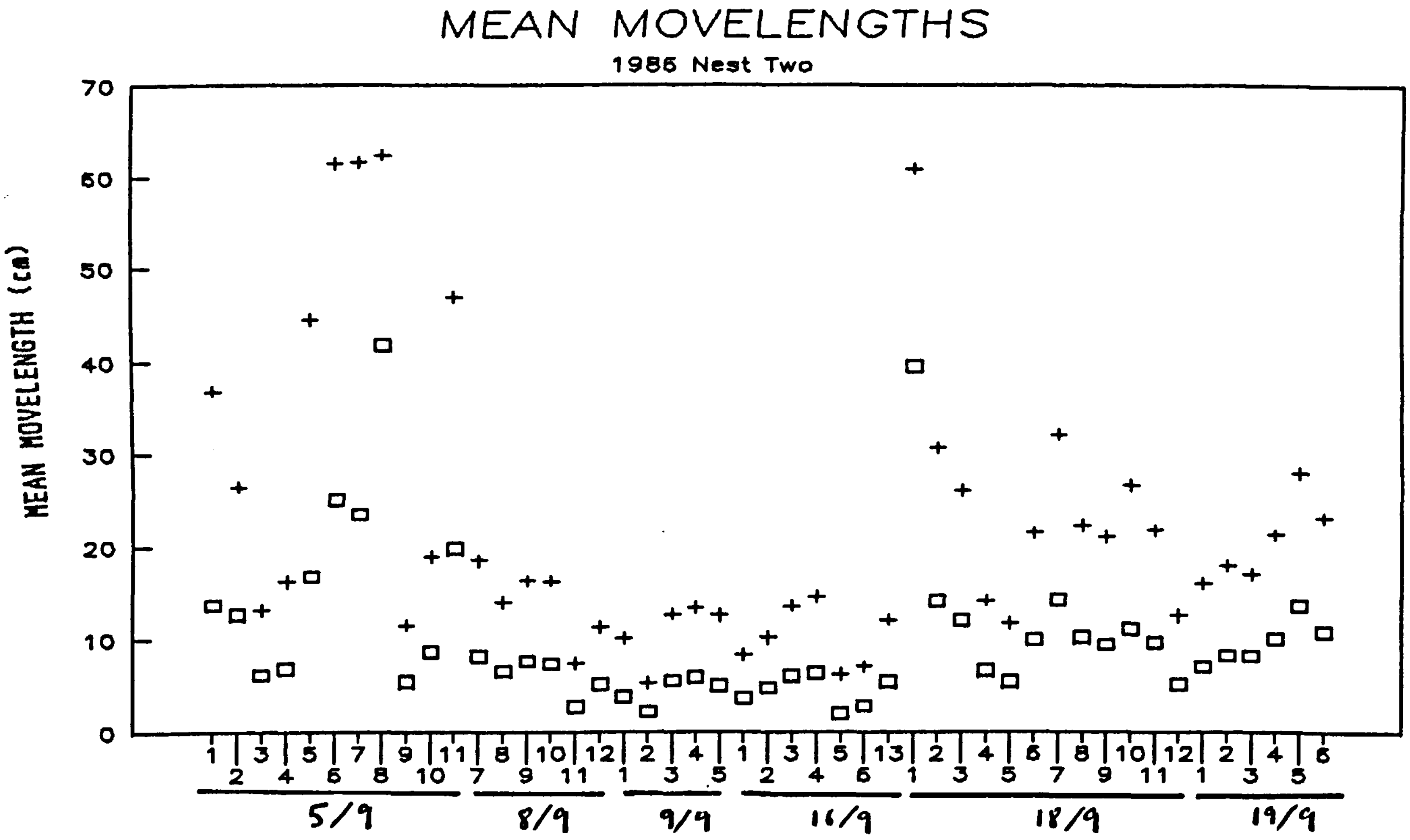

Figure 8.26 (cont.)

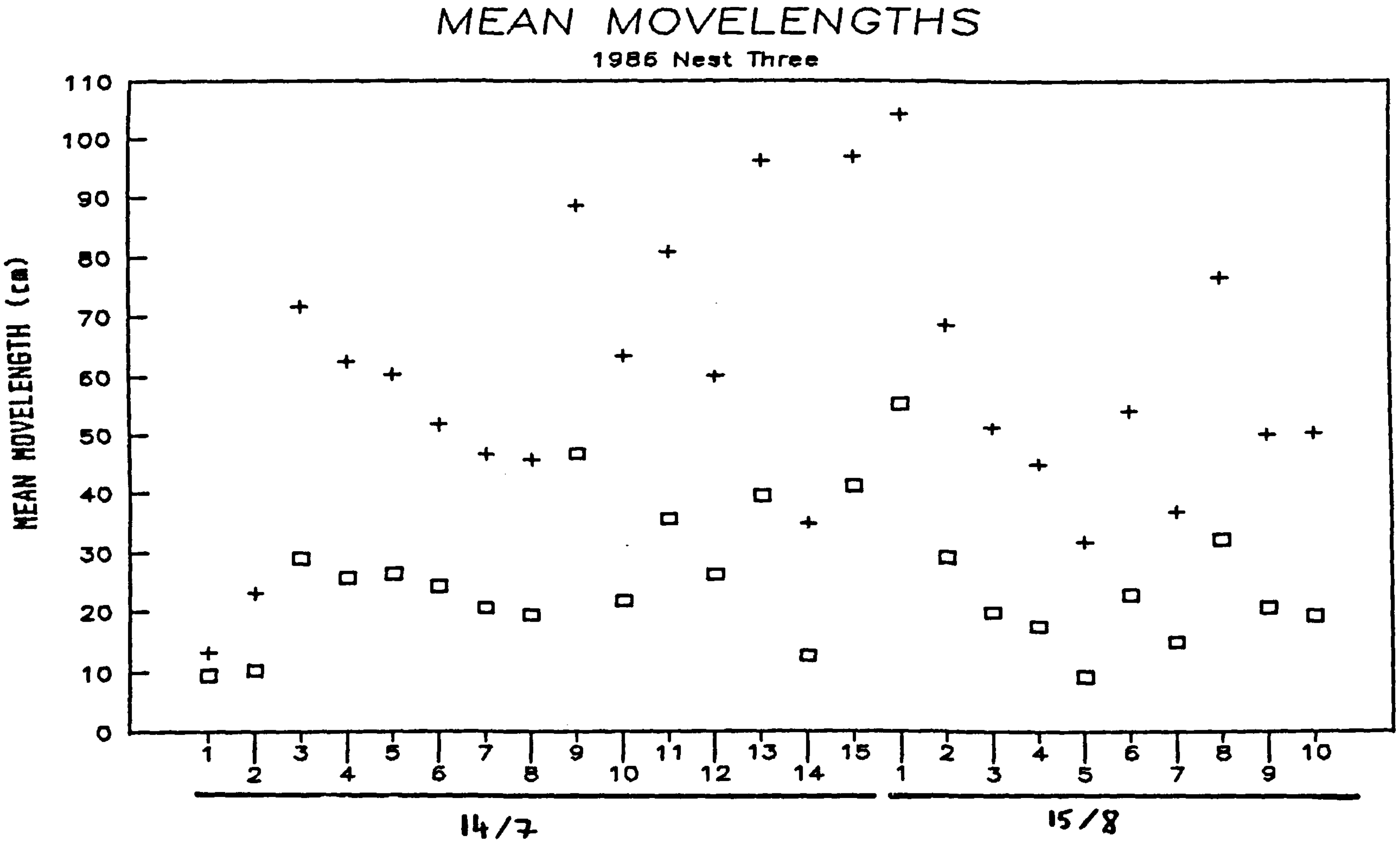

Figure 8.26 (cont.)

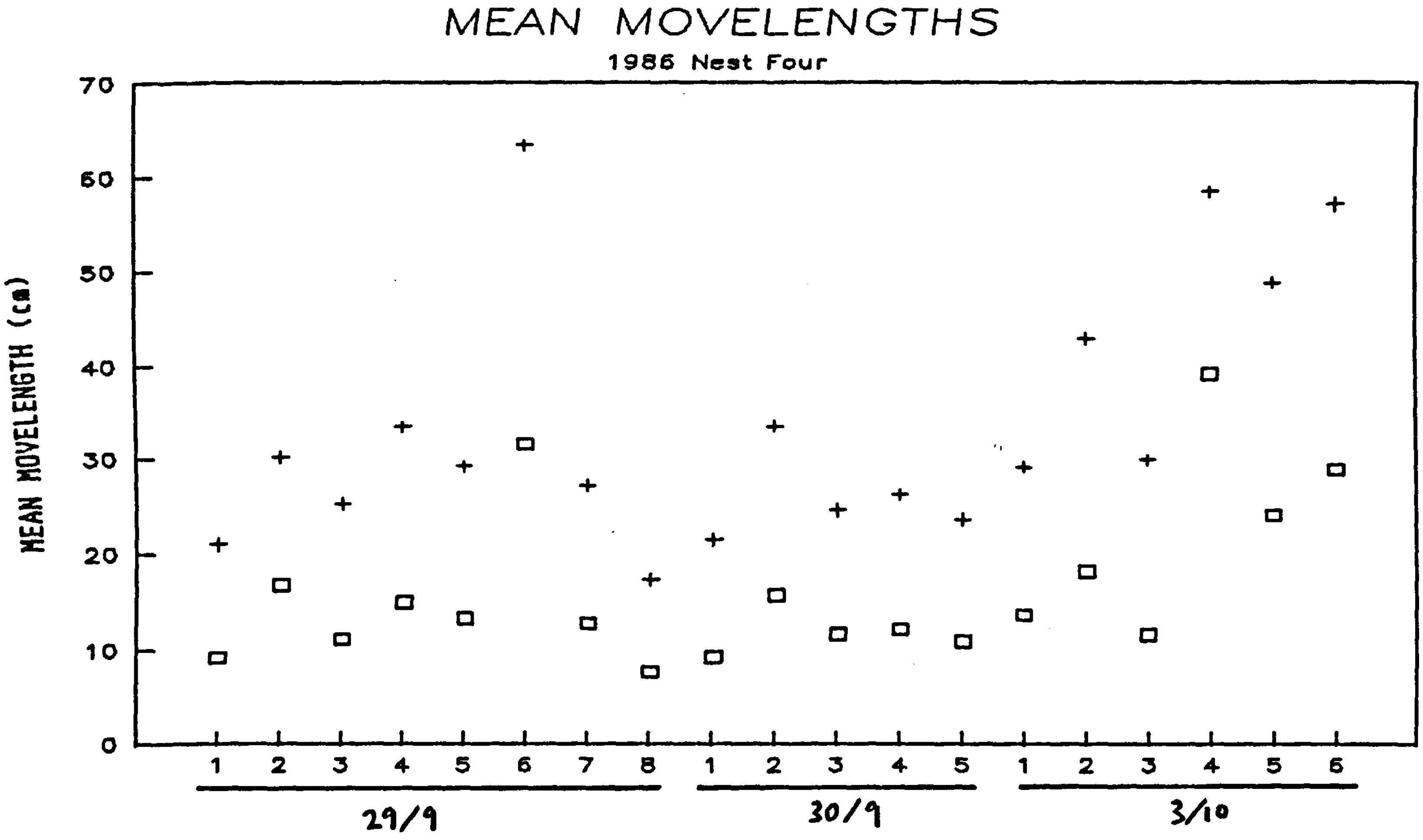

Figure 8.26 (cont.)

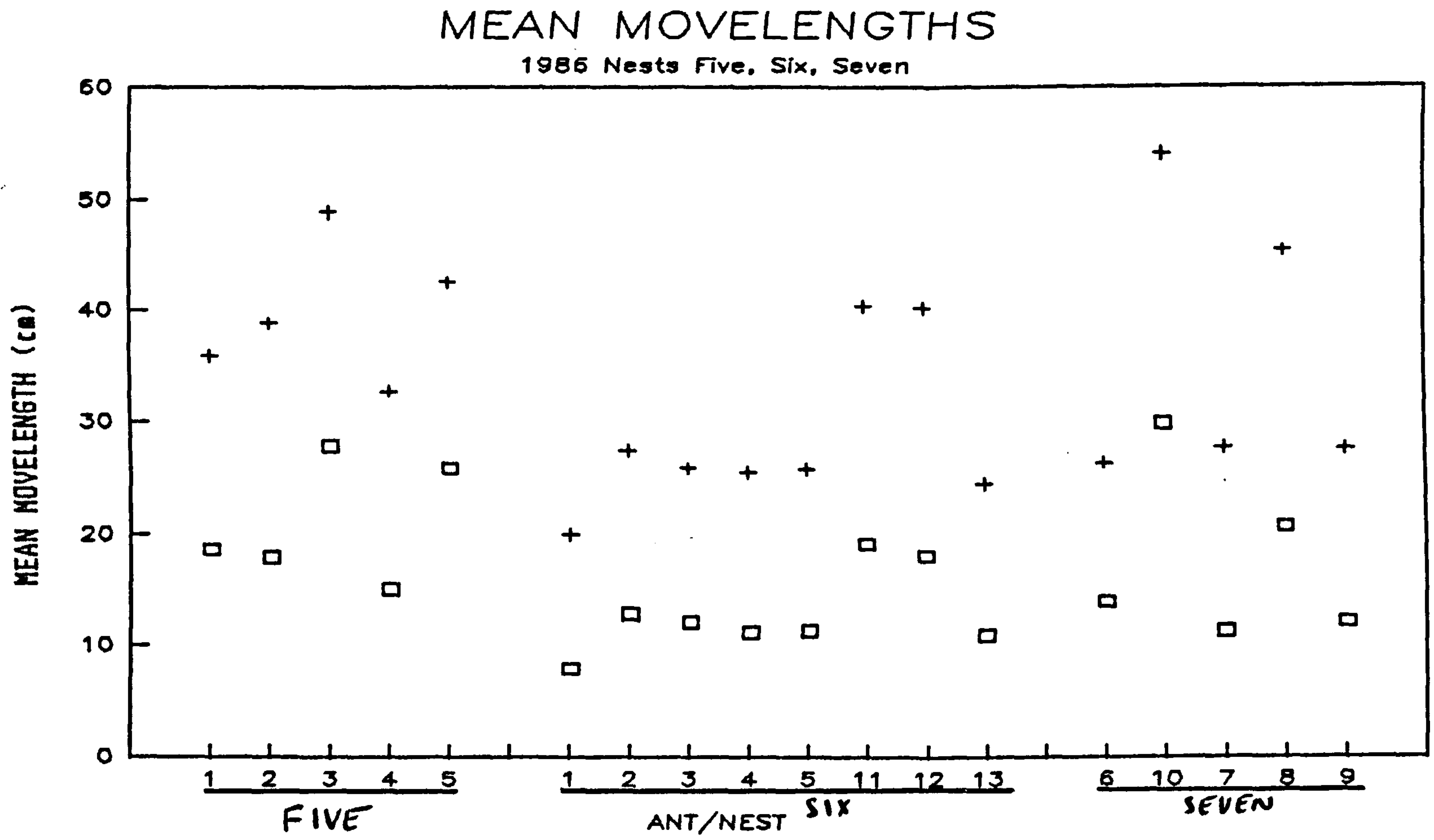

Figure 8.26 (cont.)

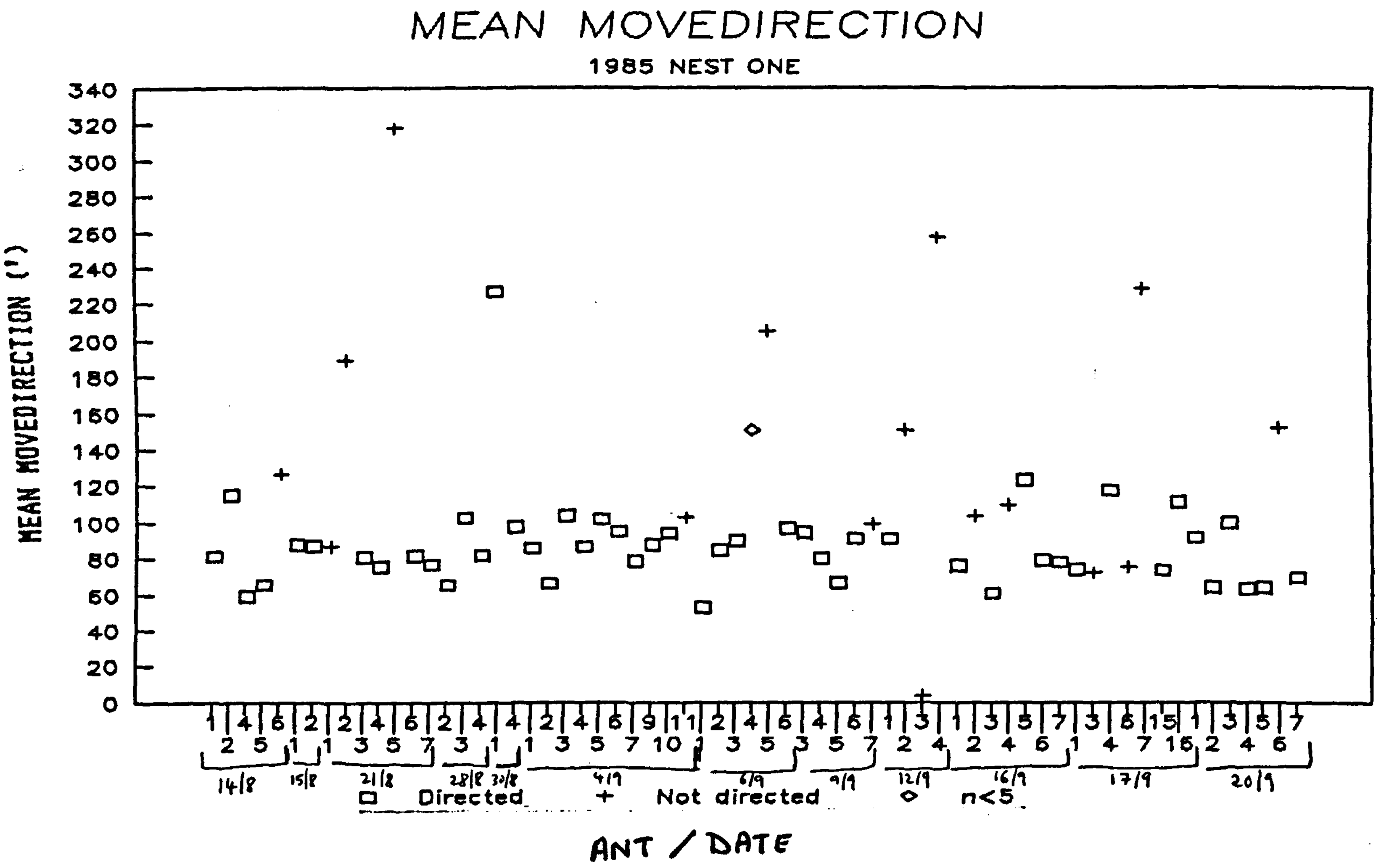

Figure 8.27. Mean movedirections of ants followed in field at Wrotham.
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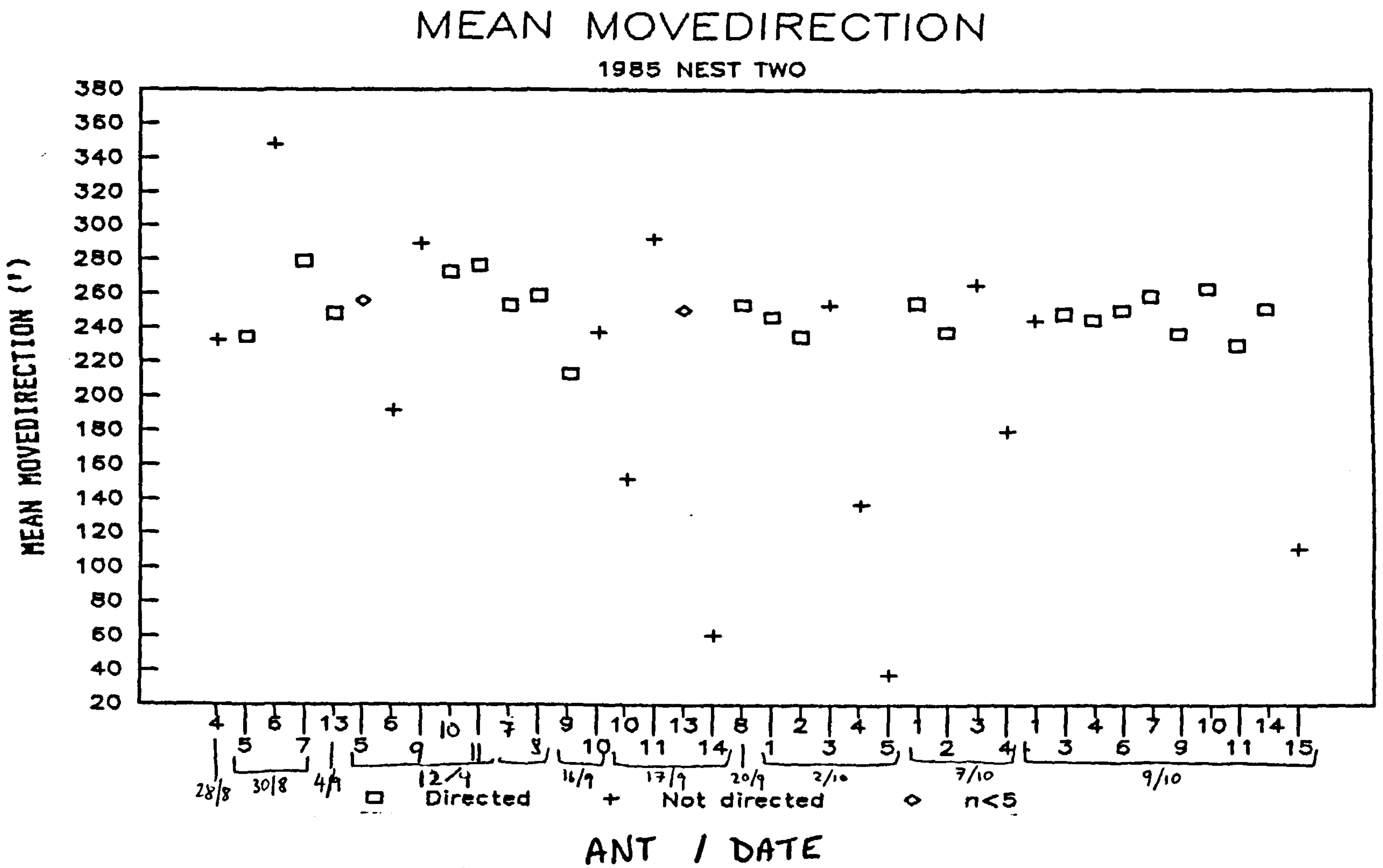


Figure 8.27 (cont.)

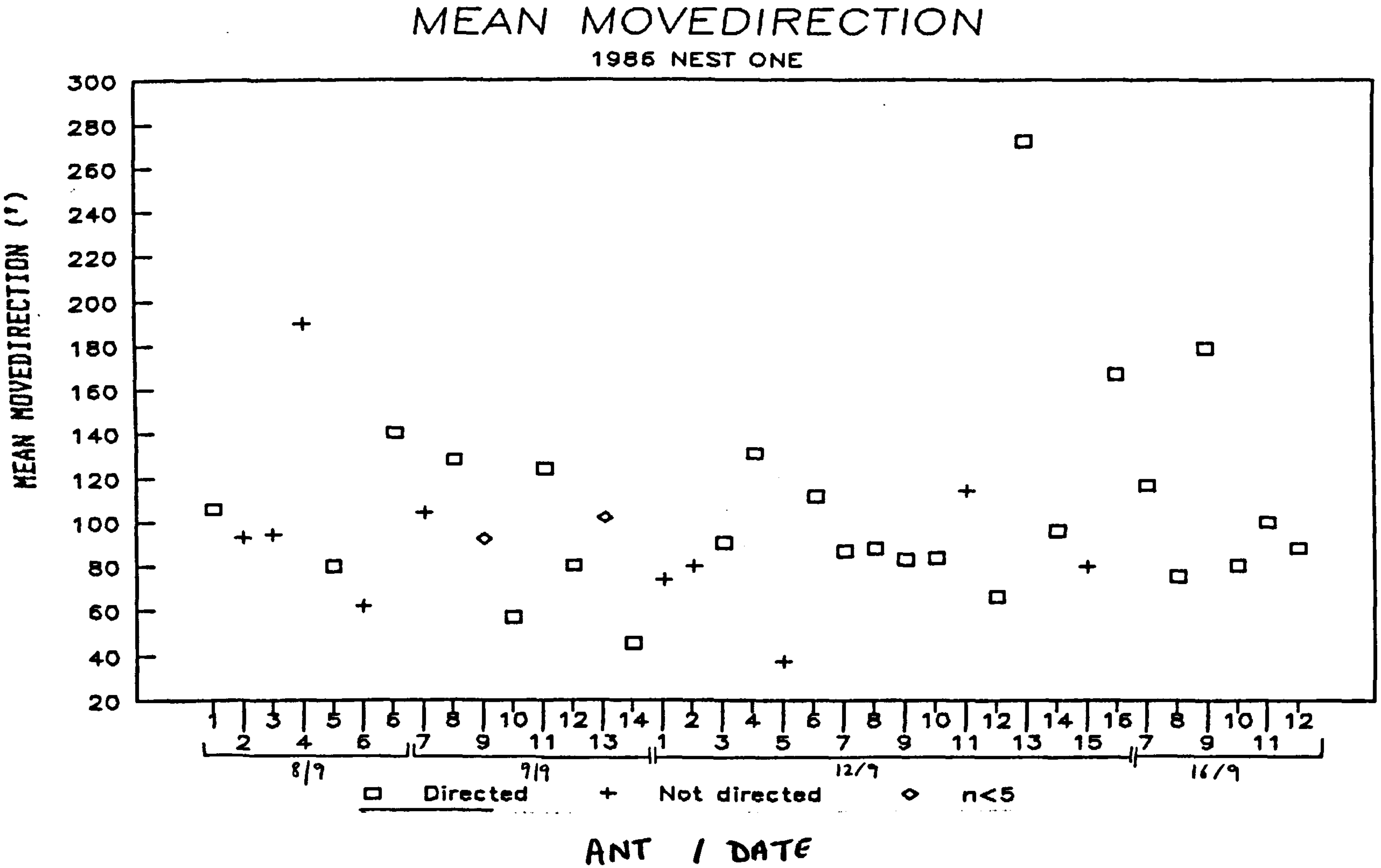


Figure 8.27 (continued)

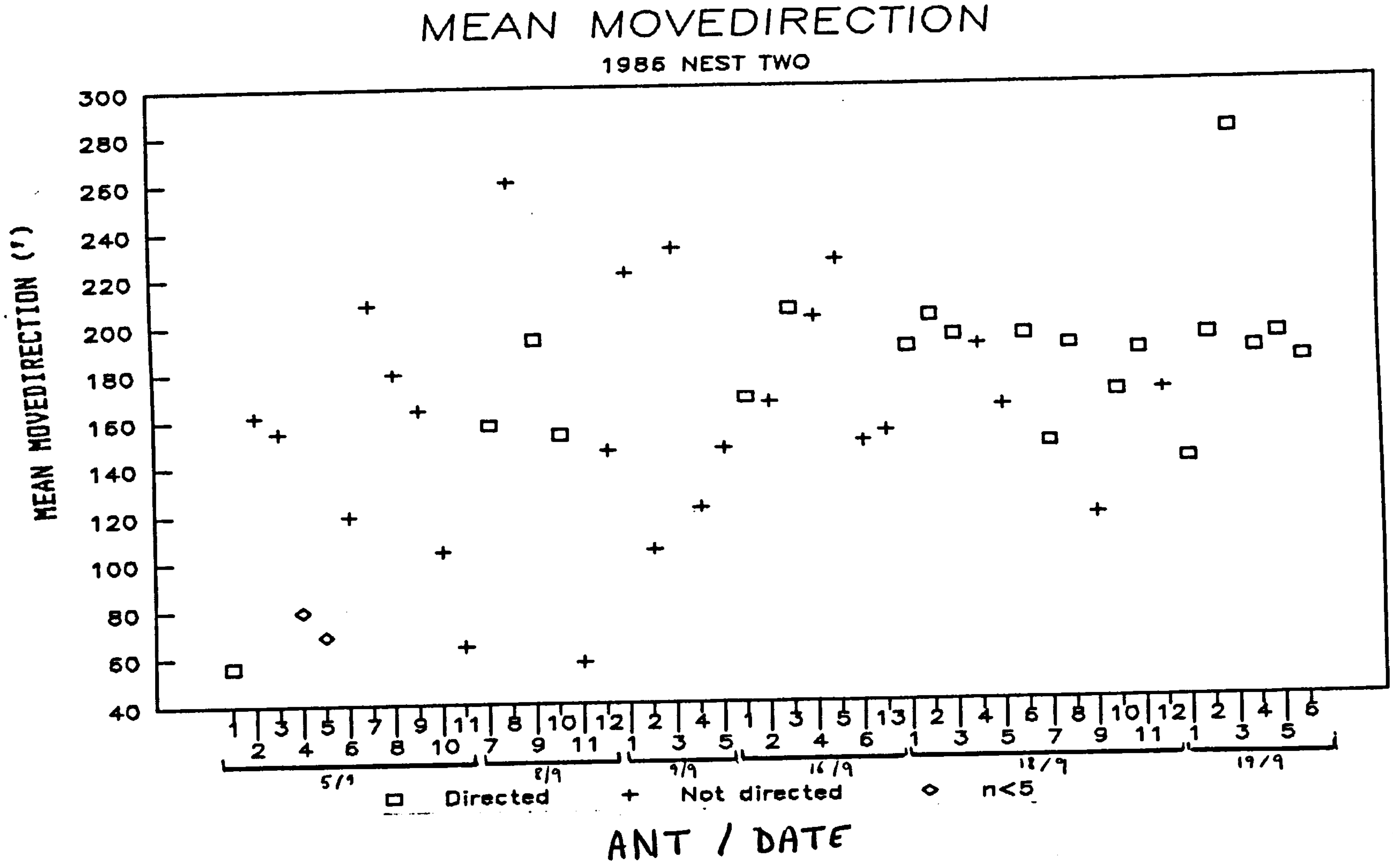


Figure 8.27 (conti

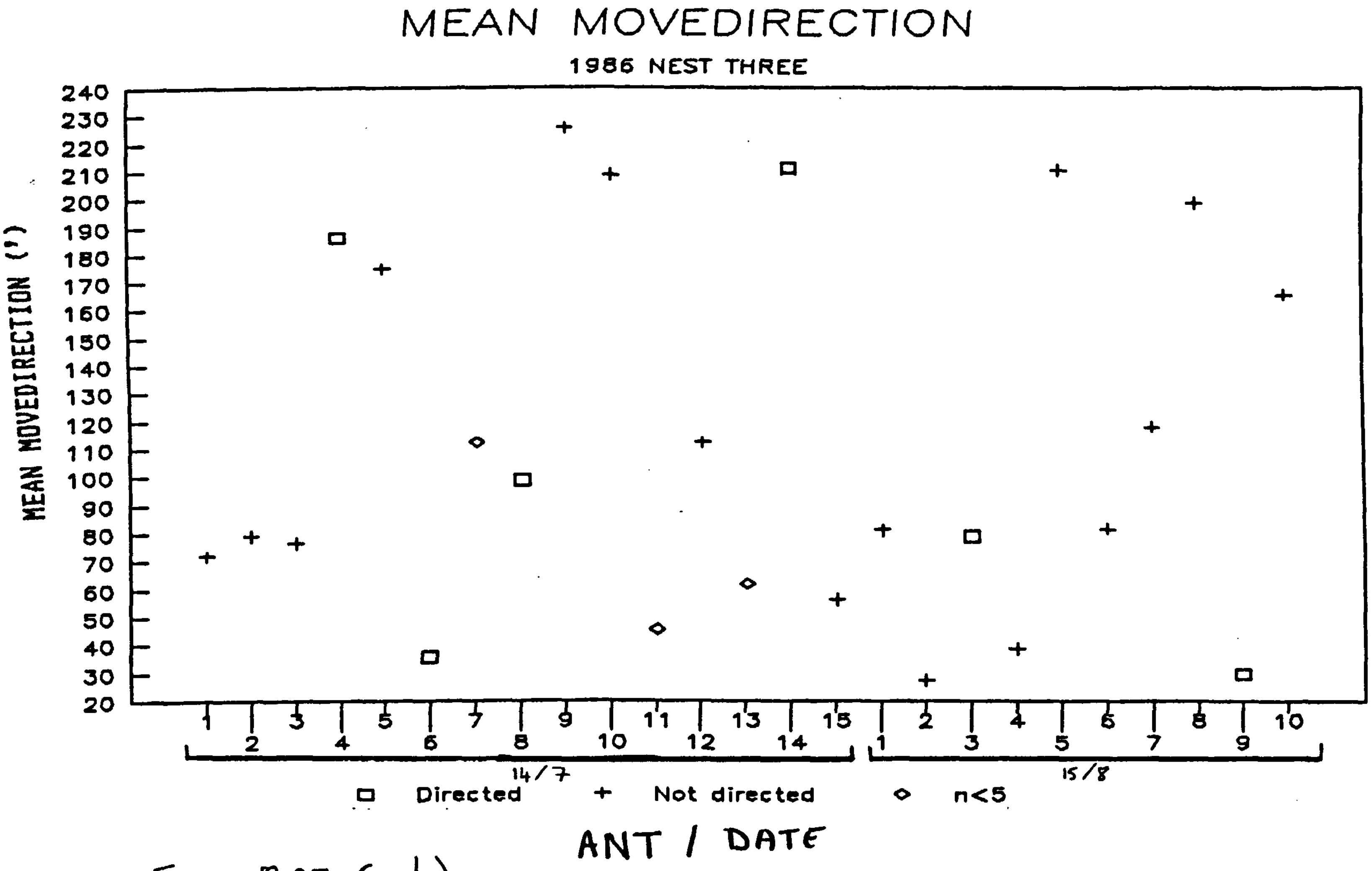


Figure 8.27 (cont.)

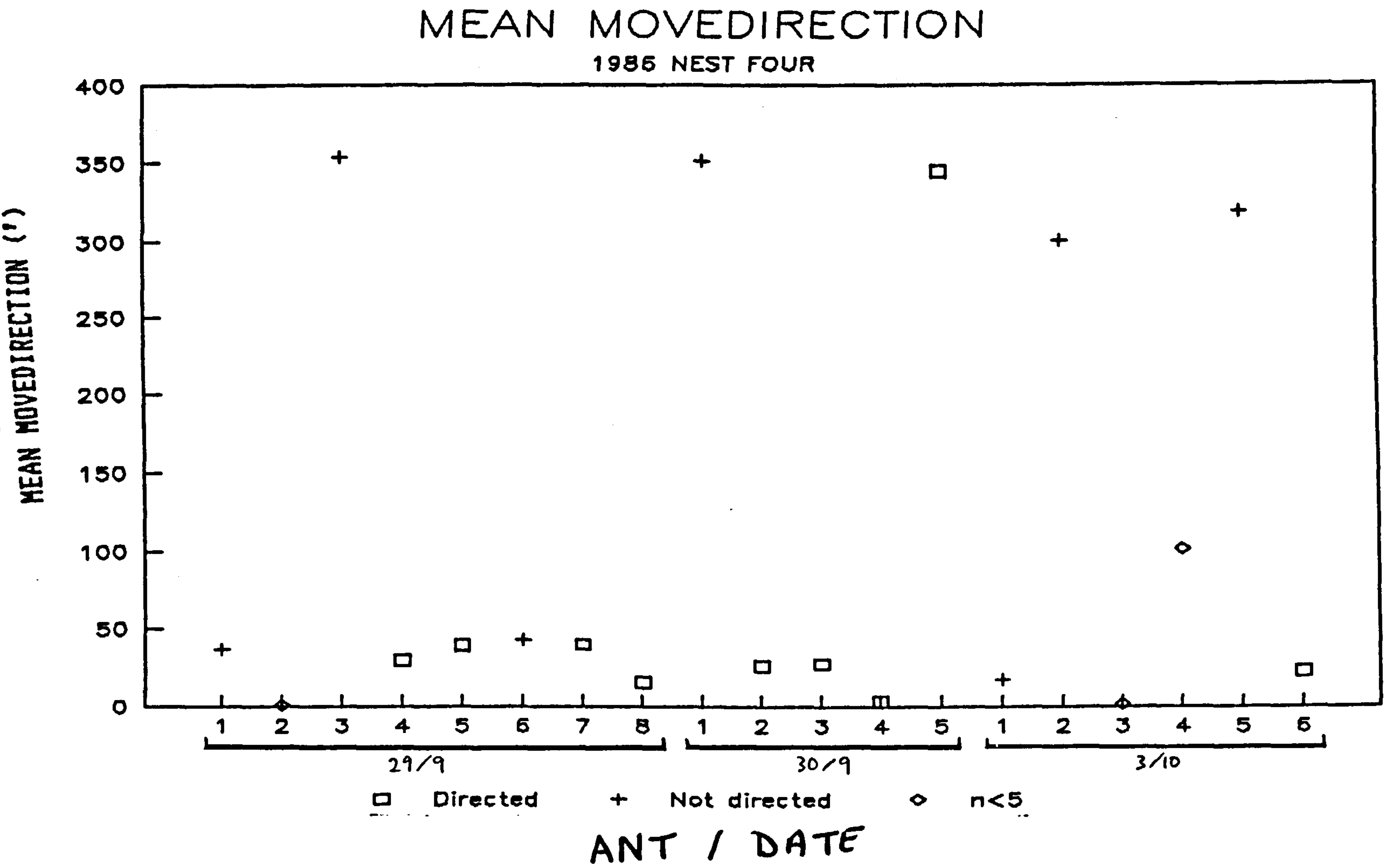


Figure 8.27 (cont.)

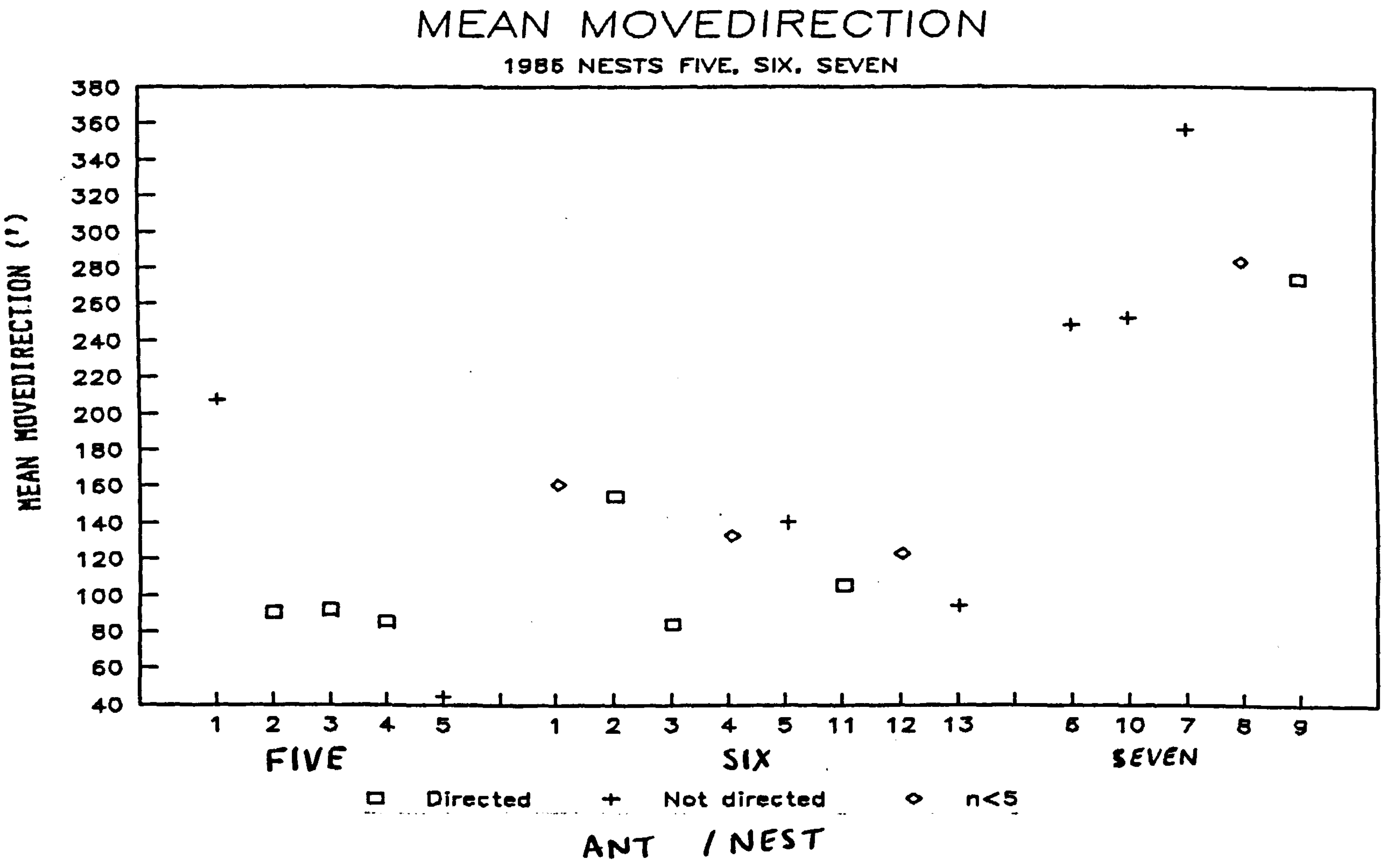


Figure 8.27 (cont.)

The proportion of ants which showed such significant clumping of sample movedirections varied between nests. For the two nests of 1985 52 out of 65, and 21 out of 38 ants travelled consistently in the same direction (80% and 55% respectively). For the seven nests of 1986 there occured 25 out of 37, 20 out of 47, 6 out of 25, 9 out of 19, 3 out of 5, 3 out of 8, and 1 out of 5 ants which were significantly clumped corresponding to 68%, 43%, 24%, 47%, 60%, 37.5% and 20% respectively. The remainder could not be said to have a prefered direction of travel.

8.4.1.1 CHANGES IN INDIVIDUALS' TRAILS OVER TIME.

Analyses were performed to investigate whether the movement parameters of the mean movement vector changed as the foraging trip progressed.

a/ movelength.

The movelengths of ants after various periods of time had elapsed are summarized in Figure 8.28. For seven of the eight nests tested there were no significant differences in movelength between the time intervals. These analyses of variance results are summarized in Table 8.40. There was a significant difference for Nest One in 1985 with ants moving shorter distances between fixes later in their foraging runs.

b/ directionality.

The directions in which the ants were travelling at various times into their foraging runs were compared. The distribution of movedirections at various time intervals are presented for each nest in Figure 8.29. Nests Five, Six and Seven of 1986 were excluded from analysis here because of their small sample sizes.

There were no significant differences in the distributions of movedirections of the ants at different time intervals. The appropriate analyses comparing these distributions are summarized in Table 8.41.

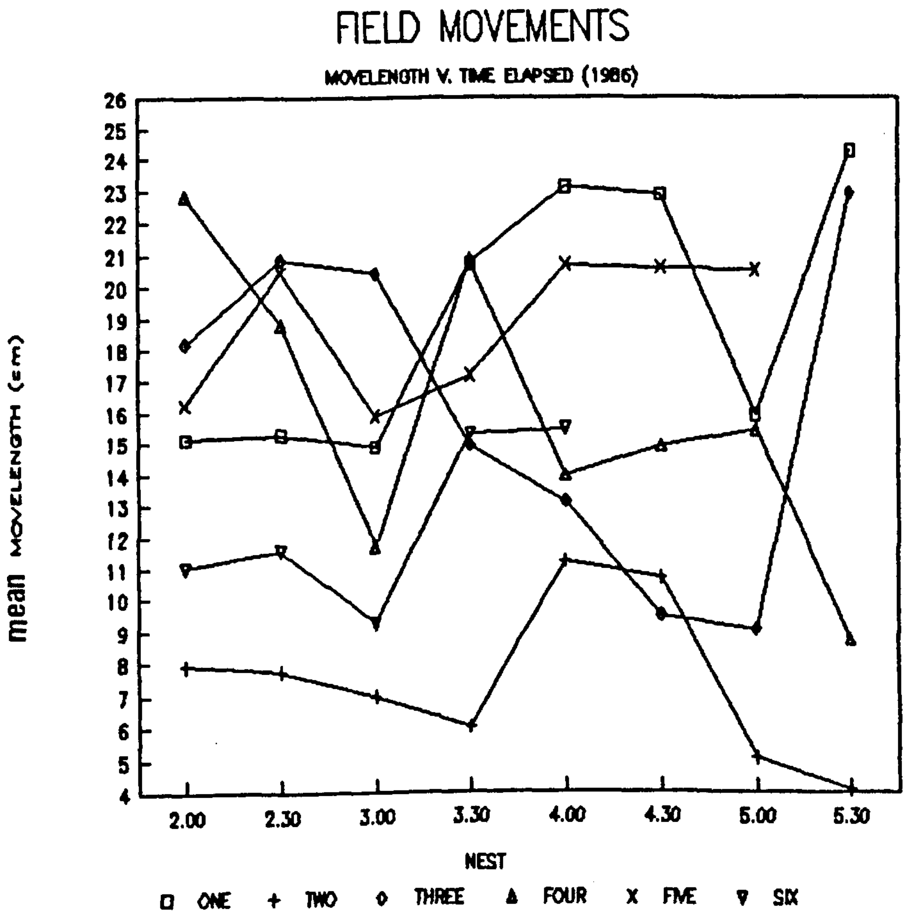


Figure 8.28. Change in movelength with time of foragers in the field.

NEST	NO. INTERVALS	F	df	SIGN.
1985 ONE	3 (1,2,3 mins)	4.6028	2, 98	p<0.025
1985 TWO	3 (1,2,3 mins)	1.6219	2, 23	n.s.
1986 ONE	8 (2.00-5.30)	1.1284	7,194	n.s.
ditto	3 (2.00-5.00)	1.154	2, 78	n.s.
1986 TWO	8 (2.00-5.30)	0.3308	7,222	n.s.
ditto	3 (2.00-5.00)	2.7269	2, 92	p<0.2
1986	8 (2.00-5.30)	0.7637	7,121	n.s.
ditto	3 (2.00-5.00)	0.8997	2, 50	n.s.
1986 FOUR	8 (2.00-5.30)	1.0542	7,103	n.s.
ditto	3 (2.00-5.00)	0.3715	2, 41	n.s.
1986 FIVE	7 (2.00-5.00)	0.0063	6, 25	n.s.
1986 SIX	5 (2.00-4.00)	1.961	4, 21	p<0.2
1986 SEVEN		NO TEST		

Table 8.40. Summary of analyses of variance tests to compare movelengths made at different times in to the foraging trip.

NEST	TEST STATISTIC	DF	PROB.
1985 ONE	X-sq = 9.31	6	n.s.
1985 TWO	M.W.W. = 1.57	2	n.s.
1986 ONE	X-sq = 7.19	9	n.s.
1986 TWO	X-sq =12.75	9	n.s.
1986 THREE	X-sq = 9.57	9	n.s.
1986 FOUR	X-sq = 3.59	6	n.s.

Table 8.41. Summary of tests to compare the distribution of movedirections of ants at different times into their foraging trips. The main test used was the circular chi-squared test but for Nest Two of 1985 a Mardia-Watson-Wheeler test was used instead. This was because the sample size was too small to allow chi-squared test (expected frequencies must be at least four).

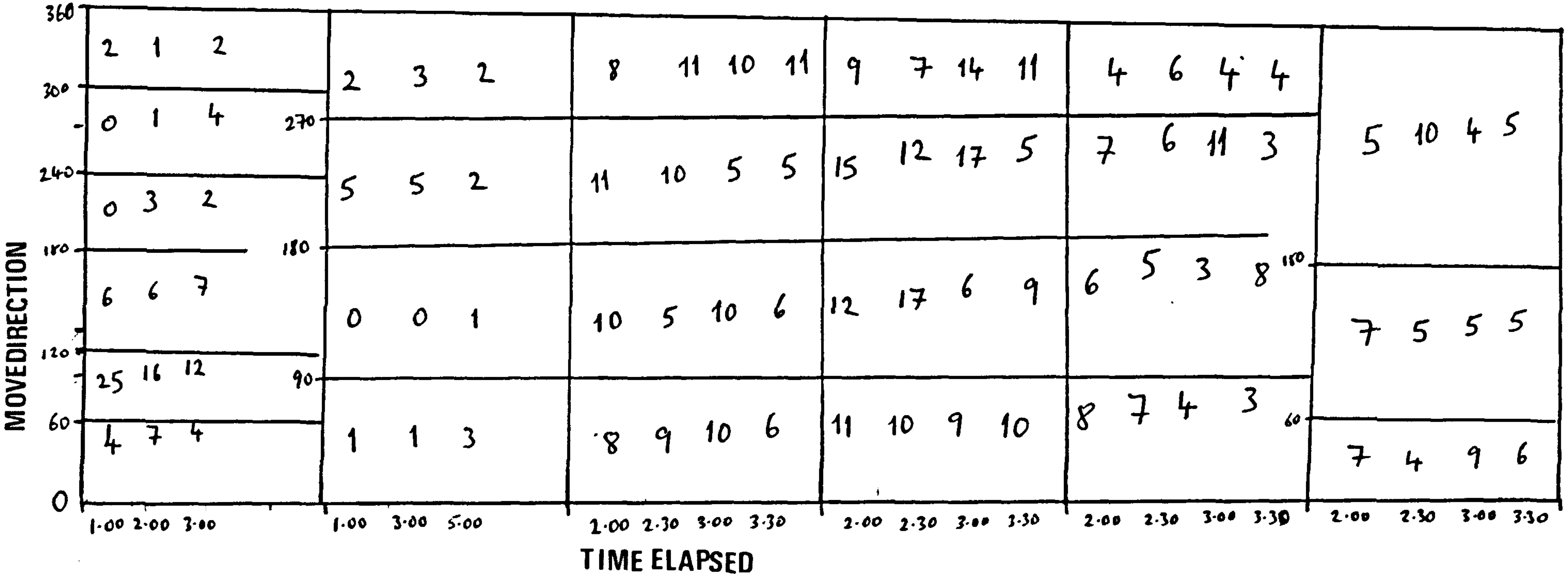


Figure 8.29. Change in directionality with time of foragers trailed in the field.

8.4.1.2 THE AREA COVERED BY FORAGING TRAILS.

The foraging paths of foragers were also used to calculate a "mean position vector" for each forager. This summarizes the distance and bearing of the forager from its nest during its foraging trip. The mean position vector for each ant is presented in Appendix 6.

The data used to calculate the mean distance is not drawn from an independent sample and so cannot be summarized as an arithmetic mean and standard deviation in the normal manner. Yet some indication of the distance from the nest at which foragers search might be obtained from the mean distance, and these are presented, for each ant, in Figure 8.30. However, only non- parametric measures can be used to analyse this data to compare between ants and between groups of ants.

The sample bearings of each forager were found to be significantly clumped around the mean bearing from the nest for all but 9 of the total of 249 foragers ($p<0.05$ at least). Such clumping might be expected because this sample is not an independent one either. This clumping does mean, however, than in all but these nine cases it can be said that the forager concentrates its search in a sector determined by its mean bearing. The mean bearings for each ant are presented in Figure 8.31.

The ants which did not show clumping of their bearings were Ant #6 (12/9/85, Nest Two), Ant #14 (17/9/85, Nest Two), Ant #3 (12/9/86, Nest Two), Ant#3 (16/9/86, Nest Two), Ant #4 (16/9/86, Nest Two), And #9 (14/7/86, Nest Three), Ant #10 (14/7/86, Nest Three), Ant #1 (29/9/86, Nest Four) and Ant #1 (30/9/86, Nest Four).

It is noticable that many of the ants which showed no significant clumping were found closer to the nest and had shorter mean distances than other foragers from that nest on that day. This is true in at least 6 of the 9 cases where no clumping was found. The mean distances from the nest were 9.54cm, 16.55cm, 4.45cm, 19.21cm, 19.7cm, 41.84cm, 55.77cm, 20.37cm, 26.13cm respectively.

8.4.2 VARIATION BETWEEN ANTS.

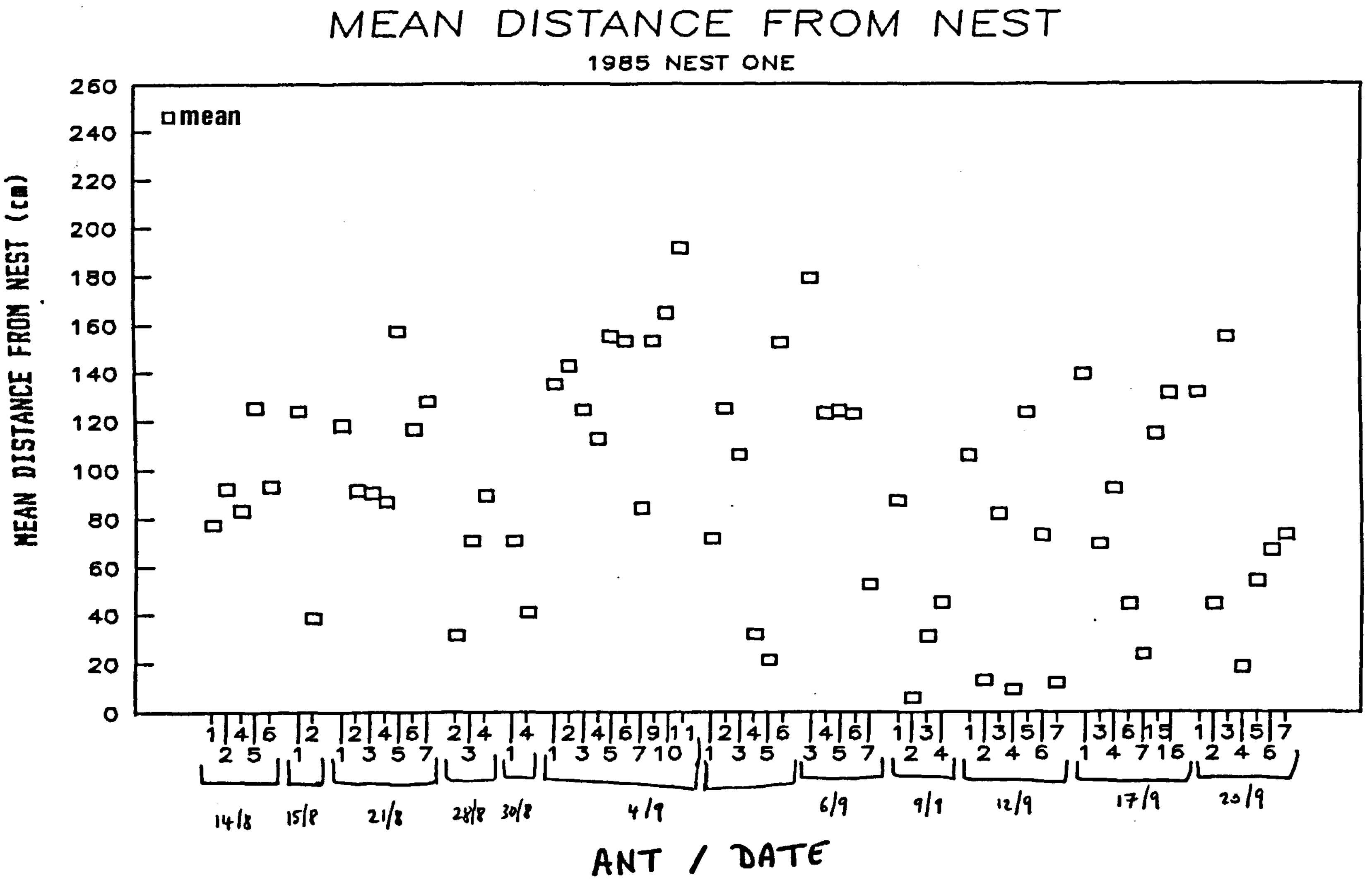


Figure 8.30. Mean distance from the nest of foragers during their forays in the field at Wrotham.

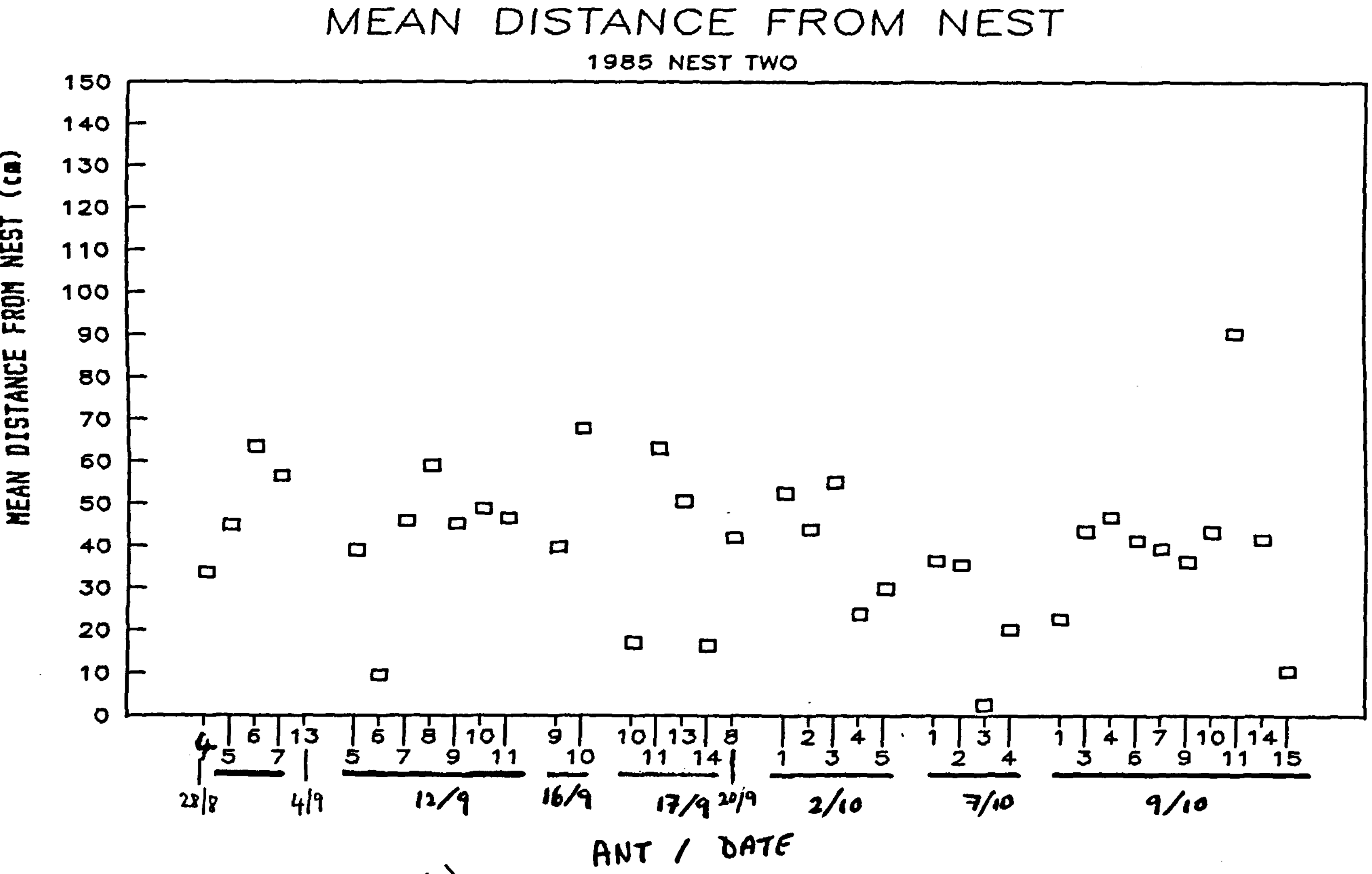
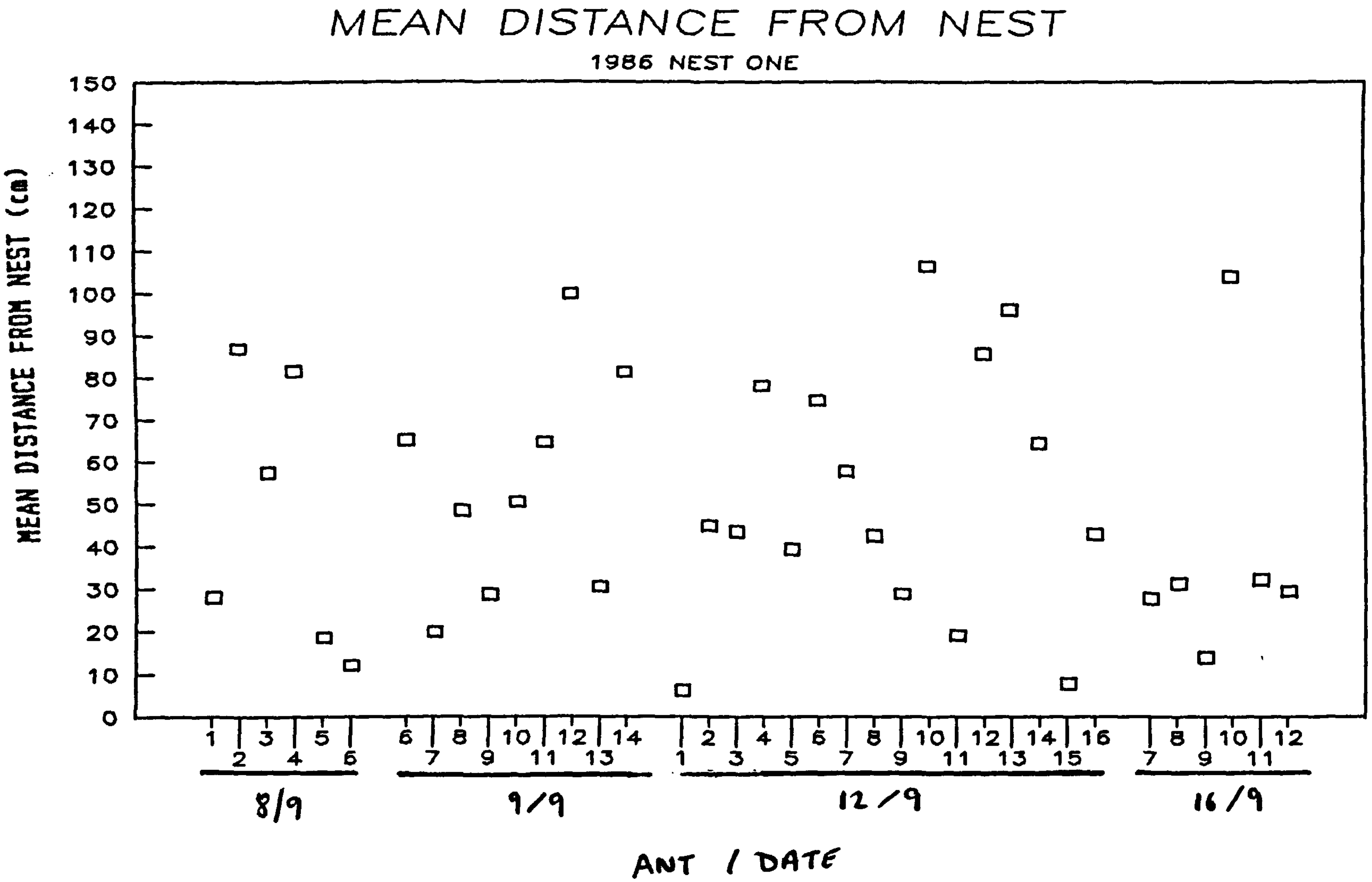


Figure 8.30 (cont.)



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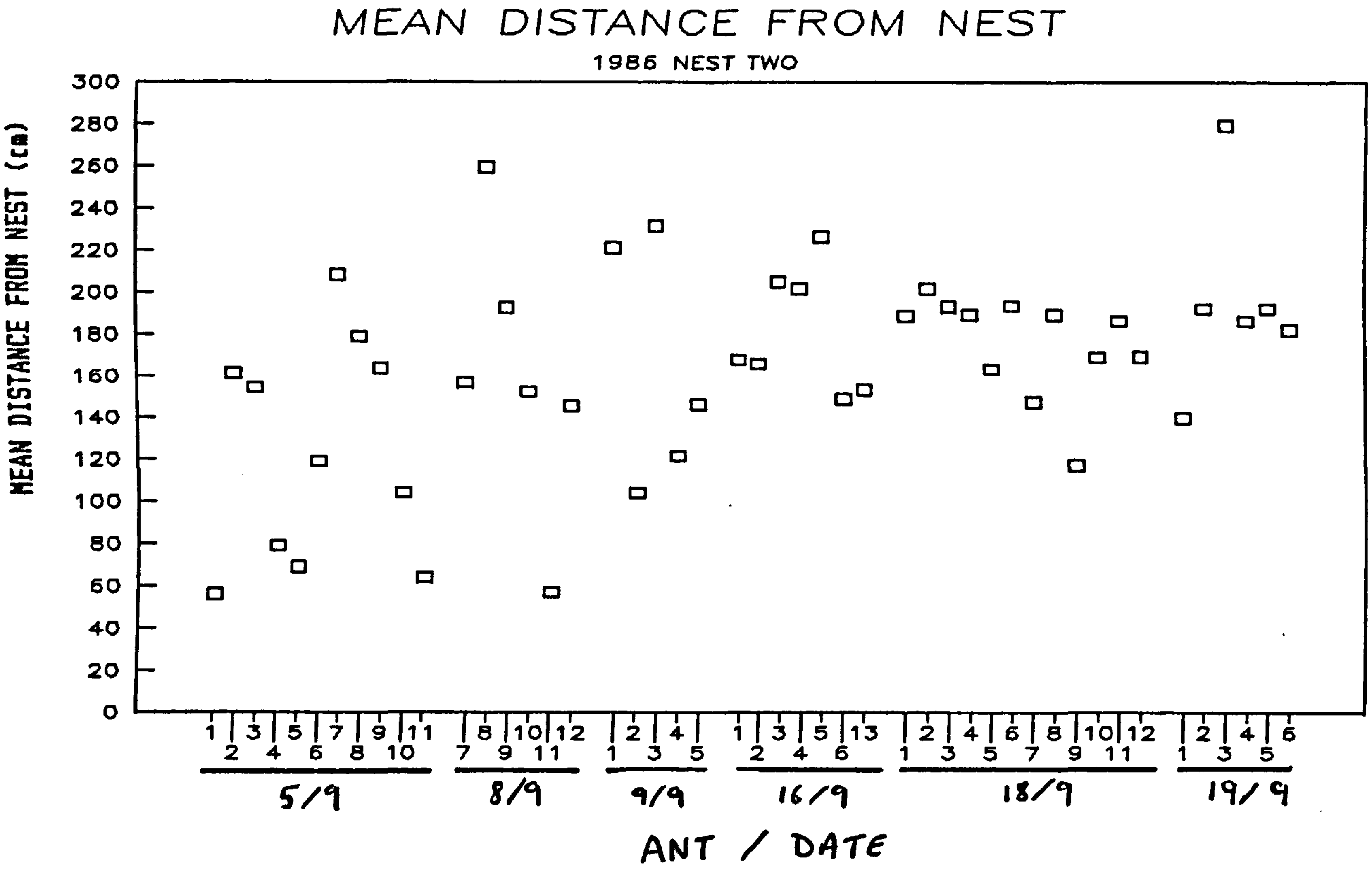

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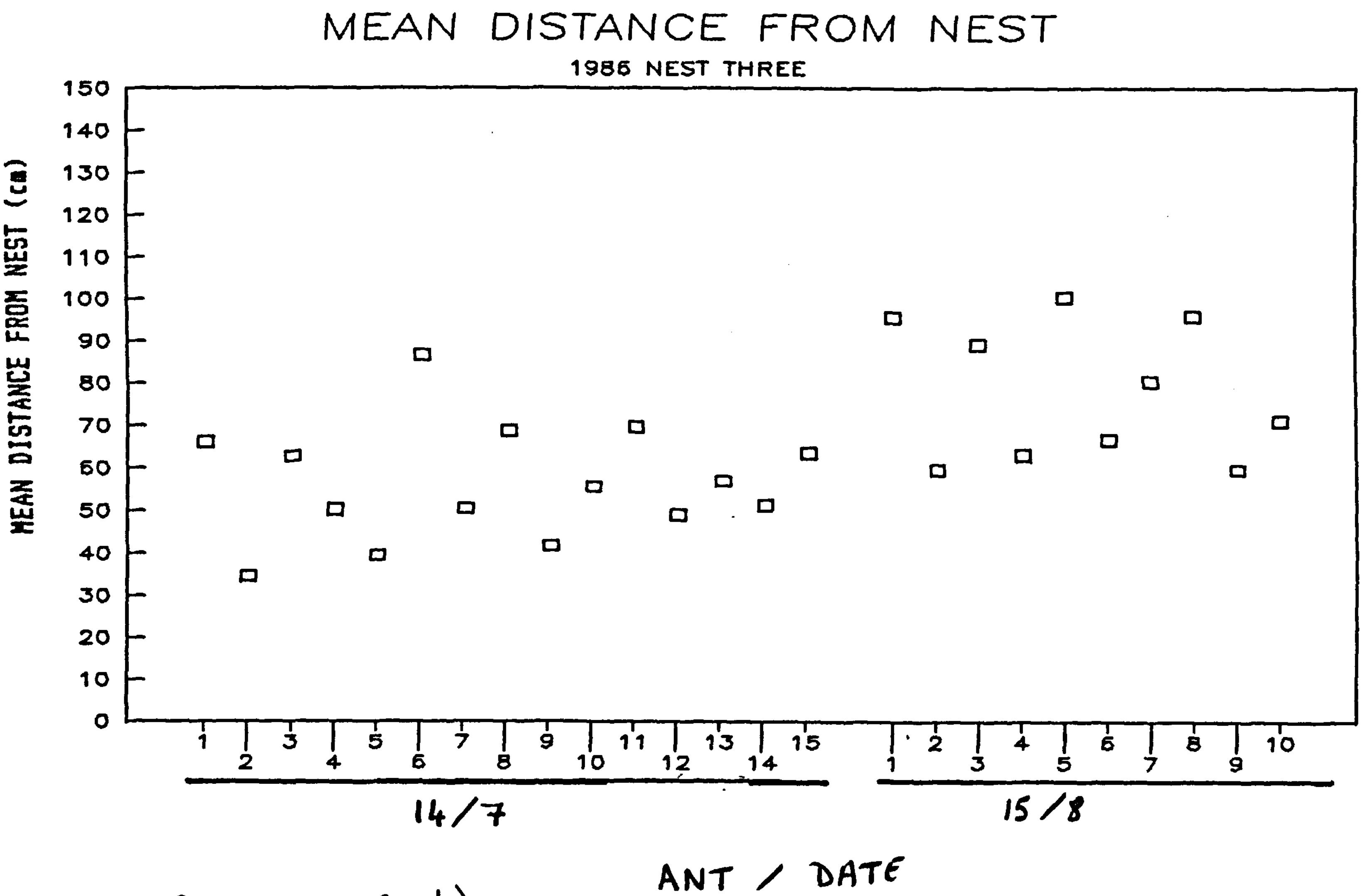

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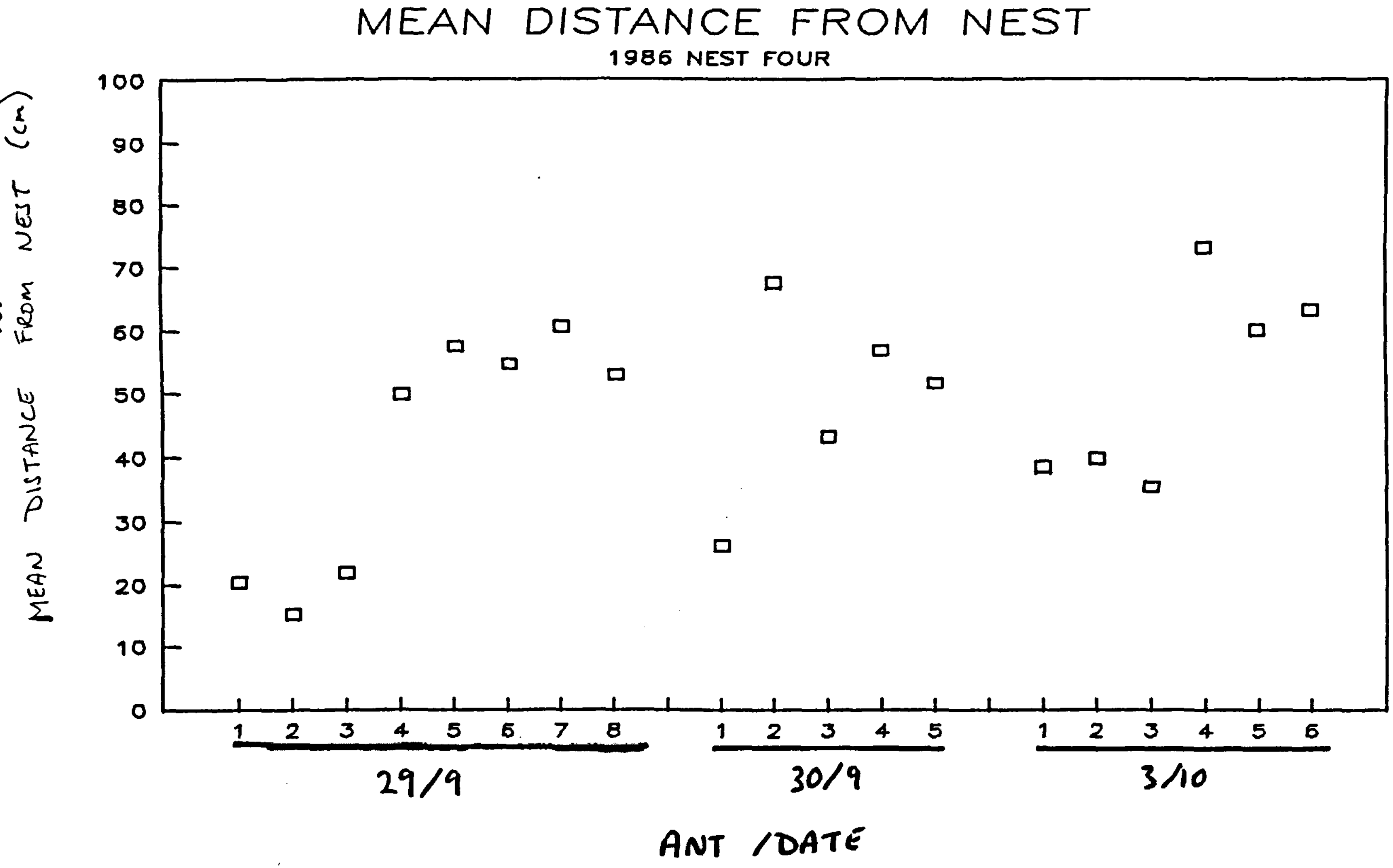

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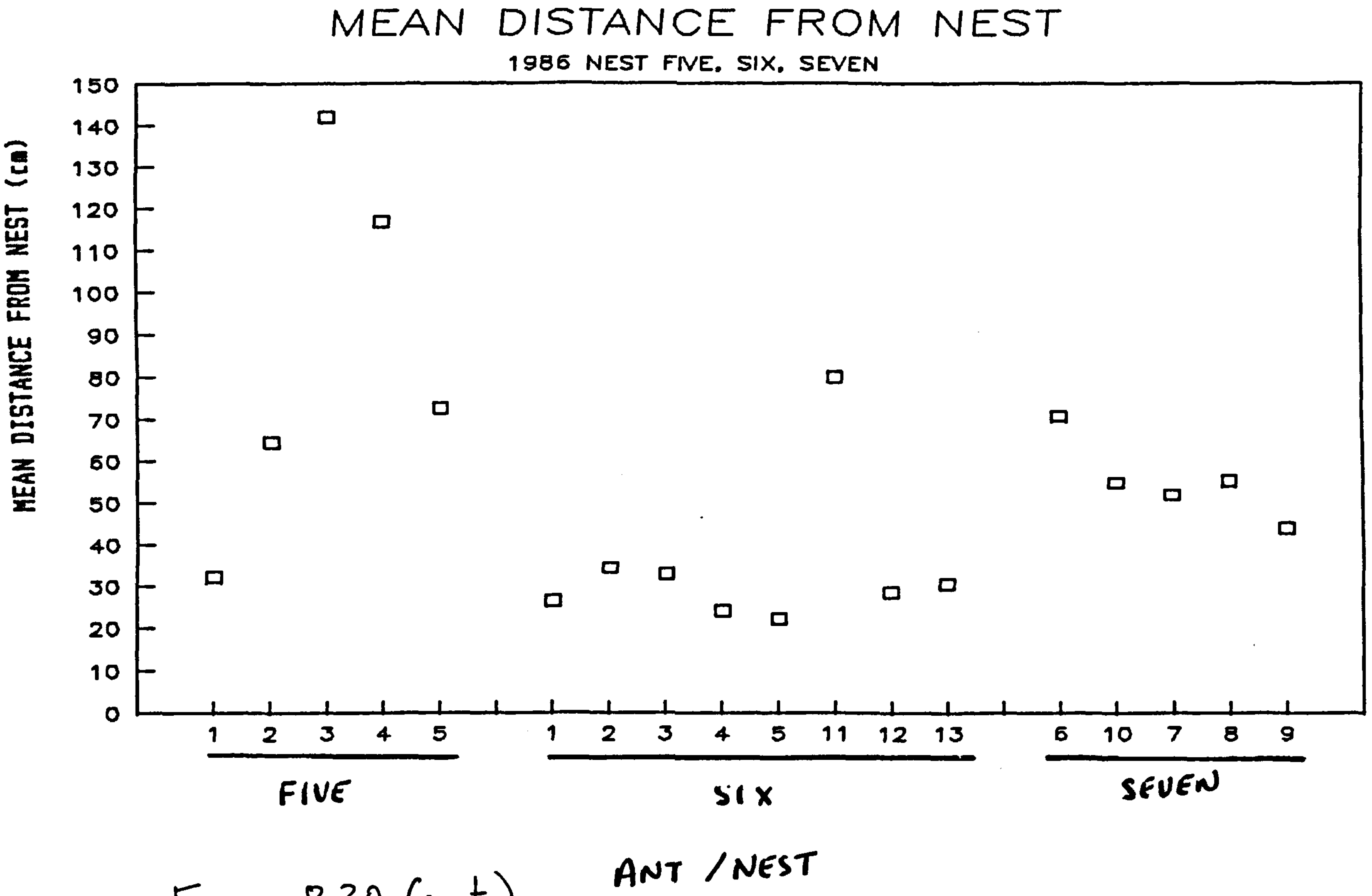

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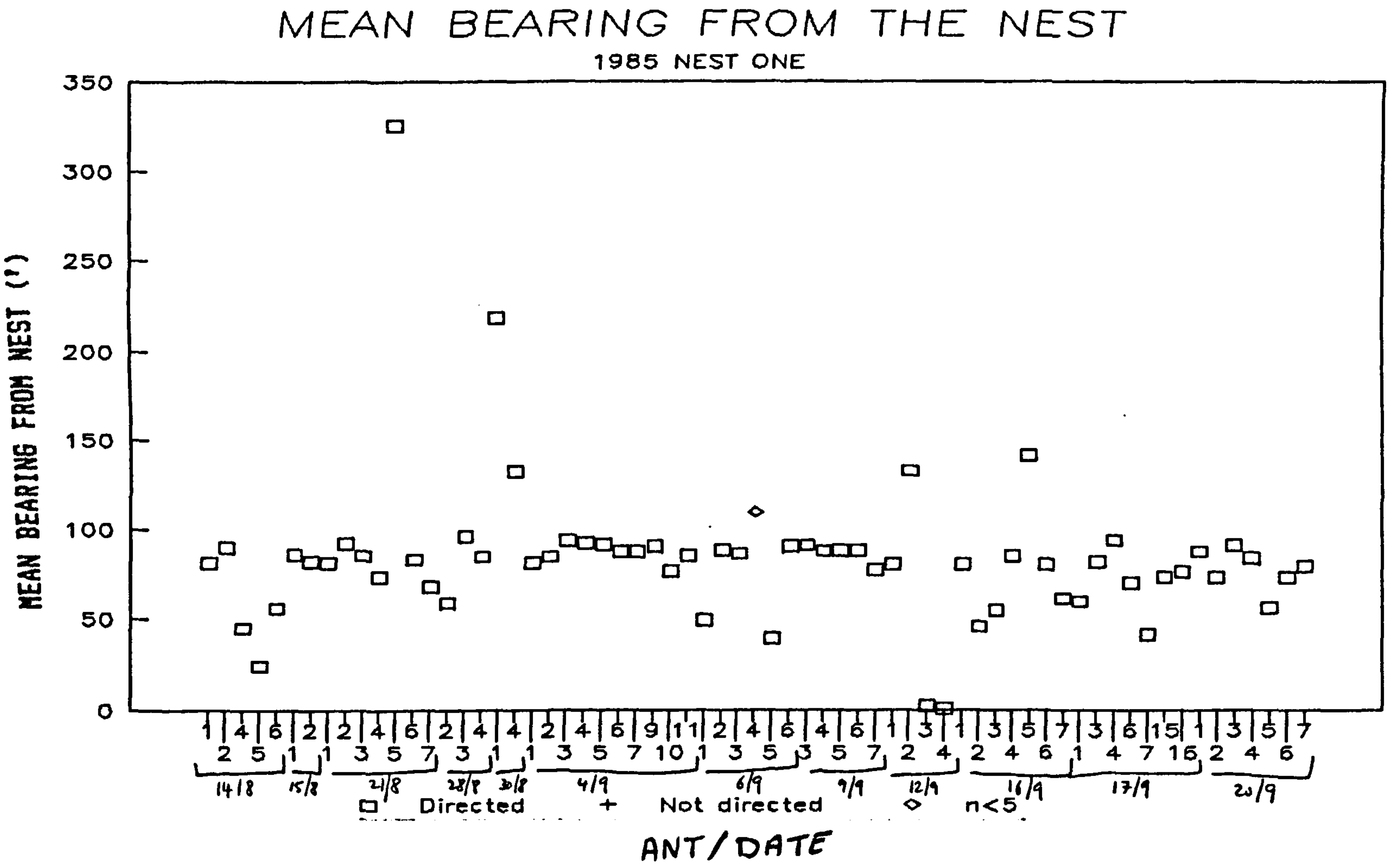
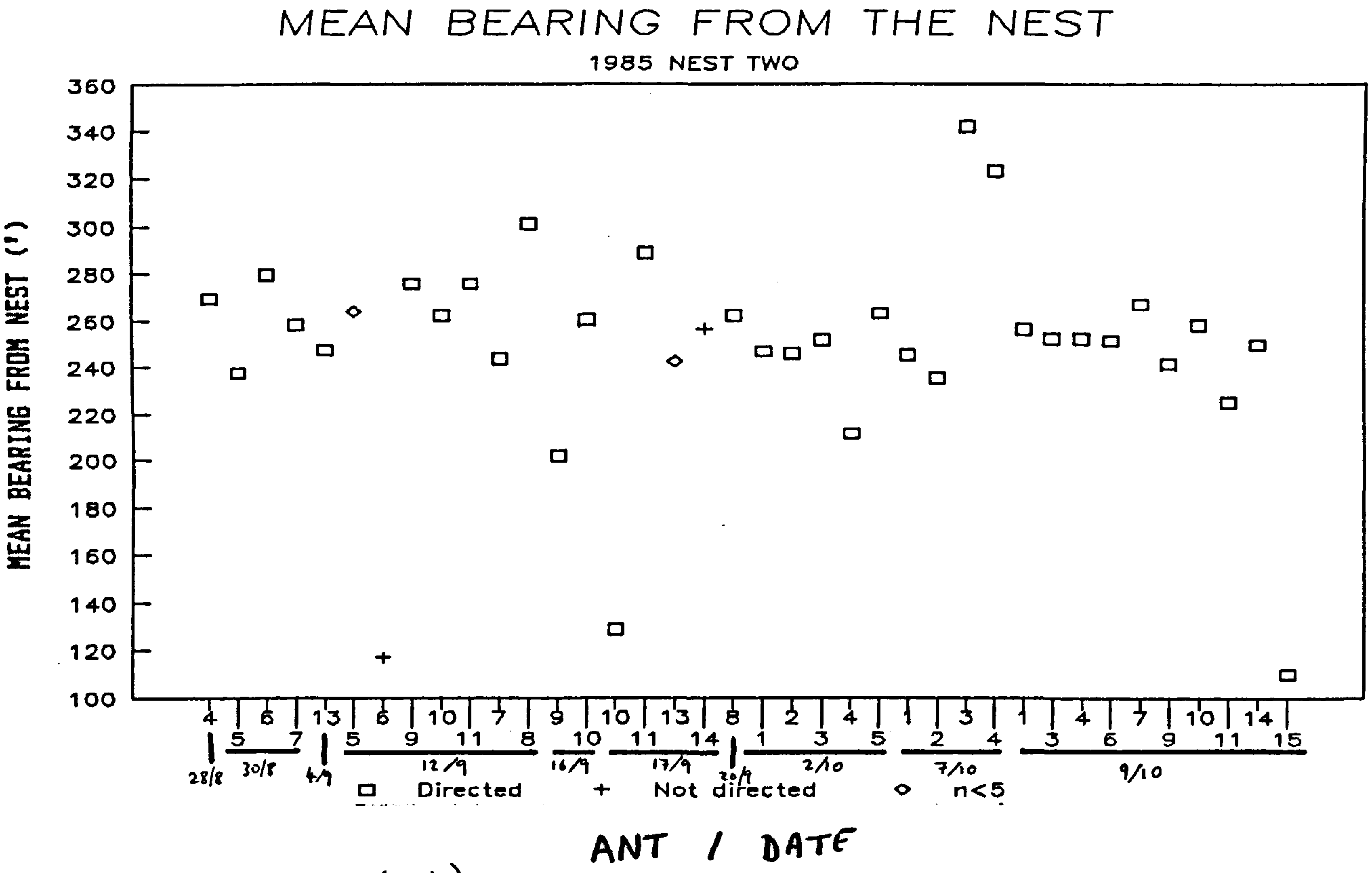


Figure 8.31. Mean bearing from their nest of foragers dutring their forays in the field at Wrotham.



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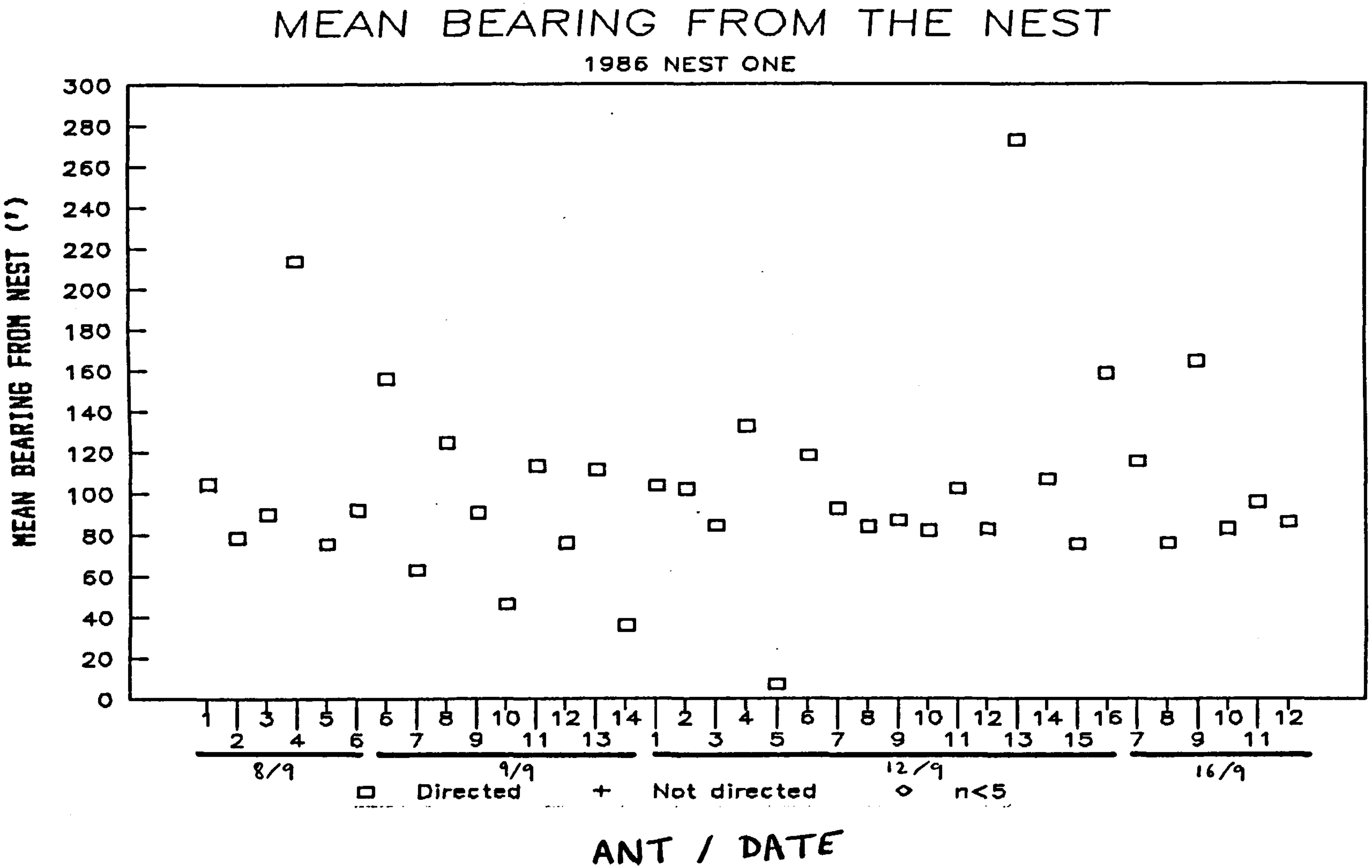

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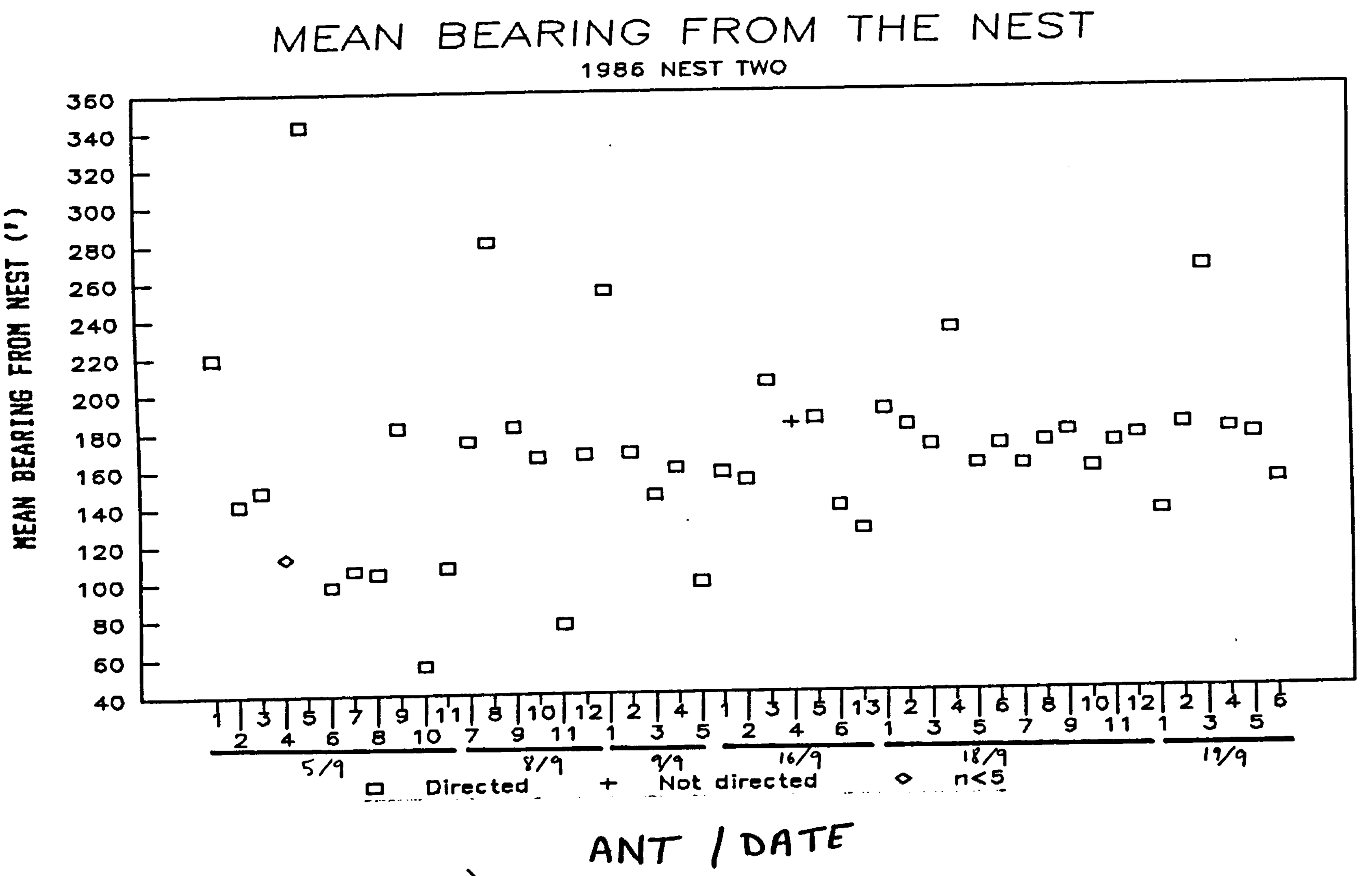

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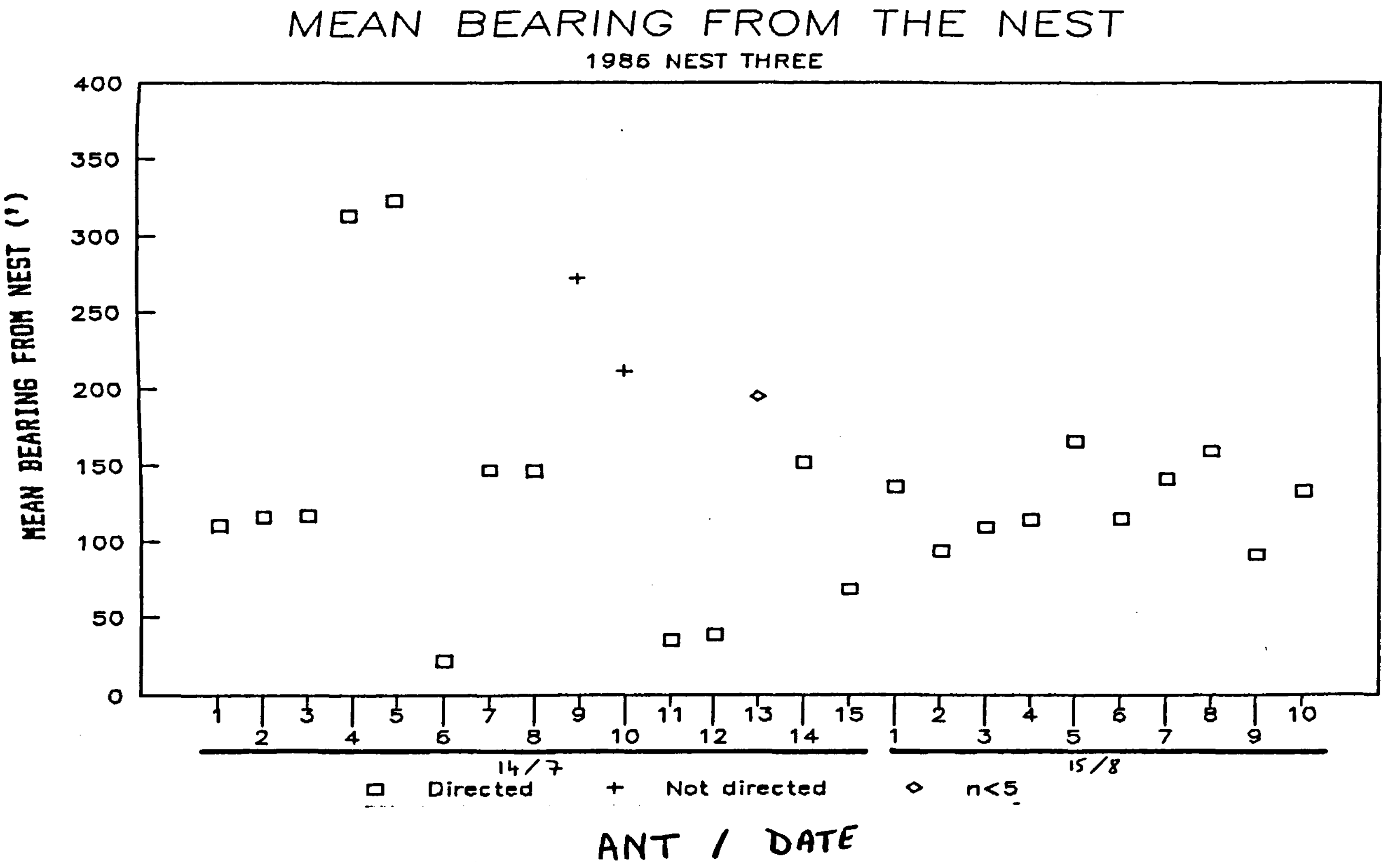

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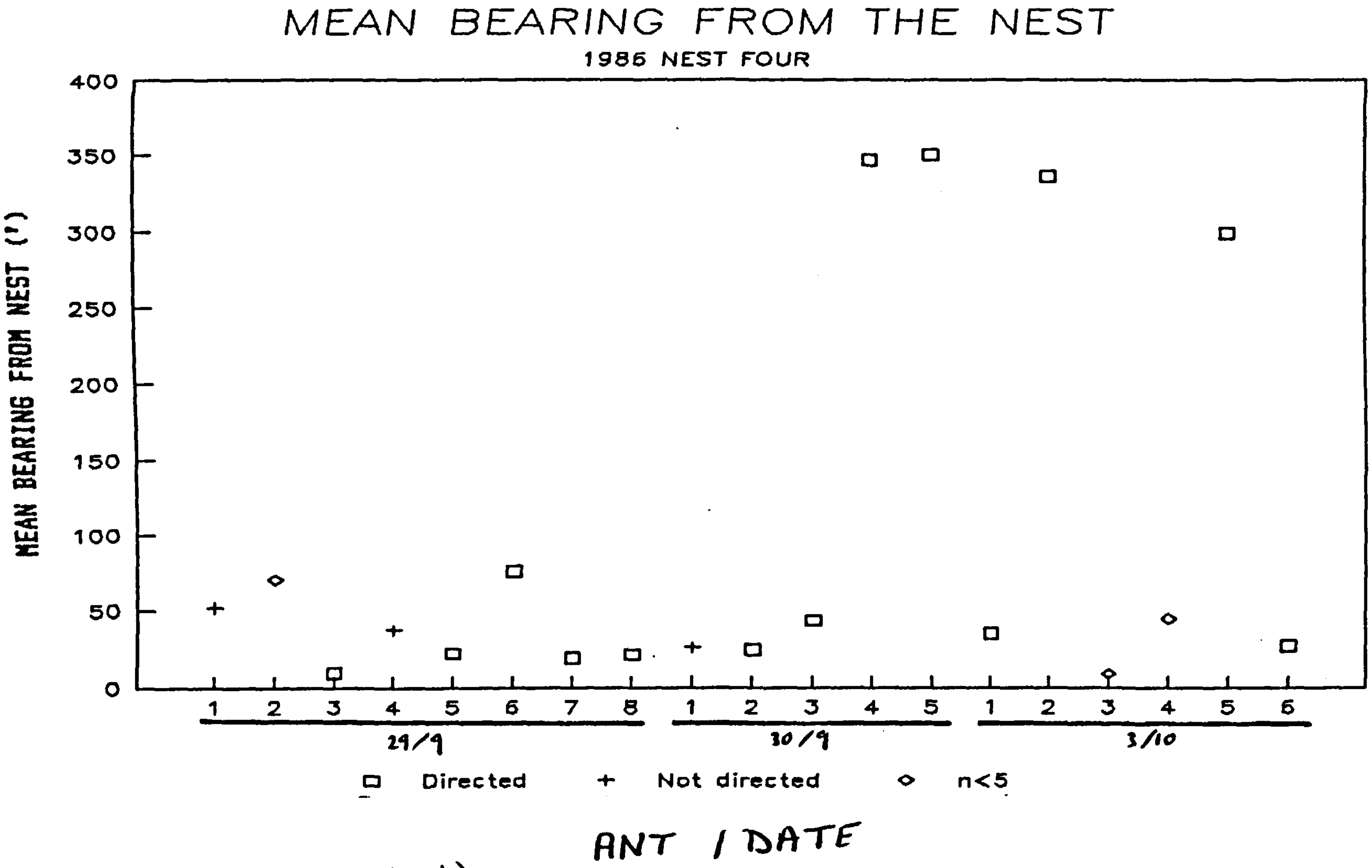

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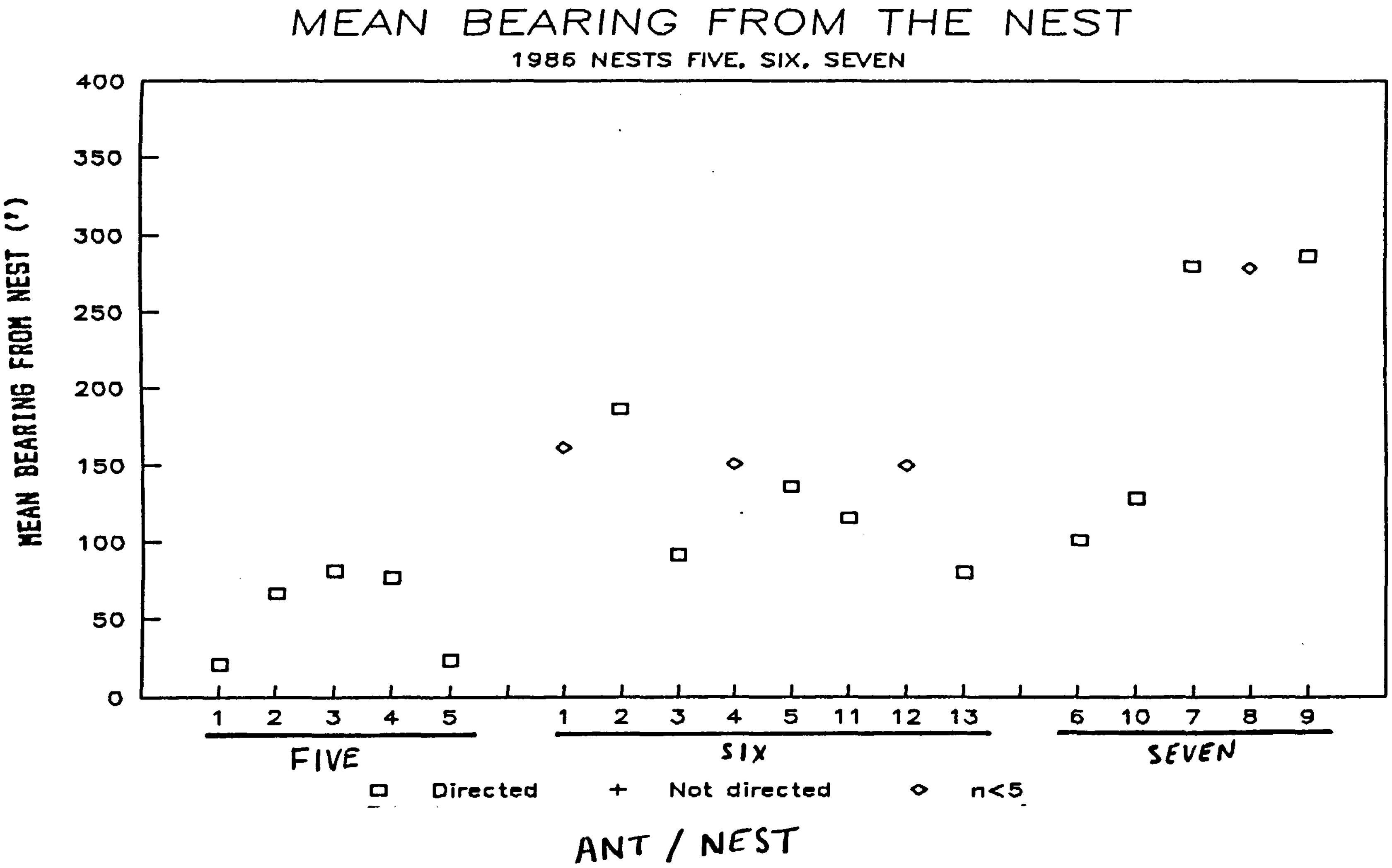

Figure 8.31 (cont.)

Both the mean movement vector and the mean position vector differ between ants (see Appendices 5 and 6). These differences between ants were analysed further to examine the variation between all the ants followed in each year, between the ants followed from each nest and between the ants followed on each separate date.

8.4.2.1 ALL ANTS IN EACH YEAR

a/ movelength.

The mean movelengths (+/- standard deviation of all the ants were presented in Figure 8.26. Movelength varied significantly between ants in both years. In 1985 the grand mean movelength of 103 foragers, which were followed for a total of 1067 30 second steps, was 15.04 +/-7.37 cm. The differences in movelengths between individual ants were significant (F=3.0865, df=102,964, p<0.001). In 1986 the grand mean of 146 ants, followed for a total of 1204 steps, was 14.18 +-10.08cm. Again there were significant differences between the individual ants (F=3.9178, df=145,1058, p<0.001).

b/ movedirection.

The mean movedirections of individual foragers were compared by means of Rayleigh tests, using the "mean of means" method permitted by circular statistics. Only the mean movedirections of individuals which showed significant clumping of their sample movedirections around their mean movedirection could be used in this second analysis. The supermean movedirections of all the (individually clumped) ants in 1985 and all the (clumped) ants in 1986 were shown in Figure 8.27.

In 1985 it was found that the supermean movedirection of the individual mean movedirections of the 73 ants (which showed significant clumping of sample movedirections) was 93.57' (angular deviation, 63.8'). The clumping index was r=0.3783; with a sample size of 73 this indicates the sample of individual mean movedirections was significantly clumped around the supermean movedirection for that year (p<0.01). Thus all of the ants which travelled consistently in one direction travelled in much the same direction.

Similarily the sample of individual means was significantly clumped around the supermean movedirection in 1986. The supermean movedirection in this case is 115.46' (angular deviation 58.43'). The clumping index was r=0.4794, which indicates significant clumping with a sample of 67 ($p<0.001$). Again all the ants which travelled consistently in one direction travelled in the same direction.

c/ distance from nest.

The spatial distribution of the individual mean distances of the foragers from their nests is also given in Table 8.42. Clearly individuals from the same year differ in the distances at which they concentrate their foraging. However no analysis was attempted to compare this measure between foragers because the distances from the nest at which each forager searched did not have a random distribution.

d/ bearing from nest.

It can be seen from Figure 8.31 that foraging effort was unevenly spread around the nests. This unevenness was confirmed by Rayleigh tests which compared the mean bearings of the ants (which showed significant clumping of sample bearing around their individual mean bearing). In both years the individual mean bearings were significantly clumped around the supermeam bearing. In 1985 the supermean bearing of 98 ants was 83.16' (angular deviation 68.27); the clumping index was r=0.2944 indicating significant clumping ($p<0.001$). In 1986 the supermean bearing of 132 ants was 57.30' (a.d.+/-57.3); clumping index r=0.5006, significant clumping ($p<0.001$).

8.4.2.2 ALL ANTS FORAGING FROM EACH NEST.

a/ movelength.

DISTANCE FROM NEST	1985	1986
0-9 cm	4	6
10-19 cm	5	19
20-29 cm	5	21
30-39 cm	12	19
40-49 cm	16	17
50-59 cm	8	21
60-69 cm	5	17
70-79 cm	6	6
80-89 cm	7	10
90-99 cm	6	4
100-109 cm	1	3
110-119 cm	5	1
120+	22	2
TOTAL	103	146

Table 8.42. Distribution of mean distances of ants from their nest in 1985 and 1986.

YEAR	NEST	ANTS	STEPS	MEAN	S.D.	F	DF	SIGN.
1985	ONE	65	757	16.58	8.28	3.0509	64, 69	p<0.005
1985	TWO	38	310	11.28	3.98	2.6439	37,272	p<0.001
1986	ONE	37	290	15.98	9.22	4.347	36, 25	p<0.001
1986	TWO	47	379	8.75	7.01	4.496	46,332	p<0.001
1986	THREE	25	277	17.01	11.62	4.48	25, 25	p<0.001
1986	FOUR	19	136	17.5	8.63	2.42	18,117	p<0.001
1986	FIVE	5	50	15.89	5.49	2.159	4, 4	p<0.2
1986	SIX	8	41	13.97	3.78	0.651	7, 33	n.s.
1986	SEVEN	5	31	15.69	7.79	0.822	4, 2	n.s.

Table 8.43. Summary of analyses of variance of the movelengths of foragers followed in the field between the ants which foraged from the same nest.

There were significant differences in movelength between the individual ants foraging from the same nest. The movelength of each ant, and their standard deviations, have been presented in Figure 8.26. Analyses of variance tests revealed such significant differences between the foragers in 6 of the 9 nests. The analyses are summarized in Table 8.43. It is noticable that the 3 nests which showed no significant differences had the smallest number of recorded trails (5, 8 and 5 respectively).

b/ movedirection.

The distribution of the mean movedirections of individual ants from each nest were presented in Figure 8.27 along with the supermean movedirection for each nest. The mean movedirections are only included in this figure if the sample movedirections were significantly clumped around the individual mean movedirection.

The individual movedirections were found to be significantly clumped around the supermean movedirection for 5 of the 6 nests where there was sufficient data for a significance test to be carried out. Rayleigh tests revealed that in both nests in 1985 and in each of Nests One, Two and Four in 1986 all the ants which had a prefered direction of travel (52, 21, 25, 20 and 9 respectively), travelled in the same direction.

In Nest Three in 1986 there was no evidence of such clumping of the six ants which could be tested (only six ants from this nest showed a significantly clumped individual distribution). For Nests Five, Six and Seven of 1986 there was not enough information to do a significance test.

c/ distance from nest.

There were no significant differences between foragers in the distance from the nest at which they were located. Freidman analyses of variance tests were used to compare distance from nest. In this non-parametric test the distances of all the ants at each intercept were ranked so that if an ant was consistently further from the nest (say) than its nestmates it would score higher ranks. These analyses are summarized in Table 8.44. There were no occasions when some ants were consistently closer or further from the nest than others.

Not all the ants which were followed were used in this analyses, those which travelled for shorter durations than the rest were omitted due to the requirement that each ant should have the same number of ranks. The data was reduced to that from the time intervals indicated in order to reduce the workload.

d/ bearing from nest.

The distribution of the individual mean bearings, of those ants which displayed significant clumping of the sample bearings around the individual mean, are presented for each nest in Figure 8.31. This figure also includes the supermean bearing for each nest calculated from a sample of the individual means.

Rayleigh tests revealed that the mean bearings of the individuals were significantly clumped around the supermean bearing for each nest. These tests are summarized in Table 8.45. The locations of foragers from each nests in 1985 and from six out of seven nests in 1986 were all clumped in a sector around the supermean bearing from the nest. The exception was Nest Seven. Only five ants were followed from this nest, which was under a flat slab having two exit holes about 30 cm apart. It could be that the three ants leaving from one exit may have had a different destination from the two leaving the other so it might be erroneous to group all five. However, the samples of three and two were too small for independent analysis.

The locations of the nests, the supermean bearings of the ants from each nest and the position of likely "target" plants were presented in Figure 8.32. V-tests showed that for all nests except Nest Seven the bearing along which the foragers were clumped did not differ significantly from that of the "target" plant.

8.4.2.3 ALL ANTS FORAGING ON SAME DATE.

YEAR	NEST	ANTS	NO. AND TIMES OF INTERVALS (mins)		X-SQUARED	DF	SIGN.
1985	ONE	37	3	1,3,5.00	61.91	72	n.s.
1985	ditto	11	5	1,3,5,7,9.00	25.67	40	n.s.
1985	TWO	9	3	1,3,5.00	18.4	16	n.s.
1986	ONE	11	5	1,2,3,4,5.00	29.89	40	n.s.
1986	TWO	10	4	1,2,3,4.00	21.68	27	n.s.
1986	THREE	19	3	1,2,3.00	36.99	36	n.s.
1986	FOUR	16	3	1,2,3.00	24.1	30	n.s.
1986	FIVE	4	4	1,2,3,4.00	5.7	9	n.s.
1986	SIX	4	3	1,2,3.00	5.8	6	n.s.
1986	SEVEN	3	3	1,2,3.00	4.66	4	n.s.

Table 8.44. Summary of Freidman analyses of variance by ranks of the distance from nest between ants from each nest in each year.

YEAR	NEST	NO. ANTS	SUPERMEAN BEARING	ANGULAR DEVIATION	CLUMPING INDEX	RAYLEIGH TEST
1985	ONE	65	78.24	29.22	0.8717	$p<0.001$
1985	TWO	34	252.30	35.32	0.8177	$p<0.001$
1986	ONE	37	96.16	38.0	0.7788	$p<0.001$
1986	TWO	43	161.68	44.38	0.6995	$p<0.001$
1986	THREE	23	110.22	49.5	0.625	$p<0.001$
1986	FOUR	13	14.06	31.38	0.8497	$p<0.001$
1986	FIVE	5	54.26	25.62	0.8977	$p<0.01$
1986	SIX	8	134.45	32.59	0.8382	$p<0.005$
1986	SEVEN	5	258.85	70.66	0.2392	n.s.

Table 8.45. Summary of the bearings of ants from each nest. Rayleigh tests were used to determine whether the clumping index indicated significant cling for the revelant sample size.

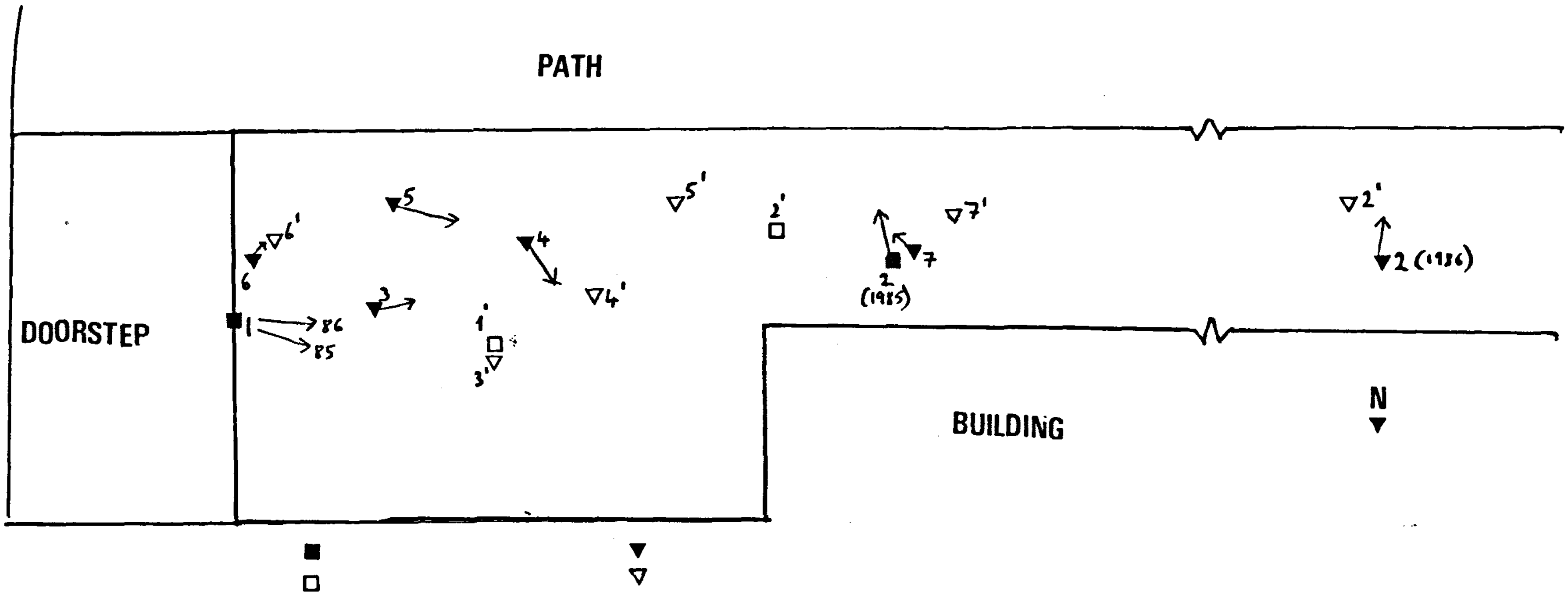

Figure 8.32. Locations of nests, prefered movedirections of foragers and probable "target" plants with aphid clusters.

a/ movelength.

The mean movelengths of the ants on all the various dates and their standard deviations were presented in Figure 8.26. On most occasions there were significant differences between the ants. Such differences were revealed by analyses of variance tests which are summarized in Table 8.46. It was found that there were significant differences ($p<0.05$ at least) between ants on 18 dates out of 31 tested. There were a further eight cases where there was some indication of differences between ants but where these did not reach the significance level ($p<0.2$). On some occasions it was necessary to pool data from adjacent dates in order to increase sample sizes before the tests could be performed.

b/ movedirection.

The distribution of individual mean moveangle of all ants (which showed significant individual clumping) followed on the same day were presented in Figure 8.27. The results of a series of Rayleigh tests performed to investigate the statistical distribution of individuals' mean movedirections are summarized in Table 8.47. The mean movedirections of individual foragers were significantly clumped around the supermean movedirection for each date whuch could be tested. In some cases it was necessary to pool the data from consecutive dates to meet the requirement that at least five dates are being compared could be met.

This shows that for both nests in 1985 and for Nests One and Two of 1986 there were significant clumping of the mean movedirections of the individual ants around the supermean movedirection for each date ($p<0.05$ at least). Thus all ants travelled in the same direction on each date. For the other nests of 1986 there was not enough ants which showed clumping on an individual basis for Rayleigh tests to be performed for each date.

c/ distance from nest.

There was no analysis of the distance from the nest of ants which foraged on the same date. This was because the sample sizes were too small to allow ranking.

DATE(S)	ANTS	STEPS	MEAN	S.D.	F	DF	SIGN.
1985 Nest One							
14-15/8	5+2	73	18.72	3.95	0.4358	6, 66	n.s.
21/8	7	106	20.96	7.45	2.7566	6, 99	p<0.025
28-30/8	5	50	14.39	4.28	1.1731	4, 45	n.s.
4/9	10	161	15.64	4.79	4.5230	9,151	p<0.2
6/9	6	55	18.04	6.77	2.7604	5, 49	p<0.05
9/9	5	42	23.92	7.32	2.0261	4, 37	p<0.2
12/9	4	50	7.92	4.51	2.7091	3, 46	p<0.2
16/9	7	72	11.85	9.75	13.6017	6, 65	p<0.001
19/9	7	69	18.51	14.46	4.4226	6, 62	p<0.001
20/9	7	79	15.27	6.14	2.9366	6, 72	p<0.025
1985 Nest Two							
28/8,4/9	5	50	12.9	4.59	3.0216	4, 45	p<0.05
12/9	7	51	11.03	4.01	1.7458	6, 44	p<0.2
16-20/9	7	61	12.03	4.25	2.9478	6, 54	p<0.025
2/10	5	36	13.3	3.46	1.3991	4, 31	n.s.
7/10	4	33	8.05	5.0	13.4555	3, 29	p<0.001
9/10	10	79	10.27	3.25	2.3201	9, 69	p<0.001
1986 Nest One							
8/9	6	57	20	16.74	0.675	5, 51	n.s.
9/9	9	63	15.54	6.55	4.881	8, 53	p<0.001
12/9	16	132	15.57	8.06	3.52	15,116	p<0.001
16/9	6	39	11.79	5.26	4.909	5, 33	p<0.2
1986 Nest Two							
5/9	11	73	16.95	10.91	2.8307	10, 72	p<0.01
8/9	6	43	6.3	2.09	1.7341	5, 37	p<0.2
9/9	5	48	4.25	1.48	0.756	4, 43	n.s.
16/9	7	66	4.6	1.67	2.92	6, 59	p<0.025
18/9	12	95	12.97	3.18	2.48	11, 83	p<0.005
19/9	6	54	8.74	2.1	4.909	5, 48	p<0.005
1986 Nest Three							
14/7	15	130	22.57	11.19	1.97	14,115	p<0.05
15/8	10	140	12.16	12.78	9.58	9,136	p<0.001
1986 Nest Four							
29/9	8	56	16.39	7.50	2.214	7, 48	p=0.05
30/9	5	42	13.62	2.37	1.942	4, 37	p<0.2
3/10	6	38	23.42	10.53	1.594	5, 32	p<0.2
1986 Nest Five							
7/7	5	50	15.89	5.49	2.159	4, 45	p<0.2
1986 Nest Six							
20/6	8	41	13.97	3.78	0.6516	7, 33	n.s.
1986 Nest Seven							
20/6	5	31	15.69	7.79	0.822	4, 26	n.s.

Table 8.46. Summary of analyses of variance tersts comparing the movelengths of different ants followed on the same date. It was necessary to group data from adjacent dates to increase sample size.

DATE(S)	NO. ANTS	SUPERMEAN MOVEDIRECTION	ANGULAR DEVIATION	CLUMPING INDEX	SIGN.
1985 Nest One					
14-15/8	7	81.62	16.2	0.9559	$p<0.01$
21,28,30/8	9	87.55	38.0	0.7848	$p<0.05$
4/9	10	86.87	8.1	0.9884	$p<0.001$
6,9,12/9	9	82.48	8.1	0.9873	$p<0.01$
16/9	5	83.06	21.4	0.9347	$p<0.05$
17/9	5	80.88	19.8	0.9457	$p<0.05$
20/9	5	78.22	16.2	0.9667	$p<0.01$
1985 Nest Two					
28/8-12/9	7	256.59	14.0	0.9689	$p<0.001$
16/9-7/10	6	240.61	14.0	0.9689	$p<0.001$
9/10	8	248.43	11.5	0.9840	$p<0.001$
1986 Nest One					
8,9/9	8	95.34	31.4	0.8449	$p<0.05$
12/9	11	99.97	42.9	0.7195	$p<0.005$
16/9	6	103.81	33.4	0.8307	$p<0.01$
1986 Nest Two					
5,8,9,16/9	6	161.31	42.1	0.7266	$p<0.05$
18/9	8	184.41	16.2	0.9611	$p<0.001$
19/9	6	191.25	14.0	0.9705	$p<0.005$
1986 Nest Three					
14/7,15/8	6	93.0	62.8	0.4038	n.s.
1986 Nest Four					
29,30/9,3/10	9	21.47	16.2	0.9617	$p<0.001$
1986 Nest Five					
7/7	3	107.66	4.5	0.999	no test
1986 Nest Six					
20/6	3	114.13	29.2	0.8719	no test
1986 Nest Seven					
20/6	1	274.22	....	n=1	no test

Table 8.47. Summary of the mean movedirections of ants foraging on each date, including a Rayleigh test of the significance of clumping of individuals' mean movedirections around the supermean bearing for each date. On some occassions it was necessary to group data from adjacent dates so that the requirement of the Rayleigh test that there be at least five angles to be compared be met.

d/ bearing from nest The distribution of individual mean bearings from the nest were presented for each date in Figure 12.31 along with the supermean bearing for each nest. Rayleigh tests, summarized in Table 8.48, revealed that on 25 of the 30 dates (or combinations of adjacent dates) tested there was significant clumping of the individual means around the date supermean. Thus it was the case on most days that the ants were clumped in a sector around this supermean bearing from the nest.

8.4.3 VARIATION BETWEEN YEARS.

The movement pattern of foragers in 1985 was compared to that of ants foraging in 1986. Similarily the spatial distributions of foraging effort resulting from these foraging patterns was also compared between years. Two kinds of comparisons could be made between the years.

In the first instance the total data gathered in each year was compared for each of the movement and distribution parameters. In the second instance such comparisons were restricted to data gathered from Nest One so that the influence of any variations between the others nests could be elimated.

a/ movelength.

There was no significant difference in movelength between the years when all the data gathered in 1985 was compared to the total gathered in 1986 (1985: mean 15.04cm +/-7.37, 1067 steps; 1986: mean 14.18cm +/-10.08, 1204 steps; F=0.3448, df=1,2269, n.s.).

Similarily there was no significant difference when the comparison was restricted to Nest One only. In 1985 the mean movelength of 65 foragers from Nest One was 16.58cm +/-8.28 (757 steps) while in 1986 the mean of 37 foragers was 15.98cm +/-9.22 (290 steps) but the difference was not significant (F=0.0216, df=1,1045, n.s.).

b/ movedirection.

DATE(S)	NO. ANTS	SUPERMEAN BEARING	ANGULAR DEVIATION	CLUMPING INDEX	SIGN.
1985 Nest One					
14-15/8	7	66.87	22.92	0.921	p<0.01
21/8	7	71.32	36.24	0.7985	p<0.01
28,30/8	5	172.79	49.49	0.6241	p<0.2
4/9	10	87.14	8.10	0.9961	p<0.001
6/9	6	77.63	24.31	0.9103	p<0.001
9/9	5	86.61	8.10	0.9968	p<0.001
12,16/9	11	69.76	40.52	0.7528	p<0.001
17/9	7	78.42	14.04	0.9771	p<0.001
20/9	8	79.28	11.46	0.9836	p<0.001
1985 Nest Two					
28,30/8,4/9	5	258.21	14.04	0.966	p<0.01
12/9	5	271.55	18.12	0.9469	p<0.01
16,17,20/9	5	238.59	51.88	0.5908	n.s.
2,7,10	9	248.94	32.41	0.8482	p<0.001
9/10	10	245.87	35.32	0.8088	p<0.001
1986 Nest One					
8/9	6	99.12	41.68	0.7354	p<0.05
9/9	9	90.45	35.67	0.8062	p<0.001
12/9	16	96.12	40.60	0.7489	p<0.001
16/9	6	101.95	28.95	0.8723	p<0.01
1986 Nest Two					
5/9	10	120.25	53.75	0.5646	p<0.05
8/9	6	171.54	51.34	0.5955	n.s.
6,16/9	9	156.53	37.13	0.7862	p<0.002
18/9	12	175.70	18.55	0.9476	p<0.001
19/9	6	176.01	37.97	0.7804	p<0.05
1986 Nest Three					
15/8	12	83.997	59.54	0.4591	p<0.1
15/9	10	125.64	23.77	0.914	p<0.001
1986 Nest Four					
29/9	8	38.32	23.07	0.9189	p<0.001
30/9	5	14.43	21.99	0.9264	p<0.01
3/10	6	7.36	35.7	0.8059	p<0.05
1986 Nest Five					
7/7	5	54.26	25.92	0.8977	p<0.01
1986 Nest Six					
20/6	8	134.45	32.59	0.8382	p<0.005
1986 Nest Seven					
20/6	5	258.85	70.66	0.2392	n.s.

Table 8.48. Summary of the bearings from the nest of individuals foraging on each date; including Rayleigh tests of the significance of the clumping of individuals' mean bearings around the supermean bearing for each date.

There were significant differences between years in the directions in which the ants travelled. For those ants for which the distribution of sample movedirection was significantly clumped around the mean. A circular chi-squared test revealed that these distributions were significantly different (X- sq=27.54, df=5, $p<0.001$).

Similarily, when the comparison was restricted to ants foraging from Nest One it was found that the distributions of mean movedirections, as seen in Figure 8.28, differed significantly between years (X-sq=7.44, df=2, $p<0.05$). Thus the ants which travelled consistently in one direction travelled in different directions between years.

There was very little variation between years in the proportion of directed ants. In 1985 47% of the ants were significantly directed compared to 51.1% in 1986. There was even less variation when the comparison was restricted to Nest One; 75% directed in 1985, 74.3% in 1986.

c/ distance from nest.

Only one comparison was made of the distance at which workers foraged between years because of the need to rank the data for analysis. The distribution of foragers' mean distances from Nest One in 1985 was compared to that in 1986. The distributions of mean distances in the two years are presented in Table 8.49. When these distributions were compared by means of a Kruskall-Wallis test it was seen that there was a significant difference between years (H=113.23, df1, $p<0.001$). Thus foragers in 1985 travelled significantly further from the nest.

d/ bearing from nest.

There was a significant difference between years in the bearing of the ants from their nests. The distribution of mean bearings for each nest in each year were shown in Figure 8.31. A circular chi-squared test revealed that these distributions were indeed significantly different (X-sq=61.45, df=6, $p<0.001$). However, the distribution of mean bearings of ants from

DISTANCE FROM NEST	1985	1986
NO. ANTS	66	37
0-19 cm	4	7
20-39 cm	6	9
40-59 cm	5	8
60-79 cm	8	5
80-99 cm	11	6
100-119 cm	7	2
120-139 cm	12	0
140+ cm	10	0

Table 8.49. Distributions of mean distances from nest of ants from Nest One in 1985 and in 1986.

NEST	NO. ANTS	NO. DIRECTED	PROPORTION
1985 ONE	65	48	0.74
1985 TWO	38	21	0.55
1986 ONE	37	24	0.65
1986 TWO	47	20	0.43
1986 THREE	25	6	0.24
1986 FOUR	19	9	0.47
1986 FIVE	5	5	1.00
1986 SIX	8	3	0.38
1986 SEVEN	5	1	0.20

Table 8.50. Proportions of ants which were significantly directed ants from each nest.

Nest One did not differ significantly between years (X-sq=5.97, df=3, n.s.). These distributions were also presented in Figure 8.31.

8.4.4 VARIATION BETWEEN NESTS.

The duration of the foraging trips varied between nests. A significant variations was found between the nine nests (F=6.3480, df=8, 240, $p<0.001$) when all the recorded durations were considered, with the longest durations recorded for Nest One in 1985. When consideration was restricted to the durations of round trips only it was found that the ants from Nest One (1985 and 1986 combined) took longer forays than the ants from the other nests (F=9.084, df=1,20, $p<0.01$).

a/ movelength.

Movelengths varied significantly between nests. Figure 8.33 shows the mean movelength, and standard deviation, for each nest. Analyses of variance tests revealed that movelength differed significantly between all nine nests (F=6.0752, df=8, 2262, $p<0.001$),between both nests in 1985 (F=19.4895, df=1, 1065, $p<0.001$), and between the seven nests in 1986 (F=10.62, df=6, 1197, $p<0.001$).

b/ movedirection.

The movedirection of ants differed between nests. The distributions of (significantly clumped) individual means are presented for each nest in Figure 8.34. A Mardia-Watson-Wheeler test revealed that the distribution of movedirections differed significantly between all nine nests (W=130.22, df=16, $p<0.001$).

Similar tests comparing only the two nests of 1985 or the seven nests of 1986 again showed that the distributions of individuals' prefered directions differed between nests (1985: W=43.528, df=2, $p<0.001$; 1986: W=67.84, df=12, $p<0.001$). Thus the ants which travelled consistently in one direction travelled in different directions between nests.

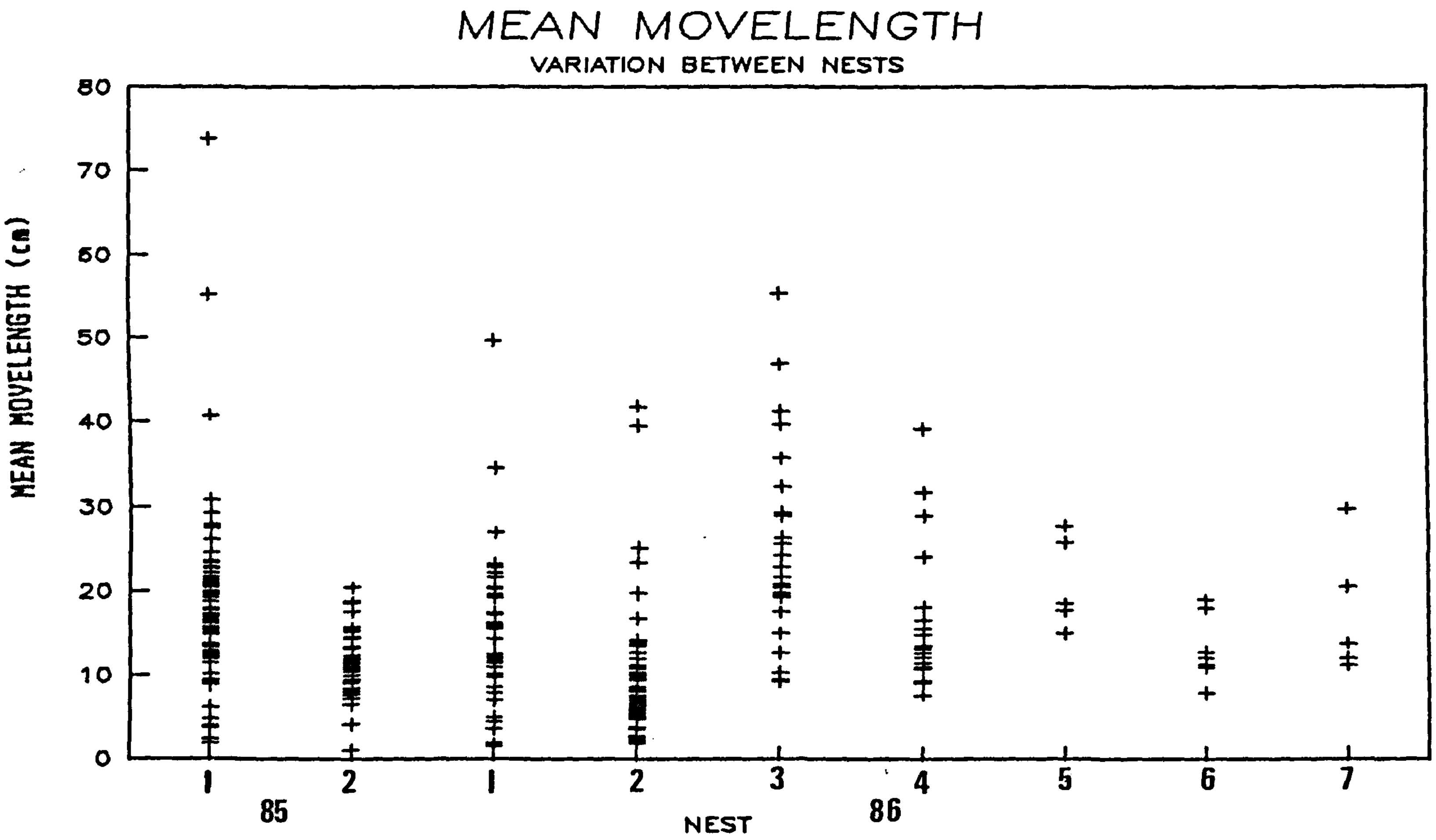

Figure 8.33. Variations in movelengths between ants from different nests.

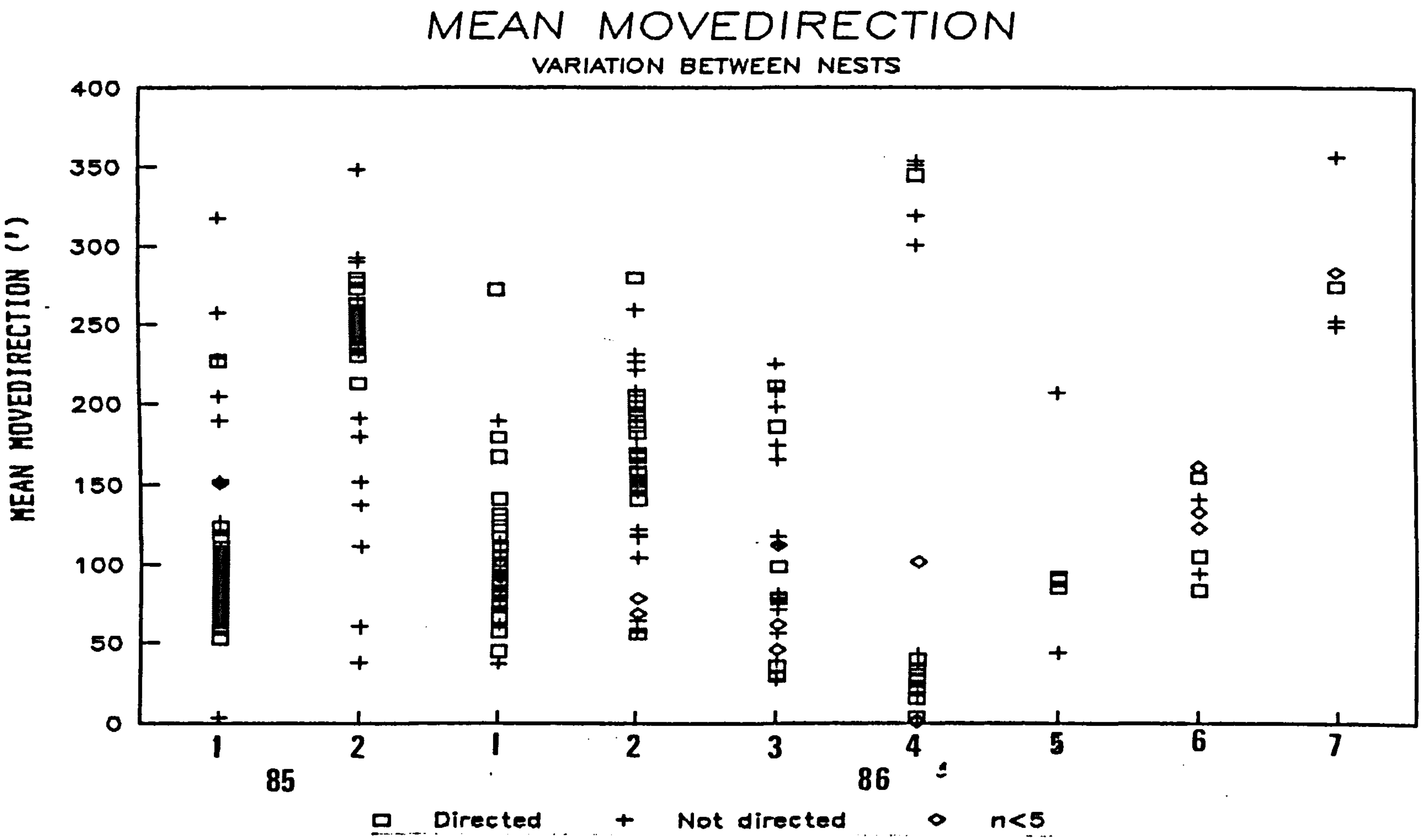

Figure 8.34. Variations in movedirection between ants from different nests.

The proportions of the ants which were found to have a prefered direction of movement varied greatly between the nests as can be seen from Table 8.50.

c/ distance from nest.

Ants from different nests foraged at different distances from their nest (Figure 8.35). The distribution of individual foragers' mean distances are presented in Table 8.51. A Kruskall-Wallis analysis of variance by ranks test showed that there were significant differences between the two nests used in 1985 ($H=31.07$, 1df, $p<0.001$) and between the seven nests used in 1986 ($H=190.02$, 6df, $p<0.001$) in the distances at which their foragers would search.

d/ bearing from nest.

The supermean bearings of Nests One and Two of 1985 and Nests One to Six of 1986 were significantly clumped around a grand mean bearing of 107.47' ($r=0.6484$, $n=8$, $p<0.05$; Nest Seven of 1986 was excluded because the individual means were not clumped around the supermean for this nest). Similarily the supermean bearings of Nests One to Six of 1986 were significantly clumped around a grand mean bearing of 100.48' ($r=0.6933$, $p=0.05$). These results indicate that foragers from each nest were located along the same bearing from their nests.

However, closer examination revealed differences between nests in the distributions of individuals' mean bearings. A series of circular chi-squared tests compared the distribution of means between the two nests in 1985 and between all pairwise combinations of Nests One to Four (there were too few data from Nests Five and Six to allow such tests to be performed). The distribution of individuals' mean bearings for each nest have is presented in Figure 8.36. The results of the chi-squared tests are summarized in Table 8.52; all revealed significant differences between nests in the distributions of bearing along which foragers were located.

8.4.5 VARIATION BETWEEN DATES.

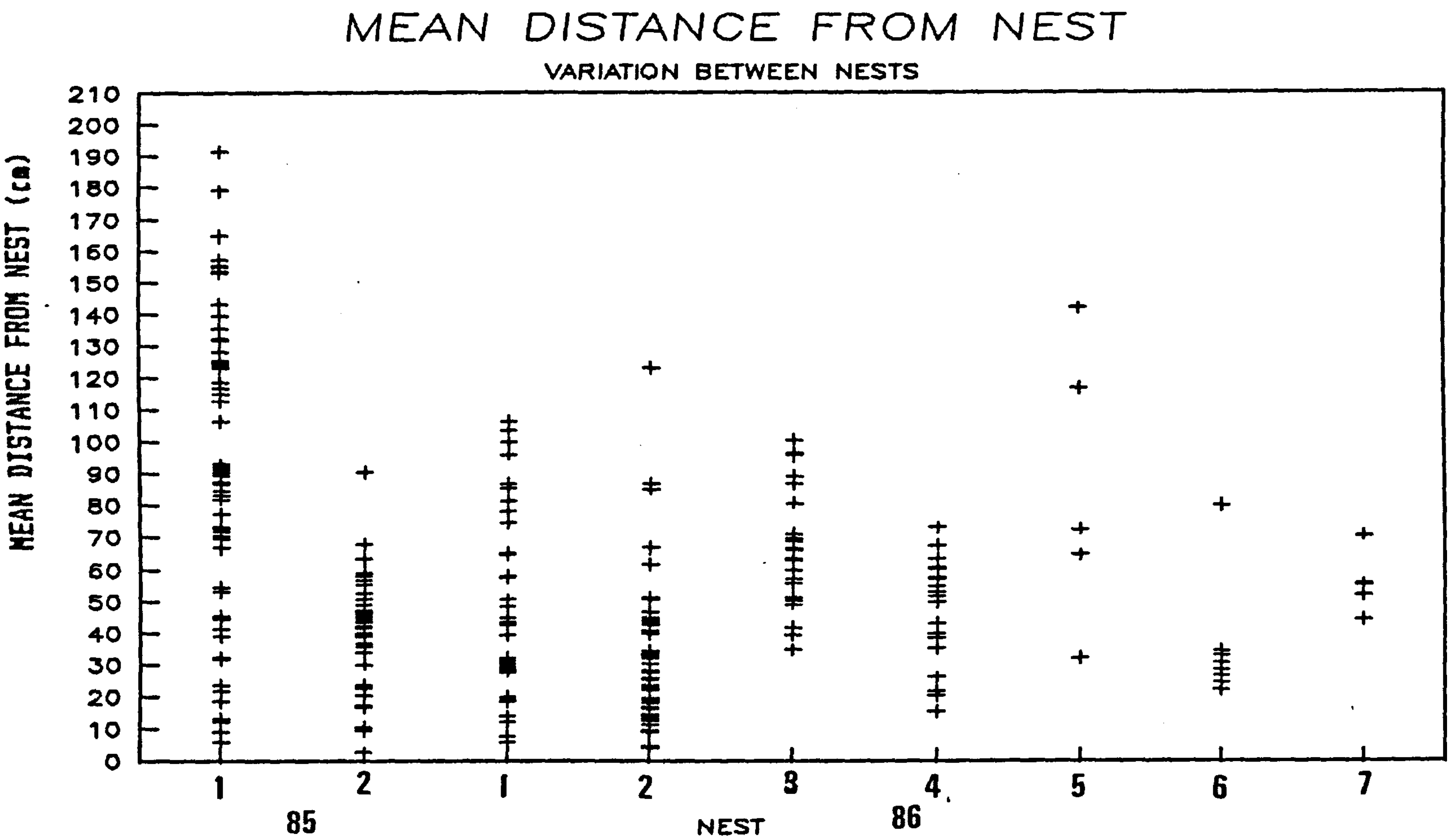

Figure 8.35. Variations in mean distance from the nest between ants from different nests.

DISTANCE	1985		1986						
FROM NEST (cm)	ONE	TWO	ONE	TWO	THREE	FOUR	FIVE	SIX	SEVEN
NO. ANTS	65	38	37	47	25	19	5	8	5
0-9 cm	2	2	2	4					
10-19 cm	2	3	5	13		1			
20-29 cm	2	3	5	9		3		4	
30-39 cm	4	8	4	6	2	3	1	3	
40-49 cm	4	12	5	7	2	2			1
50-59 cm	2	6	3	3	7	5			3
60-69 cm	2	3	3	2	7	4	1		
70-79 cm	6		2		1	1	1		1
80-89 cm	7		4	2	3			1	
90-99 cm	5	1	2		2				
100-109 cm	2		2		1				
110-119 cm	5						1		
120+	22			1			1		
TOTAL	65	38	37	47	25	19	5	8	5

Table 8.51. Distribution of mean distances from nest of foragers from each nest.

NEST	CHI-SQUARED	DF	SIGN.
1985 ONE v TWO	79.40	2	n.s.
1986 ONE v TWO	23.95	3	n.s.
1986 ONE v THREE	8.22	2	n.s.
1986 TWO v FOUR	11.26	1	n.s.
1986 TWO v THREE	11.01	2	n.s.
1986 TWO V FOUR	5.297	1	n.s.
1986 THREE V FOUR	11.85	1	n.s.

Table 8.52. Summary of the circular chi-squared tests to compare the distributions of individuals' mean bearing from the nest between different nests.

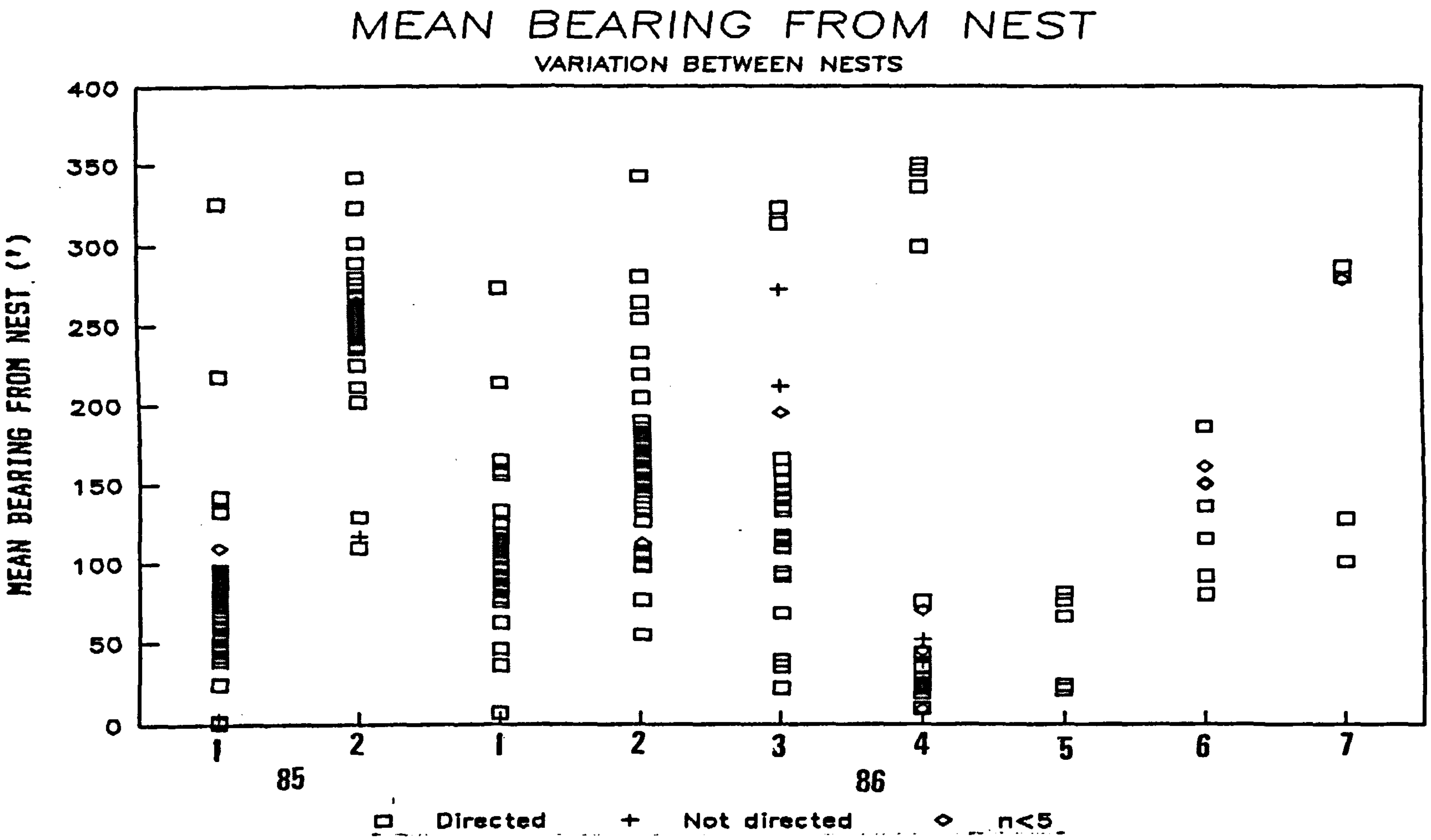

Figure 8.36. Variations in mean bearing between ants from different nests.

Foragers were trailed from some of the nests on several separate dates. Thus it was possible to compare the movement and spatial distribution parameters between the separate dates for Nests One and Two of 1985 and for Nests One to Four in 1986.

a/ movelength.

The movelengths of foragers varied between dates as can be seen in Figure 8.37 which summarizes the movelength of ants followed on each date as mean movelengths with their standard deviations. Analyses of variance tests revealed that these differences were significant for five of the six nests which could be so tested. Nest One in 1986 was the exception; there was no significant difference in movelength between the four dates on which foraging movements were followed. The results of these analyses of variance tests are summarized in Table 8.53.

b/ movedirection.

The prefered movedirections of the ants on each date are presented in Figure 8.38. The distribution of these movedirections were compared between dates by means of a series of Mardia-Watson-Wheeler tests; these revealed that there were no significant differences between dates for any of the five nests which could be tested (there was too little data for Nest Three in 1986 for a test to be performed). Thus the movedirections of the ants which travelled consistently in one direction did not change significantly between dates. These results are summarized in Table 8.54.

As can be seen from Table 8.55 there was considerable variation in the proportion of directed ants between each dates but this variation did not follow any particular pattern.

c/ distance from nest.

The distance of foragers from their nests on each date, presented in Figure 8.39, was compared by means of Kruskall-Wallis analyses of variance by ranks tests. These tests,

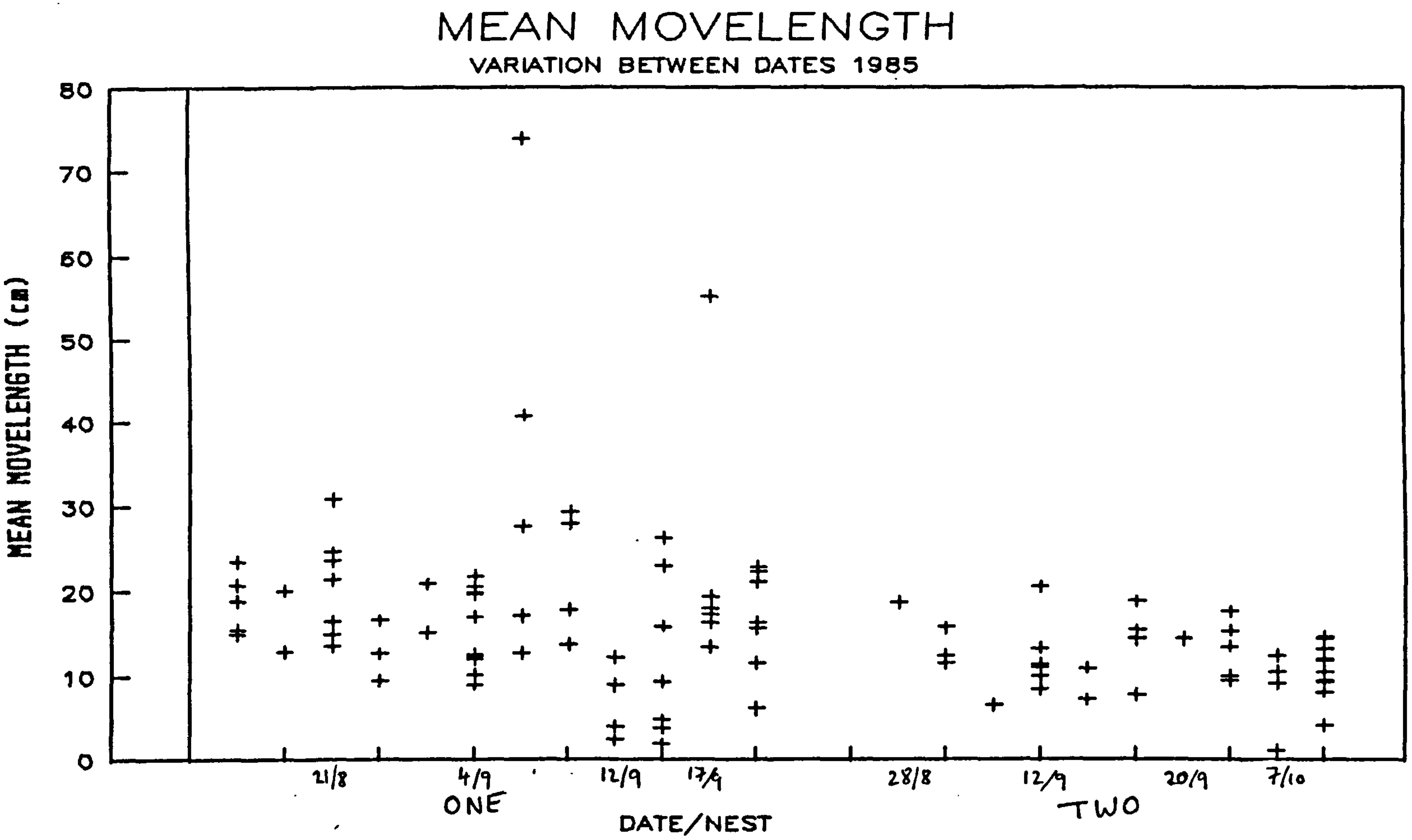

Figure 8.37. Variations in movelengths between ants from different dates.

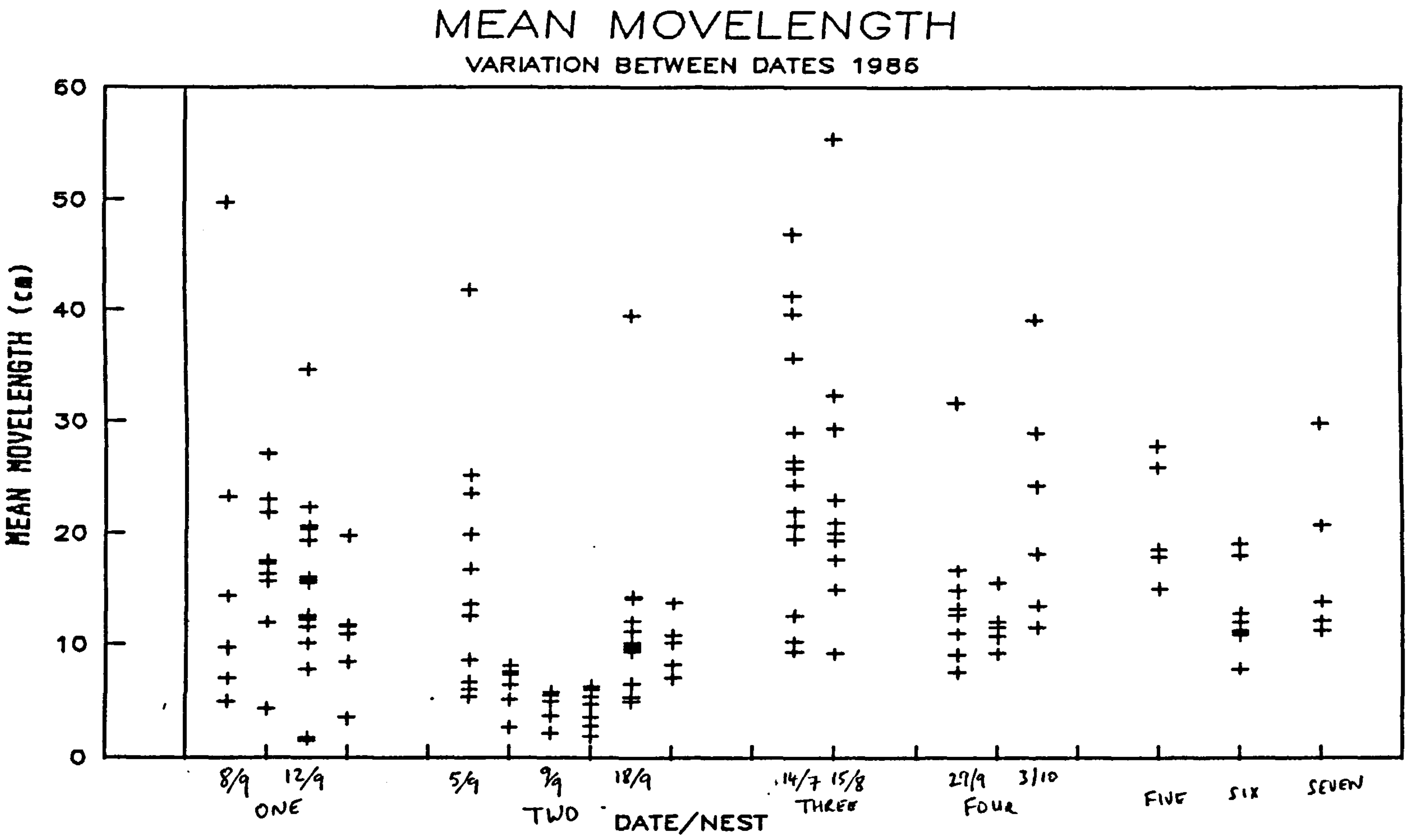

Figure 8.37. Variations in movelengths between ants from different dates.

YEAR	NEST	NO. DATES	NO. STEPS	F	DF	SIGN.
1985	ONE	10	757	5.03	9,747	$p<0.001$
1985	TWO	6	310	2.74	5,304	$p<0.025$
1986	ONE	4	290	2.15	3,286	$p<0.2$
1986	TWO	6	379	46.47	5,373	$p<0.001$
1986	THREE	2	277	117.42	2,275	$p<0.001$
1986	FOUR	3	136	24.76	2,133	$p<0.001$

Table 8.53. Summary of analyses of variance of movelengths of ants followed in the field between dates.

YEAR	NEST	NO. DATES	NO. ANTS	W	DF	SIGN.
1985	ONE	11	52	24.5	20	n.s.
1985	TWO	8	21	14.3	14	n.s.
1986	ONE	4	25	2.38	6	n.s.
1986	TWO	5	20	8.16	8	n.s.
1986	THREE	2	6	INSUFFICIENT DATA FOR ANALYSIS		
1986	FOUR	3	9	3.54	4	n.s.

Table 8.54. Summary of Mardia-Watson-Wheeler tests comparing the distribution of ants' prefered movedirections between dates.

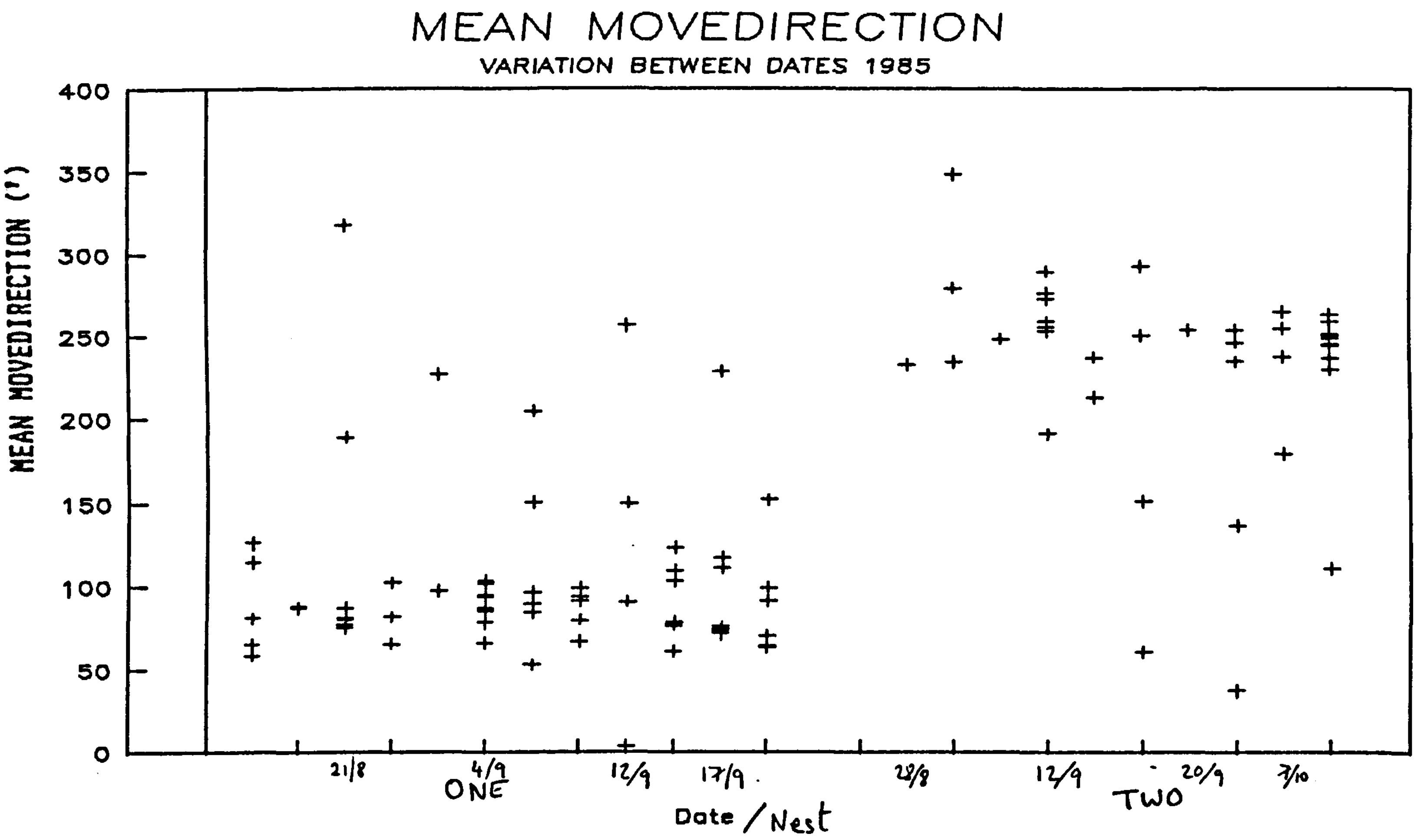

Figure 8.38. Variations in movedirection between ants from different nests.

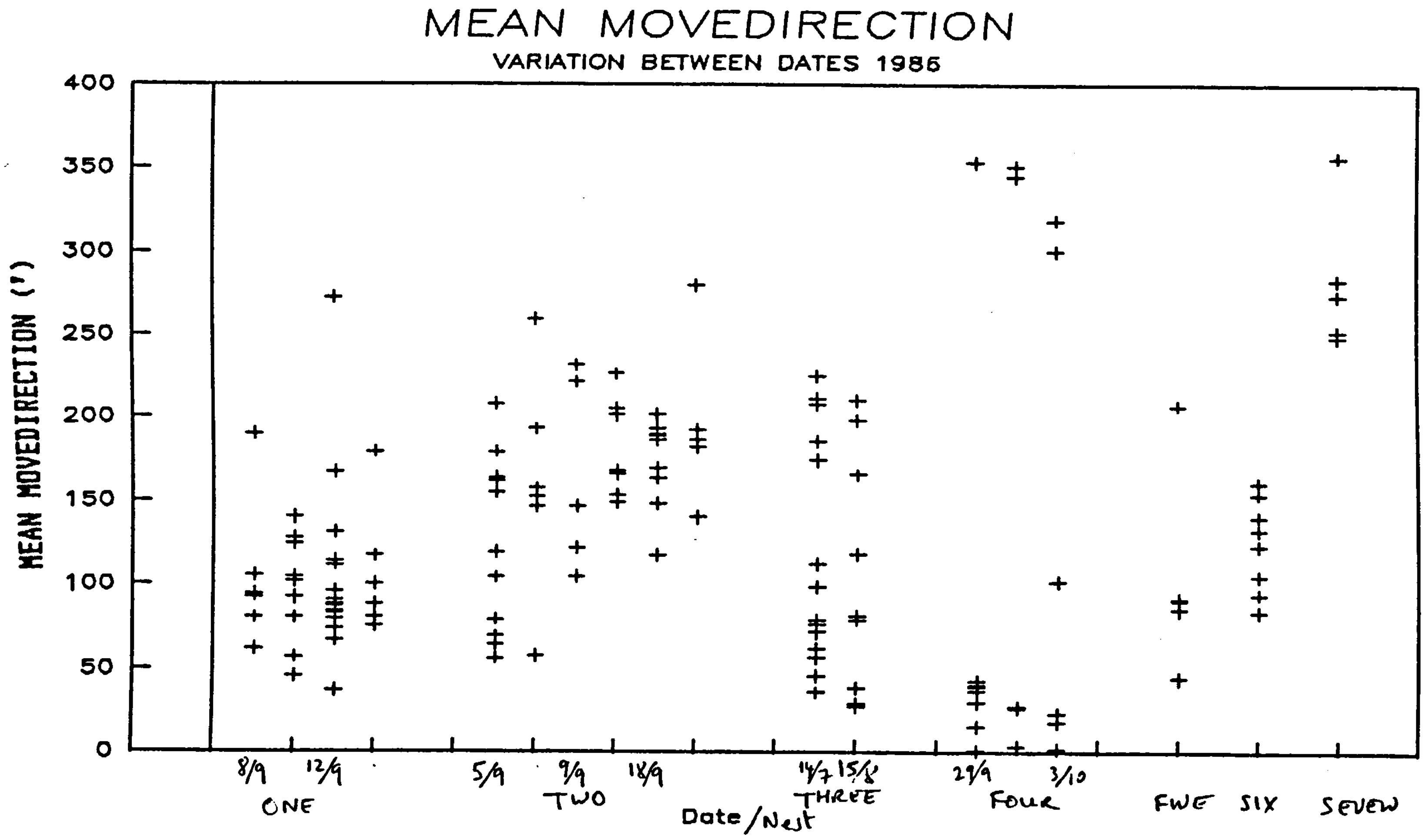

Figure 8.38. Variations in movedirection between ants from different nests.

DATE	1985		NEST			1986
DATE	ONE	TWO	ONE	TWO	THREE	FOUR
1	4/4	3/5	2/6	1/9	4/12	4/7
2	2/2	4/6	6/7	3/6	2/10	4/5
3	5/7	1/2	11/16	0/5		1/4
4	3/3	1/4	6/6	2/7	4/12	
5	2/2	1/4				
6	10/11	1/4				
7	4/5	8/10				
8	4/5					
9	1/4					
10	5/7					
11	5/7					
12	6/7					

Table 8.55. Proportion of ants which moved c#onsistently in one directeion on each date.

YEAR	NEST	NO. DATES	NO. ANTS	H	DF	SIGN.
1985	ONE	10 (12)	65	24.96	9	p<0.01
1985	TWO	6 (9)	38	3.38	5	n.s.
1986	ONE	4	37	1.45	3	n.s.
1986	TWO	6	47	20.9	5	p<0.001
1986	THREE	2	25	8.64	1	p<0.01
1986	FOUR	3	19	1.05	2	n.s.

Table 8.56. Summary of Kruskall-Wallis analyses comparing distribution of mean distances of foragers from their nests between dates. For both nests of 1985 it was necessary to merge data from adjacent dates before analysis; the actual number of dates is given in parenthesis.

summarized in Table 8.56, revealed that for three of the six nests there were significant differences between dates in the distance of the foragers from the nest. Thus on some dates the ants foraged further from the nest than on other dates.

For Nest One in 1985 and for Nests Two in 1986 there was no apparent pattern in this variation. For Nest Three in 1986 there were only two dates for comparison; ants foraged further from the nest on the second occasion. For the other three nests there was no indication that foraging distances varied between dates.

d/ bearing from nest.

The distribution of individual mean bearings from the nest on each date are presented in Figure 8.40. These bearings were compared between dates by means of either Rayleigh tests or Mardia-Watson-Wheeler tests.

Rayleigh tests were used for those nests where there was significant clumping of individual's mean bearings around the supermean bearing for five or more dates. Rayleigh tests were used to compare bearings between dates for Nest One in 1985 and for Nest Two of 1986.

For Nest One of 1985 the supermean bearings of eight dates were significantly clumped around the grand mean bearing of 76.45' ($r=0.9926$, $n=8$ dates, $p<0.001$) showing that the ants were located in the same direction on the different dates.

Similarily, the foragers from Nest Two of 1986 were located in the same direction on different dates. The supermean bearings of 5 dates (merging 8 & 9 September) were significantly clumped around the grand mean bearing of 160.58' ($r=0.9342$, $n=5$ dates, $p<0.01$).

For Nest Two of 1985 and Nests One, Three and Four of 1986 Mardia-Watson-Wheeler tests were used to compare the distribution of individual mean bearings between dates. There were no occasions where the distributions varied significantly between dates. Hence

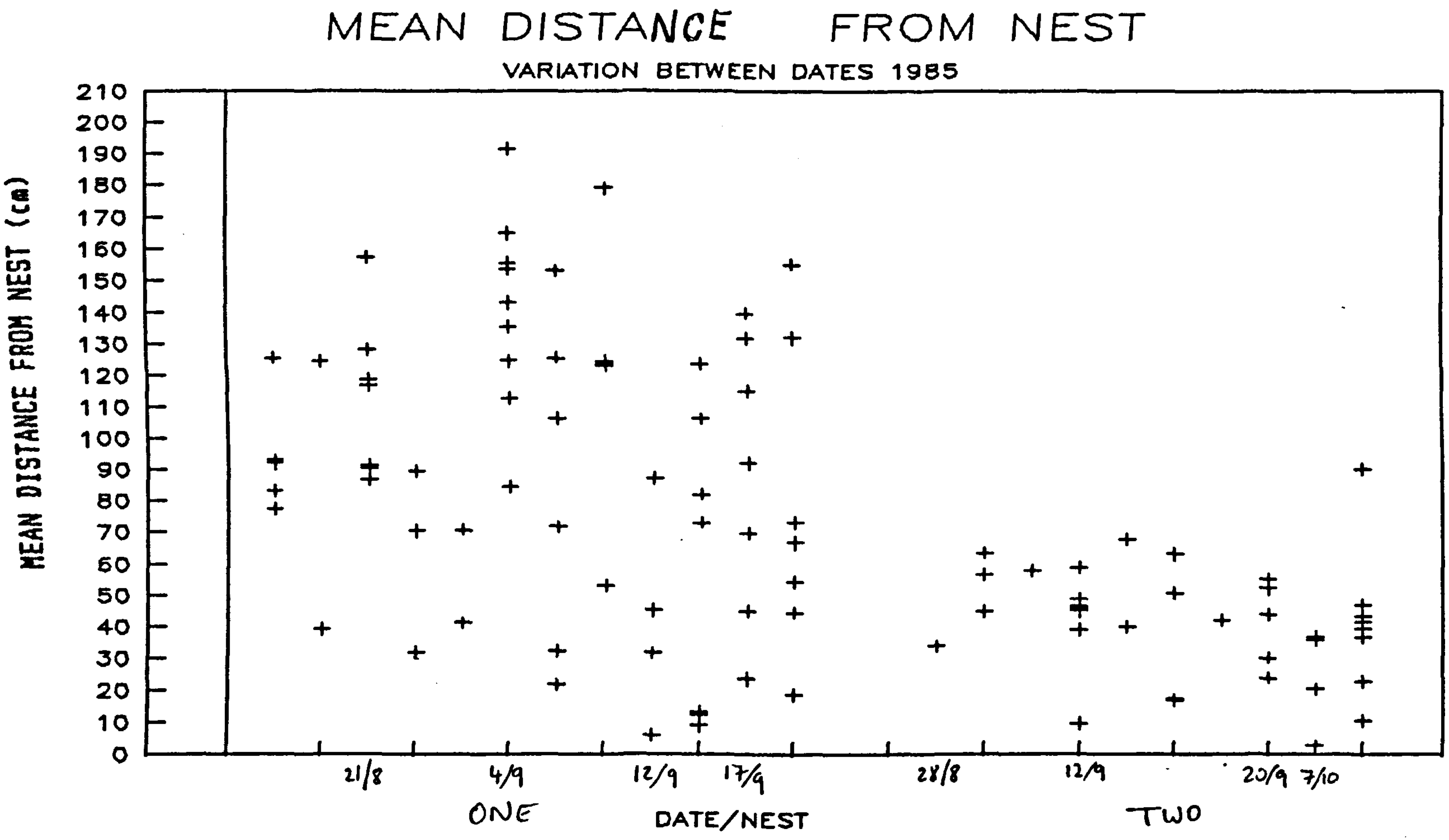

Figure 8.39. Variations in mean distance from the nest between ants from different dates.

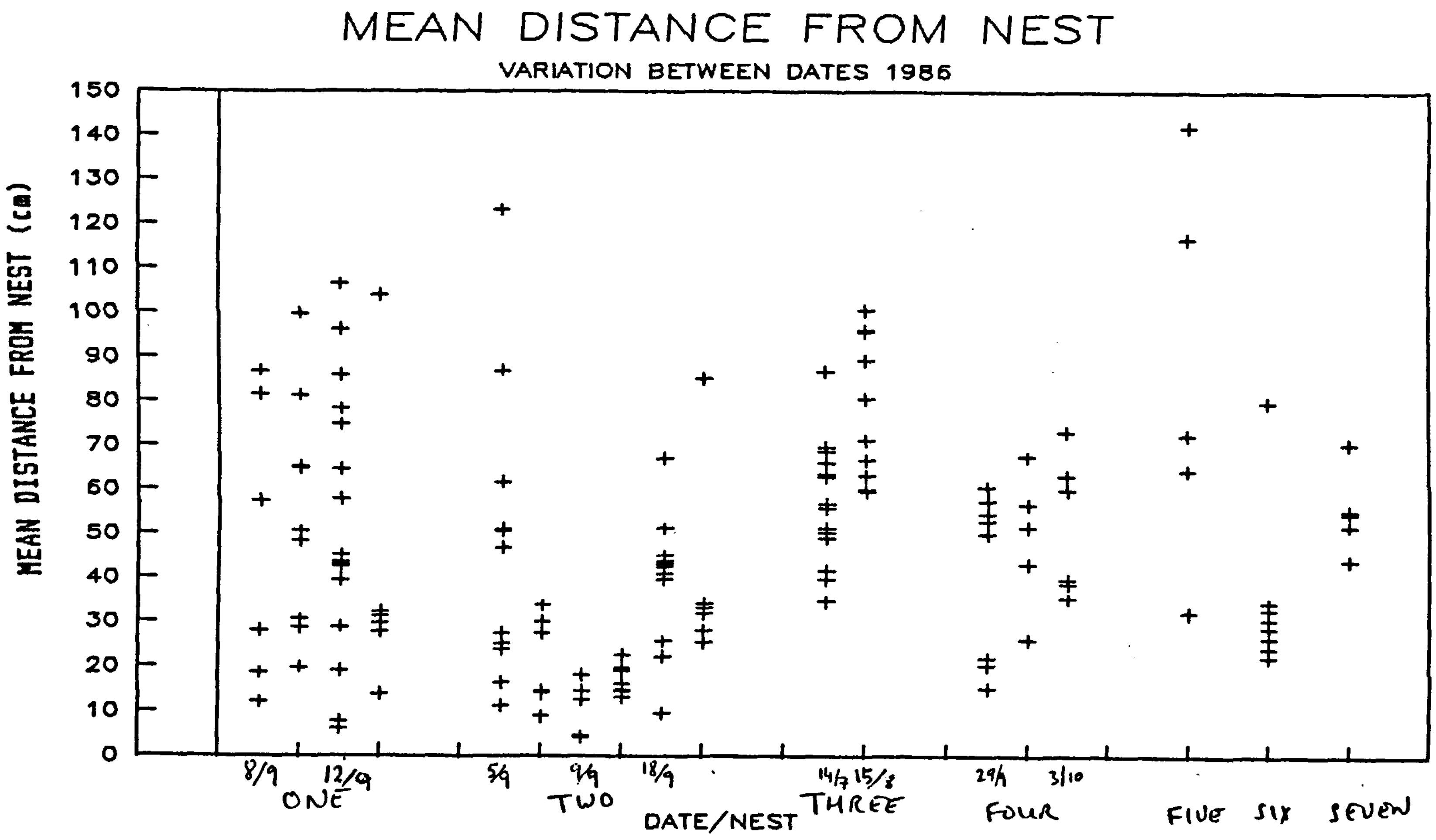

Figure 8.39. Variations in mean distance from the nest between ants from different dates.

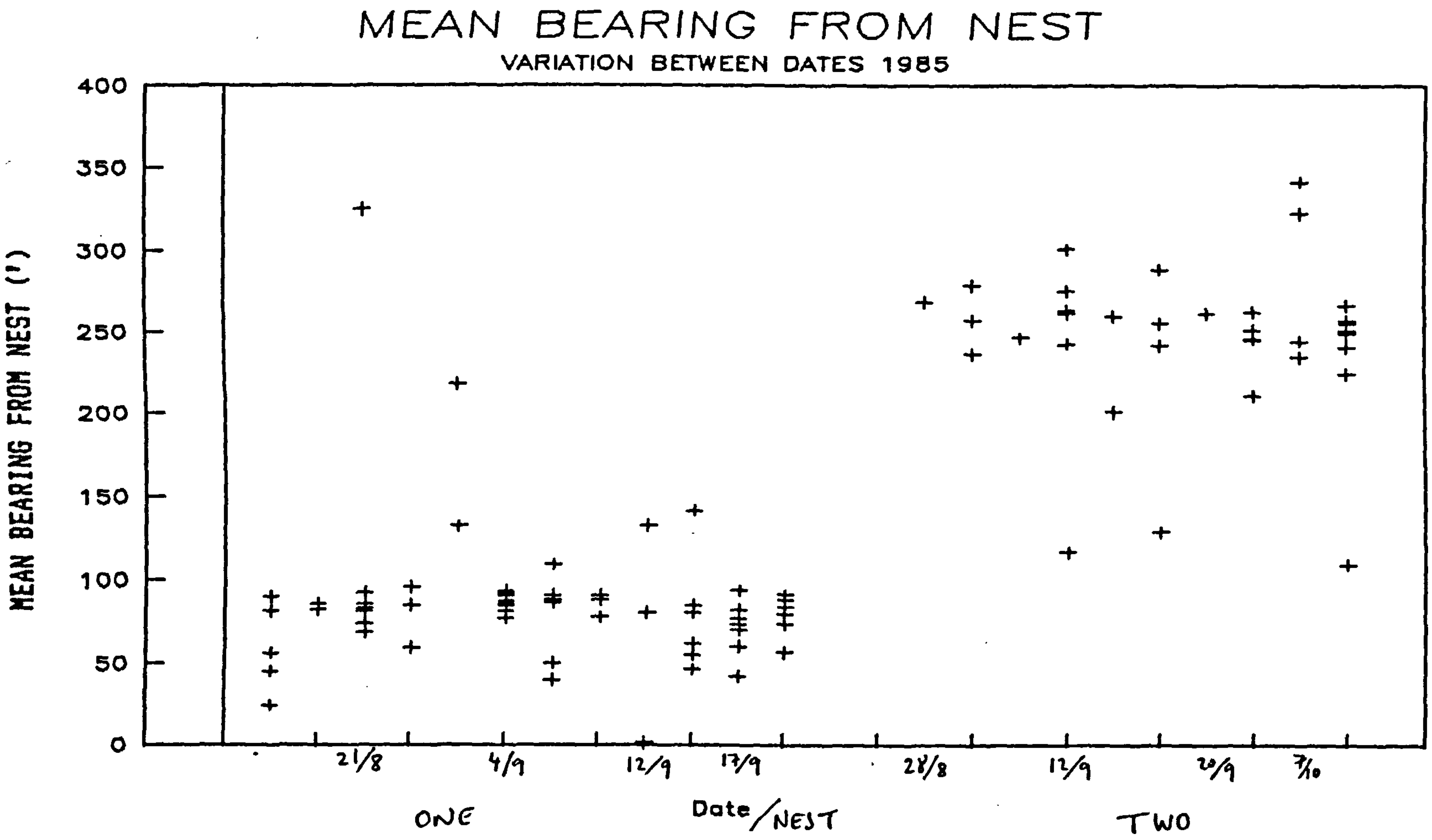

Figure 8.40. Variations in mean bearing between ants from different dates.

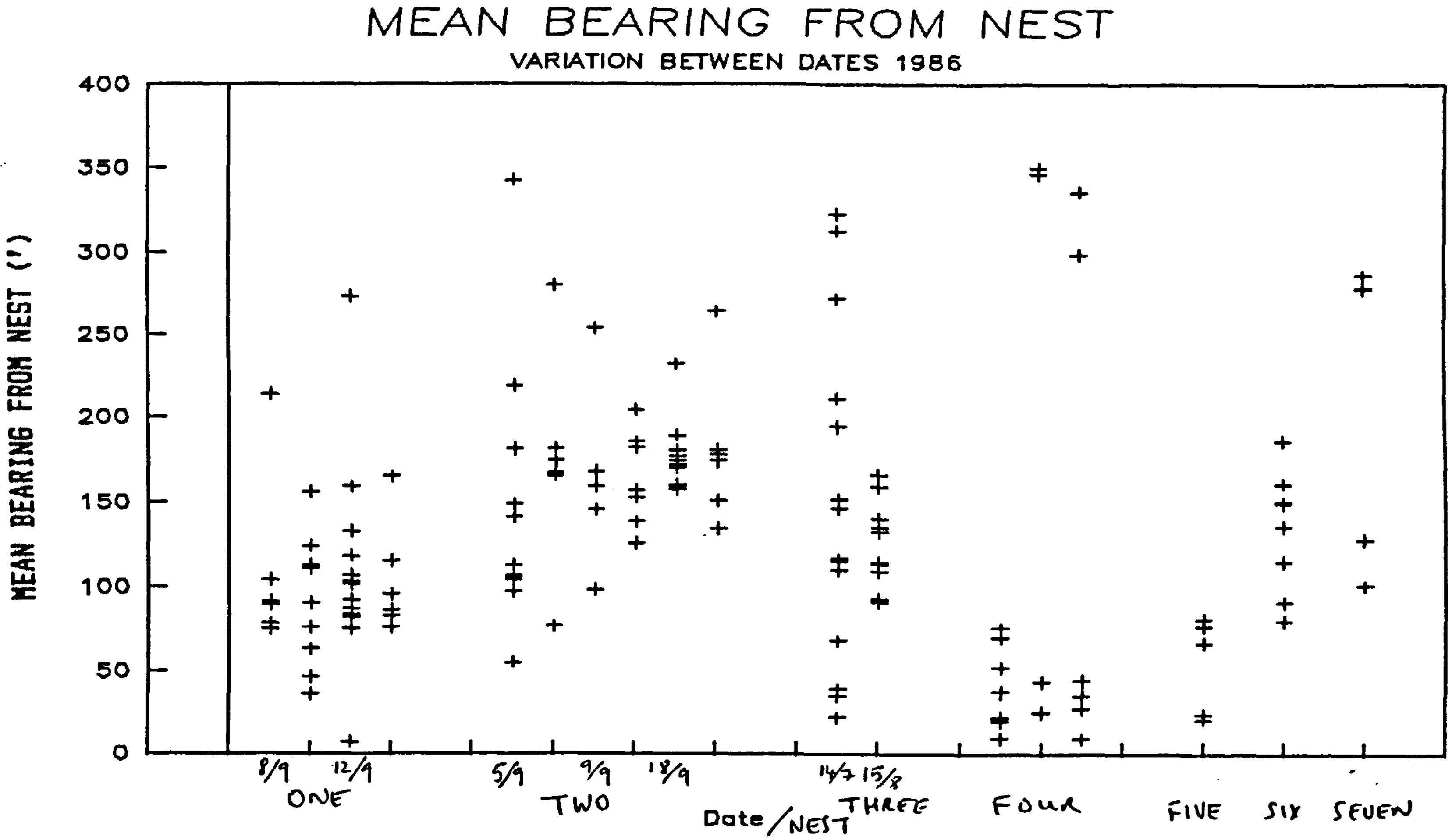

Figure 8.40. Variations in mean bearing between ants from different dates.

the ants were equally likely to be located in the same direction from the nest on each date. (1985, Nest Two: W=11.01, df=8, n.s.; 1986, Nest One: W=3.69, df=6, n.s.; 1986 Nest Three: "2-sample test" X-sq=1.04, df=2, n.s.; 1986 Nest Four: W=4.996, n=5,4,4, n.s.).

8.4.6 VARIATION BETWEEN "APHID-TENDERS" AND "SCAVENGERS".

The durations for which the trails of aphid-tenders and scavengers were followed are displayed in Figure 8.41 which reveals that there there were no great differences between the groups. In some cases, such as for Nest One of 1985, the range of durations of scavengers trails extends further than that for aphid tenders. Such discrepancies can be explained by the fact that aphid-tenders trails come to a definite conclusion whilst those of general scavengers do not.

a/ movelength.

The movelength of aphid-tenders, unsuccessful round-trippers and scavengers are displayed in Figure 8.42. From this it would seem that the mean movelengths of aphid-tenders are less variable than those of other foragers. This consistency even seems to extend between nests for, with the exception of Nest Three, the majority of aphid-tenders mean movelengths fall within 10 and 30cm. The range for the other foragers was greater as they include both shorter and longer mean movelengths.

Analyses of variance (by ranks) revealed that for Nests Two and Three of 1986 there were significant differences in the movelengths of aphid-tenders and scavengers. These analyses are summarized in Table 8.57.

b/ movedirection.

The distributions of the mean movedirections of aphid-tenders and general scavengers are presented in Figure 8.43 from which it appears that the mean movdirections of the aphid-tenders are less variable. A series of Mardia-Watson-Wheeler tests were used to compare

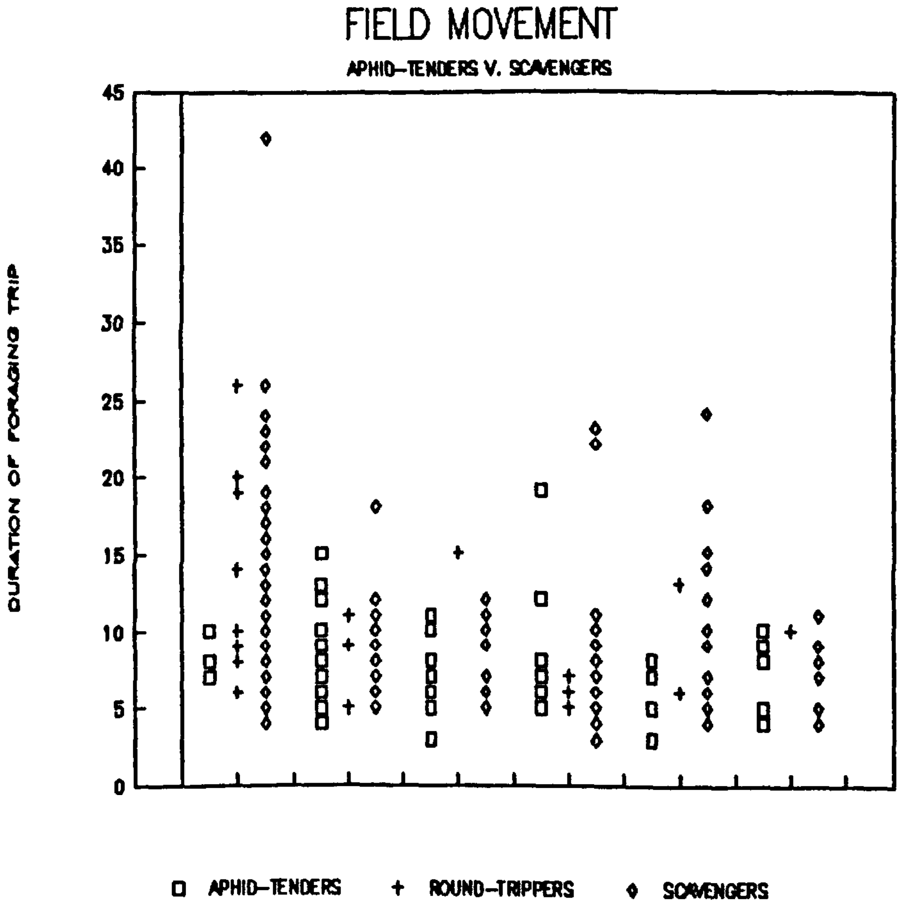

Figure 8.41 Comparison of durations of scavengers and aphid-tenders trailed in the field.

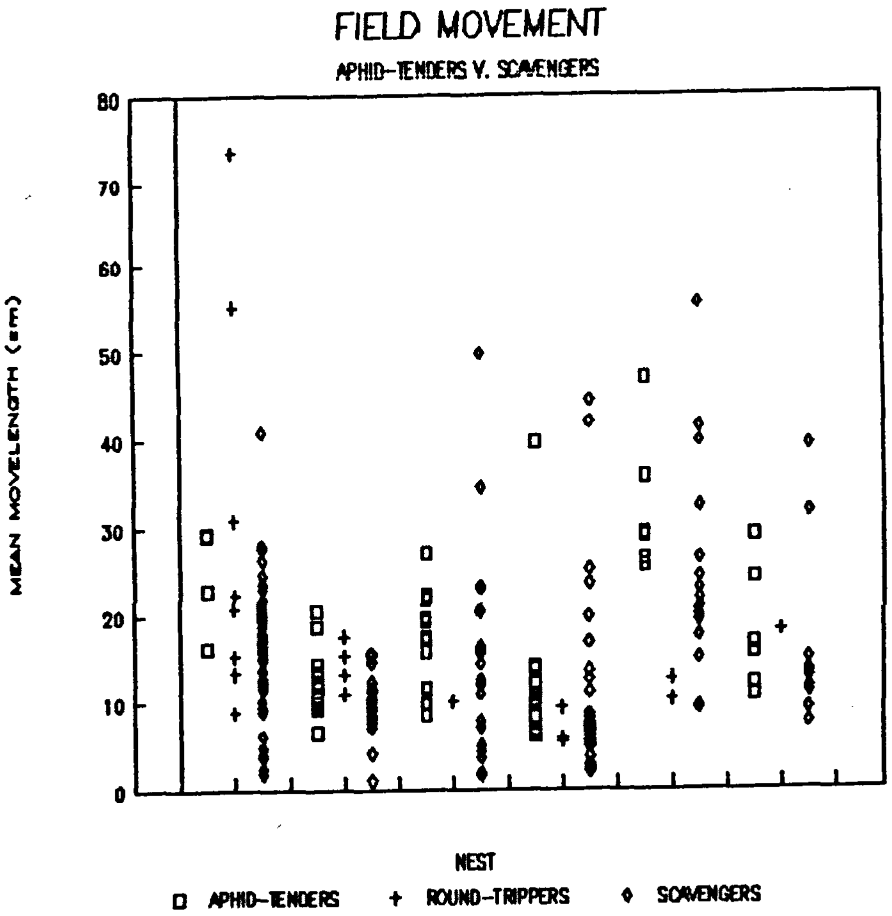

Figure 8.42. Comparison of movelengths of scavengers and aphid-tenders trailed in the field.

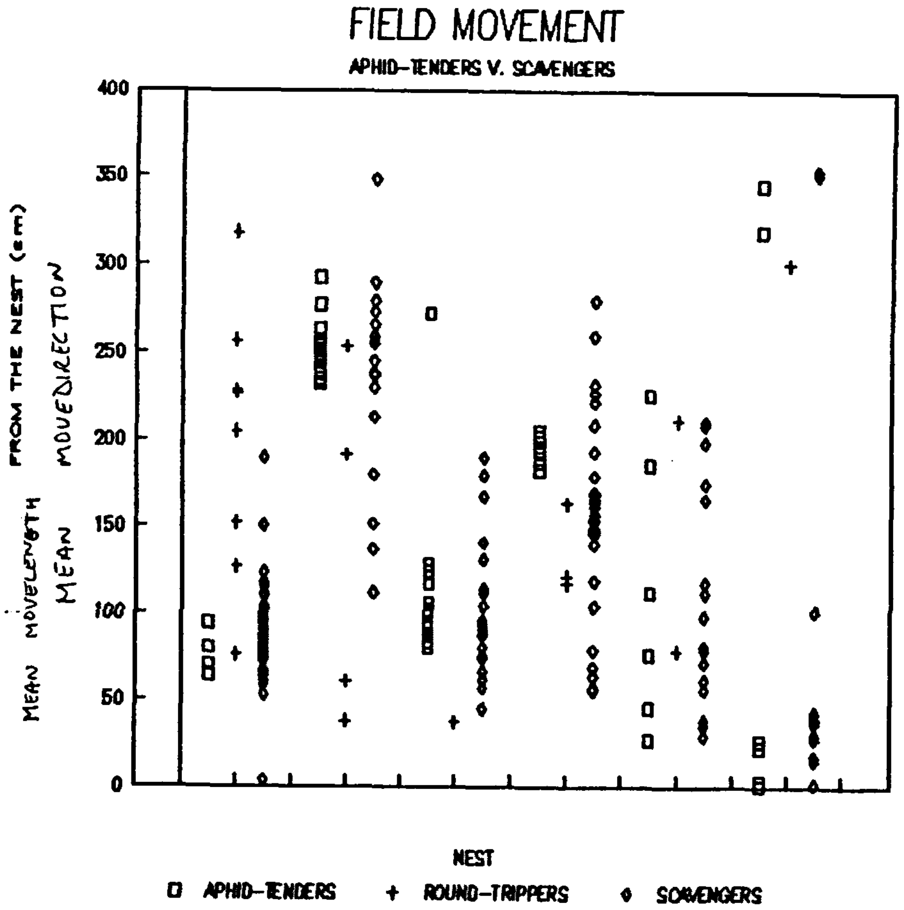

Figure 8.43. Comparison of movedirections of scavengers and aphid-tenders trailed in the field.

YEAR	NEST	No ANTS	No. AT	MOVELENGTH H	p	DISTANCE FROM NEST H	p
1985	ONE	65	4	3.6513	<0.1	0.2154	n.s.
	TWO	38	17	2.1980	n.s.	6.0092	p<0.05
1986	ONE	37	13	1.1700	n.s.	0.4049	n.s.
	TWO	47	13	4.3801	p<0.05	4.2811	p<0.05
	THREE	25	6	4.9595	p<0.05	2.7368	n.s.
	FOUR	19	6	1.1077	n.s.	1.5077	n.s.
	FIVE	5	4	0	n.s.	2.0000	n.s.
	SIX	8	2	-12.8888	n.t.	-6.8889	n.s.
	SEVEN	5	0	------	n.t.	------	n.s.

Table 8.57. Summary of Kruskall-Wallis analyses comparing the mean movelength and mean distance from the nest of aphid-tenders and scavengers. AT = Aphid-Tenders.

YEAR	NEST	No ANTS	No. AT	MOVEDIRECTION X-sq	p	BEARING FROM NEST X-sq	p
1985	ONE	65	4	2.8349	n.s.	0.0714	n.s.
	TWO	38	17	10.3295	p<0.01	8.144	p<0.05
1986	ONE	37	13	3.5324	n.s.	1.8962	n.s.
	TWO	47	13	25.5306	p<0.01	12.6293	p<0.002
	THREE	25	6	0.7506	n.s.	3.6993	n.s.
	FOUR	19	6	2.2694	n.s.	0.8596	n.s.
	FIVE	5	4	B=1.0	n.t.	B=1.0	n.t.
	SIX	8	2	B=3.41	n.t.	B=3.41	n.t.
	SEVEN	5	0	------	n.t.	------	n.t.

Table 8.58. Summary of Mardia-Watson-Wheeler tests comparing the mean movedirections and mean bearings from the nest of aphid-tenders and scavengers.

these distributions and found that for Nest Two in 1985 and Nest Two in 1986 these differences were indeed statistically significant (Table 8.58).

The proportions of aphid-tenders, round-trippers and scavengers which were moved consistently in a constant direction are presented in Table 8.59. For most nests it was the case that a greater proportion of the aphid-tenders were directed. Less round-trippers were directed than for either of the other two groups.

c/ mean distance.

The mean distances of aphid-tenders, round-trippers and scavengers from their nests are presented in Figure 8.44. Analyses of variance (by ranks) revealed that for Nest Two in 1985 and in 1986 there were significant differences between the groups in this measure with the aphid-tenders generally being found further from the nest. These analyses are summarized in Table 8.57.

d/ mean bearing.

The distributions of the mean bearings from the nest of aphid- tenders and general scavengers are presented in Figure 8.46, from which it appears that the mean bearings of the aphid-tenders are less variable. A series of Mardia-Watson-Wheeler tests were used to compare these distributions and found that for Nest Two in 1985 and Nest Two in 1986 these differences were statistically significant (Table 8.58).

YEAR	NEST	NO. ANTS	APHID TENDERS		ROUND TRIPPERS		SCAVENGERS		N<5
1985	ONE	65	4/4	1.00	1/8	0.125	43/52	0.83	1
	TWO	38	11/15	0.73	1/4	0.25	9/17	0.53	2
1986	ONE	37	10/10	1.00	0/1	0.00	14/24	0.58	2
	TWO	47	11/13	0.85	0/3	0.00	9/29	0.31	2
	THREE	25	1/5	0.20	1/2	0.50	4/15	0.27	3
	FOUR	19	4/5	0.80	0/0	----	5/10	0.50	2
	FIVE	5	3/4	0.75	0/1	0.00	0/0	----	0
	SIX	8	1/2	0.50	0/0	----	2/3	0.67	3
	SEVEN	5	0/0	----	0/0	----	1/4	0.25	1

Table 8.59. The proportion of aphid-tenders, round-trippers and scavengers which moved consistently in the same direction throughout their foray.

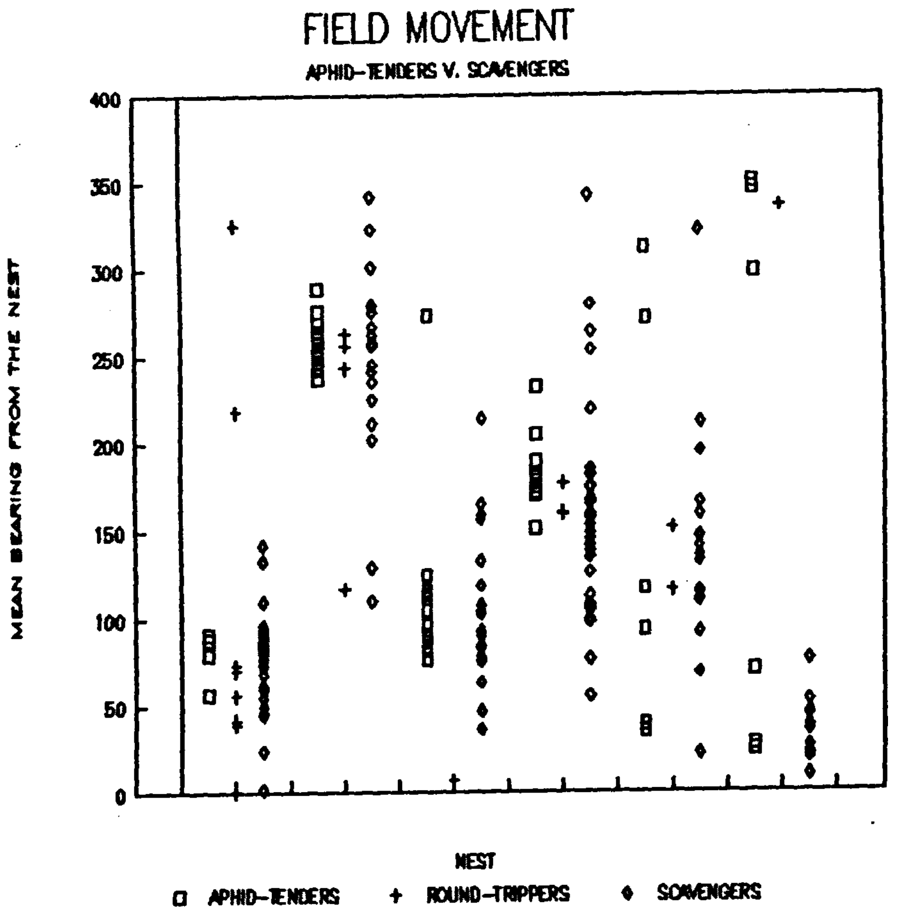

Figure 8.45. Comparison of mean bearings from the nest of scavengers and aphid-tenders trailed in the field.

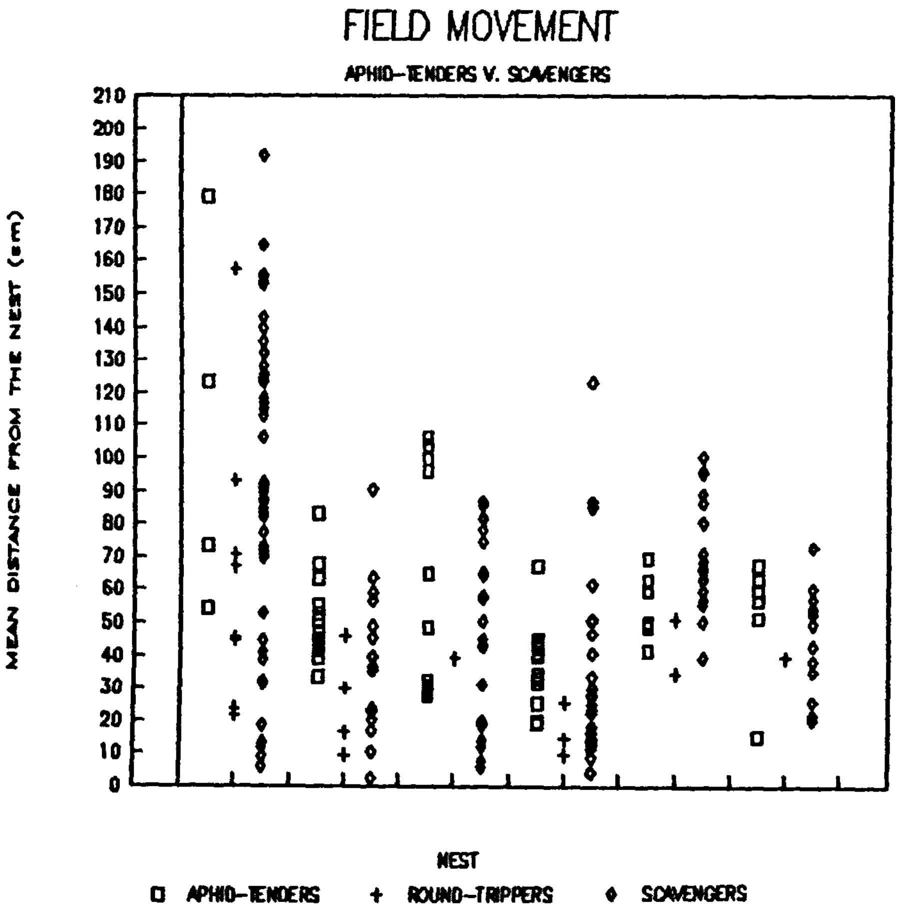

Figure 8.44. Comparison of mean distances from the nest of scavengers and aphid-tenders trailed in the field.

DISCUSSION

I first discuss the results relevant to each of the four aspects of foraging behaviour separately and try to interpret these results on each aspect within the framework of optimal foraging theory. I then attempt to marry all these aspects together to give a fuller picture of foraging behaviour. From this fuller picture I will attempt to discern some of the pressures of natural selection which may have shaped the foraging behaviour of ***Myrmica rubra***.

9 FOOD CHOICE *IN MYRMICA RUBRA.*

Observations and experiments on food choice, and observation of foraging movements in the field reveal that the diet of ***M. rubra*** is composed of a mixture of honeydew collected from aphids and of scavenge and prey items.

9.1 LIQUID FOODS.

Honeydew collected from aphids on rosebushes and on other plants was the food source most frequently exploited by field colonies in the study area of the Wrotham rosebeds. Between a quarter and a third of all the ants followed were found to be going to tend aphids.

Moreover, of the ants whose paths were followed to a positive conclusion (i.e. until they reached an aphid bearing plant, found an item of food or returned to the nest, rather than getting "lost") almost three-quarters tended aphids; 73% in 1985 and 70% in 1986. Now it may have been easier to follow foragers which travelled directly to plants with aphld clusters than other foragers which took more elaborate paths as they searched for other foods; hence it is possible that the proportion of aphid- tenders is exaggerated by the extrapolation. Either way, honeydew made up a major portion of the diet.

Choice tests, performed with laboratory colony fragments revealed that some of the individual components of honeydew; sucrose, fructose, glucose and alanine solutions, were also included in the diet. Ants were also observed to drink pure water.

These choice tests revealed something of the ability of these ants to discriminate between potential foods and so illucidate the foodselection processesinvolved in determining the diet.

The ability to discriminate between the test solutions and pure water depended on the concentration of the test solutions. Of the sugarstested the ants were most sensitive to sucrose, for a positive response occured at the lowest concentration, followed by fructose and glucose in that order.

This pattern of responsiveness is not universal amongst insects. Hassett, Dethier and Gans (1950), for example, found that the acceptance threshold of blowflies, ***Phormia spp*.** was lower for fructose (0.0058M) than for sucrose (0.0098M). Glucose, they found, had a much higher threshold again (0.13M).

However, the concentrations at which preferences are first displayed for sugar solutions match fairly well to the observation of Schmidt (1938) on taste thresholds in ***M. rubra*** (Table 2.3). He also found that foragers were more sensitive to sucrose than to fructose or glucose, a preferential response to sucrose occured at 0.0066M (my results show that the threshold concentration was between 0.001M and 0.01M).

Schmidt found that fructose and glucose solutions of 0.02M were prefered to water; these results show that fructose was prefered in (some) trials at 0.01M concentration and that glusose was prefered at 0.1M concentrations but not at 0.01M.

These results therefore support Schmidt's findings that sensitivity to sucrose solutions is much the same as in ***Lasius niger*** and "***Myrmica rubida***", and that sensitivity to fructose and glucose is about the same as in ***M. rubida***, but that ***M. rubra*** foragers are more sensitive to the former sugars than ***L. niger***.

These results also indicate that ***M. rubra*** foragers are more sensitive to sucrose than ***Formica lugubris*** foragers for Sudd and Sudd (1985) found that sucrose solutions had to be 0.15M before half of the ants of this species tested responded by drinking. However Sudd and Sudd tested their foragers in the field where other food sources were available. Indeed they found that when honeydew from aphids became available the concentration which caused half of the ants to drink increased from 0.15M to 0.9M. Now if all the aphids could be removed again, and all the other food sources removed as well, it could be that this response threshold would fall to below 0.15M.

A similar change in pattern to that observed by Sudd and Sudd was found here. Whilst the ants drank glucose solutions when they were in competition with water, they did not drink glucose when an equimolar solution of sucrose was also available.

The pattern of sugar sensitivity derived from the tests in competition with water is reinforced by the taste trials where sugars were in direct competition with each other. The observation that sucrose was prefered to fructose and to glucose when presented in equimolar (0.1M) solutions is fully consistent with this acceptability series and with the findings of Schmidt. However, the finding that fructose was prefered to glucose, while in keeping with the acceptability series conflicts with the findings of Schmidt. His finding that these sugars had the same acceptance concentrations; therefore no preference would be exhibited between equimolar solutions of these two sugars.

Now if leucine were to be placed in the series of acceptability with the sugars it would take first place for it was accepted in preferenceto water while ten times more dilute than the weakest sucrose solution which evoked a preferential response. Such sensitivity to amino acids in insects has been noted elsewhere, by e.g. Hansen (1978) who demonstrated that blowfly, ***Phormia*** were 100 times more responsive to the amino acid phenylalanine than to sucrose solutions.

However, this placement is confounded by the trials where 0.01M leucine was placed in direct competition with 0.1M sucrose:- the sucrose solution was prefered in each trial.

These results would certainly seem to be anomalous; on the one hand the minimum threshold at which ants respond is 10 times lower for leucine than sucrose but on the other hand more ants drink from sucrose droplets than from leucine droplets at one tenthoftheconcentration when in direct competition.

It was also noticable that the amount of drinking from 0.01M leucine droplets was more or less the same whether it was in competition with pure water or with 0.1M sucrose. It might be speculated that the demand for leucine is the same under both experimental regimes and that this demand is satisfied by allocating a certain number of workers to the task of retrieving it. The fate of the remaining workers depends on the other choice available; if pure water is also available a few might drink but the majority ignore it - thus a preference for leucine is demonstrated; if 0.1M sucrose is the alternative many ants will drink from these droplets - a preference for sucrose would be exhibited.

Perhaps the anomality might be resolved by considering the actual concentrations used in the trials. In the direct competition tests the concentrations were ten times higher (leucine 0.01M, sucrose 0.1M) than the lowest detected concentrations (leucine 0.001M, sucrose 0.01M). Perhaps the responses to leucine and to sucrose do not increase in the same manner with increasing concentration.

The work of Cammaerts (1977) illustrates a behavioural mechanism whereby the pattern of response to increasing concentrations may vary. She found that on finding pure water some foragers would drink but none recruited nestmates. However when an ant found a weak sucrose solution more drank and some recruited nestmates on their return to the nest. Moreover as the sucrose concentration increased above 0.01M so too did the intensity of the recruitment response and the number of workers responding to the recruitment signals. Thus the possible responses run from "all ignore" through "drink, no recruitment" to"drink and recruit".

These changing responses might explain the anomaly in the sucrose/leucine results. It is possible that the switch from treating a weak solution as if it was water to drinking without recruitment occurs at lower concentrations for leucine than for sucrose. And that the switch from drinking without recruitment to drinking and recruiting occurs at lower molarity for sucrose than for leucine.

It was noted that the pattern of response to the test solutions over time varied depending on the substance tested. For solutions of sucrose, fructose and leucine the numbers of ant-minutes spent drinking increased greatly within the first 10-20 minutes and tailed off after 30 minutes or so. The initial rise in number is certainly indicative of recruitment behaviour. Tailing off in some cases can be attributed to the drying up of the test solution but in other cases there seemed to be no obvious cause. Perhaps interferance between workers at the droplets meant that many could not get access to drink and so the number of foragers peaked at a maximum determined by the size of the droplet. Perhaps also recruitment declined as workers became sated.

The response to glucose solutions did not generally follow the time pattern exhibited for the other solutions, although the peak and decline pattern was observed on some occasions. When glucose was in competition to pure water the typical pattern was one where the numbers drinking gradually increased throughout the 60 minutes of the trial. Why such a pattern should appear is unclear - perhaps the recruitment response to 0.1M glucose is weaker than that for 0.1M sucrose and fructose.

The variations observed in the glucose response pattern depending on the nature of the competing substance might reflect the ability of the other solution to cause recruitment. Thus the slow increase in competition with water could have been because neither caused strong recruitment. But in direct competition with sucrose this pattern for glucose echoed the sucrose pattern because the presence of the sucrose solution caused much recruitment.

9.2 SOLID FOOD ITEMS.

The remainder of the foraging population followed in the field which did not tend aphids would seem to fit a role which might be termed "scavenger". These scavengers moved over the soil surface in search of prey or scavenge items. Only a small proportion of the scavengers were successful. The proportion which found an item of food on their foray was 1 out of 12 (8.3%) in 1985 and 2 out of 16 (12.5%) in 1986 respectively. Now if the nutritive value of scavenge and prey items was 20-30 times greater than that of a crop-load of honeydew then both sources would provide much the same value of food to the colony.

The booty returned to the nest suggested that the success of "scavengers" would seem to be in two "overlapping" areas; some items were obtained by active predation while others were found dead and scavenged in the literal sense.

The beetles and caterpillars carried to the nest were certainly victims of active predation, for they were carried to the nest still alive. Indeed on occasions these preys were able to break free or were released. However as they tried to escape they were inevitably recaptured.

Several of the other items carried to the nest might also have been procured by active predation, followed by dismemberment of the carcasses. However, the general state and appearance of the items collected from returning foragers strongly suggests that they had been dead for some considerable time before they were carried to the nest.

Some items, recorded for instance as "hollow tubes", appear to have very little if any nutritive value, but this subjective assessment may well be erroneous.

Many of the items returned could not be identified and were recorded as "amorphous". Of course this should not be taken to imply anything about their food value. Such "amorphous" objects could have a very high nutritive value if, for example, it was made up of the fat bodies of a dismembered prey. Alternately such globs could be made up of some otherwise inert material soaked with a nutritous liquid, such as a prey's body fluids or honeydew rained down from or expelled by an aphid. Indeed Agbooba (1985) has observed that two species of ***Aphaenogaster* (*senilis*** and ***subterranea*)** use various materials (leaf debris, pieces of twigs or grains of sand) as media to transfer liquid foods to the nest. These species do not perform trophallactic exchanges. Instead the foragers used these materials to soak up sugar solutions and prey juices and then used these "sponges" to transfer these liquids foods to the nest.

As food items were only collected from foragers returning to one nest entrance (of a colony which operated through several entrances) it is a restricted sample. A more complete picture of the diet of this ant might have been obtained if foragers returning to the other entrances had also been robbed of their booty.

Indeed as different entrances were used to exploit different areas of the surrounding terrain it is possible that local differences in potential prey populations may have been reflected in the booty returned, such as that found by Ayre (1959) in ***Formica subnitens*** where the number of insect prey returned varied between four foraging trails. However it is probable that this restriction was not too severe as the entrance used was the main one in the vicinity. Anyhow the sampling method may have been too crude to detect differences in the type of prey returned. No assessment was made of potential prey populations.

The range of dietary items collected from returning foragers is similar to Brian's (1977) summary list (#2.3 above). The discrepancies can easily be accounted for by sampling error (my collection of booty would only have been a small fragment of the total returned to the nest) and by habitat differences in the availablility of food (e.g. Brian reports that seeds of tormentil are taken in acid grassland; tormentil was not among the plants found in the Wrotham rosebeds). The range of food types making up the diet of this ant confirms its standing as a generalist forager combining active predation and scavenging with aphid tending.

The range of items in the booty returned to the nest would suggest that foragers make little choice in the selection of the solid items to include in the diet. However, the foragers must have used some selection processes for they did exclude inert material such as grit and soil particles.

Presumably some criterion of taste was used in the selection of solid items. However, there was no evidence from any of the food trials that taste was used to discriminate between food types, even though there were considerable differences in composition between the foods offered, e.g. cheddar v. cooked ham; 17.26 kJ/g v. 17.68 kJ/g, 25.4% v. 16.3% protein, 34.5% v. 39.6% fat (Roberts, 1974).

This might suggest that the ants do not discriminate between solid food items on the basis of taste; either an item is acceptable in which case it will be removed (eventually!) or it will be regarded as unacceptable and ignored; there is no scale of relative acceptability.

However, it is possible that the ants did discriminate between types of solids but that this discrimination was not shown up as a difference in the rate or number of bait removals. It was observed that ants at baits, perhaps more particularly at cheese baits, spent time imbibing liquid from the surface of the baits.

Such foragers could provision the colony by returning with a crop full of this (lipid rich!) liquid and so satisfy the nutritional requirements of the colony without recourse to the removal of the baits. Thus there would be two components in the ants' response to finding solid food items; the "removal" and "drinking" responses.

If the "drinking" response were to be pronounced then it would eclipse, at least partially, the "removal" response. Thus real discrimination between solid food types might have been overlooked as only part of the ants' functional response was considered. Preferences might have been revealed if the amount of liquid drunk, the time spent drinking or the number of foragers accumulated at each bait type had been assessed as well as the "removal" responses. Alternatively, dry baits might be developed, perhaps styrofoam spheres, so that any "drinking" response would be eliminated.

Such drinking responses will also have occured in the trials used to determine whether the foragers had any size preference among solid baits. This complication might explain why only three of the size trials revealed a size preference in removal rates. It is noteable that the ant species where size preferences were found are predominantly seed harvesters; dry seeds do not allow for a "drinking" response!

In the three trials where a size preference was demonstrated it was because smaller baits were removed quicker. However there were no differences in the total mass of baits of each size returned, indicating that all sizes were of much the same overall value to the colony.

Nonetheless it would be interesting to extend the range of sizes downwards to see whether the preference for smaller baits continued indefinitely or if some intermediate size was prefered to very small and to very large baits. There are obvious mechanical problems to be overcome in producing very small baits but if these could be overcome, perhaps by using styrofoam spheres (see e.g. Marshall et al., 1979, Baroni-Urbani and Neilsen, 1990), this could be a rewarding avenue of study.

Of course all the baits were large relative to the ants' size, even the smallest cheese bait (1x1x1mm) had a mass of c.1.151mg - more than 50% of the weight of an average worker (given as 2mg by Brian, 1973). However, ants have an ability to carry loads much greater than their own body weights (Traniello, 1989, summarizes the loading capacity of some species).

The largest baits removed had an approximate mass of 30mg - about 15 times the average worker's body weight! Baits were not excluded because they were unmovable. Similarly the presence of prey items several times larger than the foragers themselves is testimony to the ants' ability to capture, subdue and move large prey.

9.3 TO SCAVENGE OR TO TEND APHIDS.

One of the most basic foraging choices is whether to tend aphids or to scavenge on thier foray. I was not able to mark individual foragers permanently so there is no way of telling whether foragers were consistently scavengers or aphid tenders.

If this dichotomy is not a permanent feature it is possible that recruitment would provide a mechanism to determine whether foragers emerge as scavengers or as aphid-tenders. This suggestion is supported by the observations of Cammaerts (1977, 1978) who found that when ***M. rubra*** foragers recruited to sugar solutions they conveyed directional information but when they recruited to small prey items they merely activated recruits but did not give them any directional information.

These different recruitment systems might also be in play even if the dichotomy between scavengers and aphid tenders were to be a permanent feature. This mechanism could decide what a naive forager would do on its first foray; thereafter their behaviour could be determined by whether they were successful on this first trip. For instance, a forager which, on its first foraging trip, wandered over the terrain might be reinforced to continue such scavenging if it were to be successful in finding food. Similarily foragers which located aphids on their early trips would be reinforced to return to these aphids on subsequent trips. Such reinforcing behaviour has been reported in other species, e.g. Harkness (1977) and Schmid-Hempel (1984) report that some foragers of ***Cataglypsis bicolor*** return to the location of food finds on subsequent forays.

The dichotomy between scavengers and aphid-tenders might involve a temporal change in foragers' behaviour. There might be a temporal division of foragers behaviour (foraging is activity of the oldest workers) such that younger and less experienced foragers are the ones which tend aphids and the older more experienced foragers scavenge for other food items.

Such a temporal change, from aphid tenders to scavengers, matches Porter and Jorgensen's (1981) idea that foragers, being the oldest workers represent a disposable caste. The oldest foragers would be more "disposable" than younger ones. Foragers could be "trained" to made repeated profitable trips to aphid patches while they are young and have many such foraging trips "ahead of them". Older foragers, which have fewer foraging trips left, would give less reward if they were to be trained to go to aphids - after a few trips they would die and another forager would have to be "trained up" to take their place.

Of course such ideas are just speculation for the moment. However, if foragers could be given durable individual marks then an investigation into whether such mechanisms actually occur could be undertaken. This could then be a profitable direction for further research.

9.4 THE OPTIMALITY OF FOOD SELECTION.

The food preferences exhibited by the ants must have been shaped by the processes of natural selection; therefore the pattern of preferences should be such that it affords maximum fitness to the ant colony. But what exactly are the forces which have been in action and what criterion is optimized in order for the colony attains maximum fitness?

Many of the results here indicate that a natural selection pressure has acted to increase the rate at which energy is harvested by the colony and that the criterion which the ants' food selection processes optimize is the "rate of energy return to the colony".

In this discussion only gross rates of energy gain are considered, as foraging costs are not considered. Of course an optimal central place forager might be expected to maximize the net rate that energy is returned to the nest, but it is hoped that this approximation does not introduce too much of an error.

Certainly it would seem that foraging costs make up only a small fraction of the foraging rewards. For instance, Fewell (1988) found that in ***Pogonomyrmex occidentalis*** the energetic costs of foraging were less than 0.1% of the calorific reward of harvested seeds. Similarly, Nielsen and Baroni-Urbani (1990) found that for <u>Messor</u> <u>capitatus</u> the energetic reward of an average seed (about 650J) would be sufficient to maintain a workers basal metabolism (10mJ/mg/h) for over a thousand days or to allow it to carry a seed for a distance of 6.5 km!

In ***M. rubra***, too, the energetic rewards of foraging would seem to greatly outweigh the metabolic costs of foraging for Brian's (1973) calculation of the basal metabolism of ***M. rubra*** workers and queens revealed that an average 2mg worker required 22ug of sucrose per day to maintain itself while 4.6mg queens required 40ug of sucrose per day. Thus a colony fragment of 1 queen and 100 workers (typical of the fragments used in taste trials) would require the energetic equivalent of 2240ug (2.24mg) sucrose per day. This demand is more than met by the solutions available; 1ml of 0.1M sucrose contains 34.2mg of sucrose, fifteen times the daily requirement.

However, Traneillo et al. (1984) considered foraging costs to be significant in ***Formica schaufussi*** for they found that the foragers' selectivity for prey items of different sizes changed with changing temperature. They explained this by postulating that increased temperature increased the ants' metabolic costs and therefore increased foraging costs.

The pattern of preference between the sugars, with sucrose prefered to fructose and fructose prefered to glucose is one which maximizes the rate at which energy was harvested. Of these sugars sucrose has the highest energetic content (1340.64 cal/mol) followed by fructose (671.4 cal/mol) and glucose (669.6 cal/mol) in that order. The order of preference mirrors the order of calorific value so that by consuming the most prefered sugar the ants are collecting the most energetically valuable one. The strong preference exhibited for fructose over glucose would suggest that the mechanism ensuring that food preferences maximize energy collection rates is very finely tuned.

Similarly the changing responses of the ants to increasing molarity of these solutions serve to maximize the rate at which energy is harvested. These solutions were only collected if they were above some concentration, and therefore energy content, threshold. Energetic considerations would predict that as sucrose has the highest energetic value it would pass this energy content threshold" at a lower concentration than would fructose or glucose - as indeed was found to be the case.

Moreover, the extent of the ants' responses were matched to concentration so that the more concentrated solutions, with the highestenergy content per volume, were harvested rigorously and quickly by many recruited foragers, whilst less concentrated solutions, giving lower rewards, were harvested less enthusiastically and more slowly by individual foragers without recourse to recruitment. This mechanism ensures that the colony has a greater capacity to harvest more energetically rewarding foods.

The pattern of drinking from sucrose and glucose drops over time when these were in direct competition (and in some fructose/glucose trials) means that the ants maximize the rate of energygain as they exploited the more rewarding source first and then, when the richer source is exhausted, they switch toexploit the poorer source. This pattern also demonstrated the relation between time minimization and energy maximization models. As stated this pattern ensures that the rate of energy gain is maximized.

The drinking responses of the ants in the sucrose/glucose trials are in keeping with the prediction of optimal foraging theory (e.g. Pyke, Pulliam and Charnov, 1977) that only the abundance, or scarcity, of high quality food determines whether poorer quality foods are consumed.

The division of foragers between aphid tenders and scavengers might also have maximized the rate of energy gain, especially if the proportion allocated to aphid tending was mediated by recruitment and therefore responsive to the availability and quality of honeydew.

The variability between individual foragers in their responses to liquid foods appeared to be "sub-optimal" for when "odd" individuals collected a different food to the majority they invariably collected the less energetically rewarding food. Thus the behaviour of the odd foragers reduces the rate of energy return to the colony and should be selected against. However, this behaviour would be optimal if the odd ants were unable to get access to the richer droplet, perhaps because of crowding. In such a case the energy return rate would be greater if the foragers returned some of the poorer food rather than none at all.

Individual variability would also be optimal if the odd foragers were "sampling" for other food sources. Natural selection would favour colonies which were sufficient flexible to switch from harvesting a good resource to harvesting better resources. This switch would come about only if a forager found the better resource and not if all the foragers continued to harvest the former resource. The switch would be completed if the newly successful forager recruited its nestmates to harvest the richer resource. The results presented here intimate that ***M. rubra*** colonies do indeed possess such an ability to switch but such switching was not actually tested. It would be interesting to see if such a switch would occur if the richer of two food sources was presented AFTER the poorer one had been presented and the ants had responded positively to it (i.e. the poorer one).

However, not all of the results support this optimization criterion, indeed several aspects of the ants' food selection processes are in direct conflict with the calorific maximization criterion.

The evidence that ants respond to leucine at lower concentrations than to sugars conflicts with the energy maximization premise for leucine has a lower energy content that the sugars. This evidence would suggest rather that the optimization criterion is "maximize amino acid intake rate".

It is also possible that the ants misevaluate the energetic content of leucine solutions in the sense of Hughes' (1979) optimal foraging model for cryptic prey. Leucine may be a "cryptic prey" if it is "sweeter" than the sugars. Hence it would be misevaluated as having a higher calorific value than it really has. Such a suggestion has been made by Hansen (1978) for blowflies which over-evaluate phenylalanine - plants can use a sweet nectar containing sweet amino acids, but with a low calorific value to encourage insects to visit their flowers. Some of the booty items, which had little obvious value, may have been misevaluated in a similar way.

The finding that sucrose was prefered to leucine when in direct competition means that this criterion of amino acid maximization must also be rejected. The fact that approximately the amount of time was spent drinking leucine regardless of whether it was in competition with water or sucrose would suggest that the ants are "optimizing the rate of energy intake while consuming a minimum amount of amino acid". This optimization criterion fits neatly to Pulliam's (1975) model of "benefit maximization with nutrient constraints".

There may well be other similar forces constraining the energy acquisition force, because, presumably, the colony must also obtain certain amounts of lipid and of various other nutrients. An interesting avenue for further study would be to see how food preferences are altered by a regime where the colony is pre- provisioned and sated with protein (or other "constraining" food types).

10 DISCUSSION OF THE TEMPORAL DISTRIBUTION OF FORAGING ACTIVITY.

For the purposes of this discussion the equation that "outdoor activity" and "foraging activity" are identical is assumed to be true. It is recognised, however, that this equation is only approximately true for there are other "outdoor" tasks which are quite unrelated to "foraging activity". Indeed the inequality is well illustrated by the exceptionlly high numbers of exits observed from the Doorstep Nest entrance on 12/9/85 - the vast majority of these ants were involved in the release of a swarm of sexuals rather than in foraging. This discussion might therefore be more accurately described as one concerning all the activities of workers away from their nest.

10.1 THE IMPORTANCE OF RECRUITMENT.

Recruitment appeared to have a very important role in determining the amount of foraging activity occuring at any particular time. The well established mechanism of recruitment could cause the distribution of foraging activity to deviate from random; if ants are recruited sporadically to occasional food finds then one would expect there to be periods of low activity, when few ants engage in foraging, interspersed with periods of high activity, when a group of ants are recruited to a newly discovered food source.

The total numbers of ants entering and leaving the Doorstep Nest did not fit a random distribution and the deviations from randomness were in a manner consistent with this predicted recruitment pattern.

However, these deviations from randomness cannot be taken as absolute proofthat recruitment behaviour was the determining influence. There were other factors in play which may have caused the non-random distribution.

For instance the deviations could be due to seasonal influences. In both 1985 and 1986 the amount of traffic at the Doorstep Nest varied greatly between dates. The variations in 1986 followed a regular pattern of change as both measures of activity declined from June to October. This evidence of a decline over the time period from June onwards agrees with the findings of Elmes (1982).

Thus the deviation from a random distribution could be due in part to having large counts coming in high Summer and the low counts coming as activity declined in Autumn. However, this seasonal activity cannot fully explain the variation from randomness because no such relationship was found between foraging activity and time of year with the 1985 data (even when the analysis was restricted to overlapping periods) and because deviations from randomness were also found on individual dates.

It is possible that some of the daily deviations may have been due to fluctuations controlled by time of day rather than by recruitment. However, there was only limited evidence that foraging activity was influenced by time of day. No relationship was found between traffic into and out of the Doorstep Nest and time of day when the total data for each year was analysed. Nor was any relationship found between the numbers of exits and time of day for any individual date. Thus it would appear that the amount of activity is unrelated to time of day.

The scarcity of evidence for diurnal fluctuations might be because the observation periods were too short, all being made in the period from 9.00 to 18.00 hours. This is only a fraction of the time during which Brian (1977) reports ***Myrmica*** workers to be active: "throughout the day and much of the night in hot sunny weather".

There were four dates (out of 9) in 1986 when the number of entrances increased through the day. Whilst these might explain deviations from randomness for the number of entrances on those particular dates this does not explain why the exits also varied from a random distribution (on only one of these dates was there a significant correlation between exits and entrances - differences in individuals' foray durations might explain why these two measures of activity did not match better). Nor does it explain the deviations found on other dates.

Thus although the role of recruitment in producing the non-random distributions cannot be established unequivocally from these results it does seem to be the probable explanation. Seasonal and diurnal activity changes also play a part. Indeed it is easy to envisage a situation where recruitment mechanisms might act in concert with seasonal and diurnal influences. It could be that workers are more susceptable to recruitment signals later in the day, or in mid-Summer, say, and that this plays a leading role in establishing peaks of foraging activity in late afternoon, or in high Summer.

10.2 EXTERNAL INFLUENCES.

Given that recruitment plays such a major role in determining the amount of foraging activity it follows that the availability of food would be the major external factor influencing foraging activity. Unfortunately the total availability of food was not assessed so an attempt to match these factors could not be attempted.

Still the availability of one major dietary component, honeydew, is known for aphid clusters were maintained as reliable, and renewable, food sources. Foragers would be assured of obtaining a reward at any time and successful foragers returning from the aphid clusters would be constantly returning the information that food is available. Thus there could be a continuous stream of "recruited" foragers going to the aphids at all times.

When, occassionly, a new food source is discovered, such as a large scavenge item, the number of foragers recruited to this new source might only be a small proportion of those already going to aphid clusters. Therefore the maintenance and exploitation of reliable food sources may dampen fluctuation caused by recruitment to new and short-lived resources. This would have rendered such fluctuations less detectable, and might provide a further explanation as to why clearer and even more unequivocal evidence of recruitment effects were not obtained. It would be interesting therefore to see how foraging activity pattern would change if such reliable food could be removed, or if the proportion of unreliable food sources were to be increased.

Both temperature and light intensity were correlated to the amount of foraging activity. These changes might also have helped to obscure recruitment-induced changes. It seemed, however, that the changes caused by these physical factors were themselves liable to be eclipsed by other factors.

Temperature changes had a greater effect on the number of exits from the nest that on the number of entrances to it for whilst the overall correlation between exits and temperature was significant the relationship with entrances was not quite so ($p<0.1$). Thus it would seem that increasing temperature exerts its predominant influence on foraging activity by causing an increase in the number of ants leaving the nest. The rate of returns increases as the rate of exits increases but this relationship cannot be fully syncronized for individual foragers differ in the duration of their foraging trips.

There are several mechanisms which could mediate in the relationship between temperature and traffic. For one thing, increasing temperature increases the activity of all poikiothermic animals, including ants.

An increase in temperature might increase the activity of other animals and this might potential prey more available. The increase in foraging activity would then be matched to the increased availability of food resources.

Additionally increasing temperature (and its correlate light intensity) might increase the rate of photosynthesis and of phloem movement and so increase the reward procured from tending aphids.

Increased temperatures would also increase the metabolic costs of the ants and so increase the demand for food. This increased food requirement could in turn increase the amount of effort allocated to foraging. Such a mechanism would be analagous to the one suggested for ***Formica schaufussi*** by Traniello et al. (1984). They proposed that increased temperatures acted to increase metabolic costs and food requirements so as to cause foragers to change their prey selectivity.

There was only one individual date (19/9/86) when there was a significant correlation between temperature and activity (again the predominant influence was on the number of exits).

On this date there was a great range of recorded temperatures (11.3'C to 22.2'C) which suggests that temperature must vary over a wide range before it has any noticable effect on foraging activity. Yet this was not the greatest daily range recorded: on 3/10/86 soil surface temperatures were recorded 15.7' to 31.3'C - but this had no noticable effect on the amount of foraging activity. Now on this date there was very little activity at any time, and all activity had ceased by the next visit four days later, so it would seem that on this occassion seasonal influences overrode any possible temperature effects.

Temperature also varied greatly on 18/9/86, ranging from 13.1'C to 22.0'C, but this did not have any significant effect on foraging activity either. On this date it was also found that the number of entrances (but not of exits) increased significantly with the time of day. The temperature was higher earlier in the day so it would seem in this case that diurnal changes had a greater influence than temperature effects.

On 13/6/86 temperature only ranged 5'C, from 29.3'C to 34.5'C, and did not correlate with either measure of activity. Again the number of entrances increased significantly with time of day. So again it would appear that diurnal changes outweigh temperature effects.

No diurnal pattern was detected in either measure of foraging activity on 19/9/86, when the temperature/activity relationship was detected. Thus it seems that the effect of temperature is not apparent unless there is a great range of temperature and that it is quite easily eclipsed by seasonal and diurnal factors.

It was also the case that changes in light intensity influenced the number of exits from the nest, but not of entrances. However, on none of the dates was activity correlated with light intensity. It seems, therefore, that any effect which changing light intensity might have on foraging activity is only evident when there are great variations in light intensity. Any effects that light intensity changes might have had on any individual date were readily eclipsed by diurnal and other variations.

10.3 INTERNAL INFLUENCES.

It is well established that changing conditions within the colony, in particular in brood populations and age structure, can exert a strong influence on the amount of foraging activity by determining the demand for food and the availability of workers to go foraging in search of food (#3.3 above).

It is possible that changing conditions within the colony caused the June to October decline in foraging activity observed in 1986. However, in 1985 no such change was observed yet surely the brood present would have been undergoing similar changes in each year. Perhaps in the former year the internal influences were overridden by other factors.

There could also be diurnal changes within the colony and these may also have effected changes in foraging activity. Cammaerts (1980a) observed such intrinsic diurnal changes in laboratory colonies of ***M. rubra*** and ***M. scabrinodis*** maintained under standard conditions. Such changes would have had very little impact here for there was only weak evidence of regular diurnal changes.

The difference in foraging activity between year may have been due to changes in the total population. The fact that the same nest site was occupied in both years does not neccessarily mean that it was the same colony in occupation, although this was most likely the case. Even if it was the same colony it may not have had the same sized population in both years. It is not unusual for total population sizes to change from year to year. Brian (1972) observed four nests of ***M. rubra*** in the field over a period of six years; he showed that fluctuations representing an increase or a decrease of at least 50% of the population between one year and the next occured in 9 cases out of a possible 18 (not 24 because he didn't see every nest every year). It could be that the amount of activity observed represented the same proportion of a changing worker population. If this was the case then the colony would be allocating the same relative amount of activity to foraging activity in each year.

Of course, this nest entrance was only one of several operated by this colony. The distribution of ants and brood between subnests, and nest openings, may have varied between years so that the number of workers available to forage from each entrance would have been different.

Such gross changes in colony structure between years might also explain why the seasonal pattern found in 1986, with lower overall activity, was not repeated in 1985, when activity was about twice as high. Either the changing internal conditions were not the same between years or the season influence was swamped by the greater volume of activity at all times in 1985.

10.4 THE OPTIMALITY OF FORAGING ACTIVITY PATTERN IN *M. RUBRA.*

The fact that ants indulged in foraging activity at all times within the broad constraints imposed by seasonal changes might suggest that the temporal pattern is not shaped in any optimizing manner. Still, large fluctuations in activity did occur, often within a short space of time, and it is possible that the mechanisms which controlled these changes have been shaped by natural selection.

The observed activity changes correlate only poorly with time of year and time of day suggesting that the correlations with temperature and light intensity are equally limited. Indeed only large fluctuations in temperature and light intensity effect significant changes in foraging activity.

The annual change in activity observed in 1986 may have been controlled by changing temperature as this would also decline from June towards October. On this scale low temperatures may have constrained foraging activity.

The possiblity that smaller scale diurnal changes were also controlled by changes in the physical factors can be ruled out because there were occassions where activity increased with time of day as temperature declined. Thus on a day to day basis it appears that temperature does not constrain activity; although increased temperatures led to increased activity, this influence was relatively weak and was only apparent if it did not clash with other factors.

It would seem, therefore, that there exists some internal mechanism, or mechanisms, which determines the amount of foraging activity (within the large scale seasonal and environmental constraints). Unfortunately these results do not make clear quite what these mechanisms might be.

It is possible that the fluctuations in activity were due to changed demands from within the colony. However, the limited relationships between time of year and time of day, both of which may be related to changes in the internal status of the colony, shows that such mechanisms are relatively weak.

It is easy to speculate that the fluctuations are caused by the foragers response to changes in food availability, but there was no direct evidence to support this as food availability was not independently assessed.

If recruitment was used to match foraging activity to food availability, and it certainly has the potential to do so, then it would be operating as an optimizing mechanism. Certainly the non-random distributions of activity found in these observations, while not absolute proof, is consistent with and strongly indicative of a recruitment pattern. Thus the timing of peaks and troughs in the amount of foraging activity can be optimized as recruitment will ensure that the colony allocates more resources (=foragers) to foraging when the probability of food reward is greater.

11. DISCUSSION OF THE SPATIAL DISTRIBUTION OF FORAGING EFFORT.

The extensive observations made by following the trails of individual foragers provide a description of the actual distribution of foraging effort around real nests in the field. This distribution was found to be a clumped one, both in terms of the direction and distance from the nest.

11.1 SECTORING.

The clearest result of these analyses of the foragers' trails was that virtually all the ants were consistently found along very similar bearings from their nest at all times during their foraging trip. Thus each of these foragers concentrated its foraging effort in a narrow arc defined by its mean bearing (at least for that particular foraging trip).

Now this pattern was not unexpected due to the sampling method, as the position of each 30 second fix was not independent of the position of other fixes during that foray. As the ants travelled further out from their nest so it would require a greater "sideways shift" to get the ant away from what would become its mean bearing.

Mention must be given here to the nine exceptions of the 249 ants trailed which did not display significant clumping of their bearings at 30 second fixes. These ants foraged from four different nests. They remained close to their nest throughout their foray; all had mean distances of less than 56cm, five were less than 21cm and two were even less than 10cm. Thus it would be relatively easier for them to do a "sideways shift" from one arc to another.

As it proved impossible to give ants permanent marks in this study it was not possible to determine whether each one searched along the same mean bearing on each foray (as has been found to be the case in *C. bicolor* for instance, Harkness, 1977 and Schmid-Hempel, 1984). It must be the case that the individuals return to the same sector for it was clearly the case that the majority of ants focused their foraging effort in the same arc. It would be interesting to know whether the ants which appeared as outliers in the directional distribution of foraging effort were also outliers on subsequent forays.

The sectoral clumping of foraging effort was found for all nests (with the singular exception of Nest Seven) as is demonstrated by the fact that individual foragers' mean bearings were significantly clumped around the mean bearing for each nest.

The only nest from which the foragers did not all search along the same bearing was Nest Seven of 1986 which was located under a flat paving stone and had two separate exit holes 30cm apart. The three foragers exiting from one hole had very similar bearings to each other and the two exiting from the other hole again had similar bearings to one another (these samples of three and two were too small for statistical analysis). It would appear, though, that there was a clumping of foragers into arcs from each exit hole. This leads to the suggestion that the nest used different exit holes to exploit different parts of the surrounding terrain.

In all cases the sector where foraging effort was concentrated included the position of the tended aphid clusters. Indeed the mean bearing for each nest was very close to the bearing of the aphid cluster, e.g. for Nest One in 1985 the ants' mean bearing was 079', that of the aphid cluster was 086'. In other cases this match was not so good, e.g. 1985 Nest Two 245' v 187', but the aphids were nonetheless within the main foraging sector.

Now only about 50% of the foragers actually visited aphids (many of the ants which were "lost" during trailing might also have ended up at the aphids but it it is difficult to extrapolate from the number followed to a positive conclusion to predict a total for the colony). Why should the ants which did not tend aphids also focus their foraging effort in this sector which included the aphids?

It is possible that physical features of the surrounding terrain restrict the area over which the foragers might search. Such restrictions have been found elsewhere; Cherrett (1968) reported that the presence of a sandy road restricted a colony of Atta cephalotes from foraging in the sector to the North-West of their nest, and Pickles (1935) found that the foragers from one of ten nests of ***M. scabrinodis*** studied concentrated their efforts in an arc towards the South-East as the area to the North and North- East was devoid of vegetation.

Such a restriction is very feasable for these nests located as they were in a rosegarden surrounded on one side by a building, on two sides by doorsteps and paths and on the fourth side by a tarmaced path. Of course the ants could, and did, forage over the tarmac and on the doorsteps (but not as far as I know with any regularity in the building!) but there may have been some features here to dissuade them from doing so.

This restriction would have been greatest for Nest One for it was actually in the Doorstep; thus it would have been easier for the foragers from the other nests to go in all directions. However they also concentrated their foraging to a narrow arc suggesting that the directional clumping of foraging effort is not caused by such physical restrictions.

Nor can the directional clumping be explained as the result of predation pressure or competion between neighbours for neither predation nor territorial behaviour was observed.

Another possible factor influencing the directional distribution of foraging effort might be age polyethism within the forager- force. It is known that foragers are the oldest foragers in the colony; there might be a further age division within the foragers such that older scavengers used to be aphid-tenders when younger, but switched to scavenging with age and experience.

This change could occur if an aphid-tender stumbles across a scavenge item whilst going to an aphid cluster. This success may then cause the forager to scavenge for similar items on subsequent trips. Such reinforcement by success has been reported for ***Cataglypsis bicolor*** (Harkness, 1977, Schmid Hempel, 1984).

The first success would have been in the direction of the aphids cluster and on subsequent forays the foragers might return to the same location. Thus its foraging effort would still be aggregated in the sector with the aphid cluster.

The most probable explanation is that the sector with the aphid cluster also contains the greatest abundance of other foods. Certainly food abundance is likely to be less on the tarmac than on the soil. Of course the vegetated area was far from uniform with clumps of flowering plants separated by areas where the soil was kept bare by weeding. It could be that the vegetated area had a greater availability of other foods than weeded areas. On the other hand it is possible that the process of weeding, with the disturbing of the soil that this entails, made more (rather than less) food available to the ants. However, no assessment was made of the distribution of scavenge items.

If weeding, or not weeding, influenced food availability the effect would be most pronounced for Nest One because the most extended observations were made on this nest and also that the directional distribution would change between dates (as the amount of weeding varied). However, the directional clumping of foraging effort did not appear to be any less for the other nests than for Nest One. Nor did the mean bearing vary between dates. This indicating that food resources, if this is indeed the controlling factor, have a complex distribution.

The directional distribution of food resources must have remained more or less constant throughout the study period for the the pattern of sectoring was found to be consistent over time as the prefered bearings remained the same between dates and also between years for Nest One. This consistency contrasts with the case in ***Formica rufa*** (Skinner, 1980a) where foraging trails switched between different trees as different sources of aphids became available through the Summer months and in the army ant ***Eciton burchelli*** (Franks and Fletcher, 1983) where the directions of raiding columns shift between days during the statary phase, presumably as one area is being depleted of food the column shifts to a fresh one).

Food distribution induced changes in foraging effort distribution have also been reported in *Messor regalis* (Levieux, 1979), and also in *Veromessor pergandeii* (Rissing and Wheeler, 1976). When food was abundant foraging in *V. pergandeii* was clumped at any time as the ants foraged along trails, but when it was scarce they searched individually.

It would be interesting to observe the response of *M. rubra* foragers to changing food distributions. This could be done in the field by providing potted plants with aphid clusters for the ants to forage from, and then moving the pots.

Of course some ants foraged outside the main foraging sectors. These include the few ants for which the bearings at each 30 second fix were not clumped around the individual mean bearing and also includes those ants whose mean bearings fell as outliers beyond the main aggregation of bearings. Remember also that on 5 outof 30 dates the clumping of individuals' mean bearings were not significant.

If any of these scavengers were successful in finding food they would report their success back to the nest and possibly recruit nestmates and encourage them to travel to the location of their success. This would then boost the amount of foraging effort allocated to these areas.

Indeed the fact that so much of the scavengers' foraging effort was concentrated in this sector would suggest that this is the area which ants were being recruited to, and therefore had a high food content.

11.2 DISTANCE DISTRIBUTION.

The foraging effort of nests was also clumped at various distances from the nest for in 3 out of 6 cases the distribution of individuals' mean distances was not uniformly spread between annuli. In these cases there was less foraging effort (at least less mean distances) close to the nest and more at middle distances than might be expected. The prefered distances did not match very well to the distance of aphid clusters.

A note of caution must be added when comparing mean distances because there was great variance of sample distances (at 30 second fixes) around the mean distance, particularly as a comparison of the distances at each time interval showed no distance specialism between individuals. The great variance was largely because all the ants started at the nest (when distance was zero) and so their early sample distances were all necessarily low. Thus there are complications in using any measure of distance distribution. However the same error was introduced for each ant and non-parametric tests were used throughout.

The distance distribution of foraging effort varied between dates for 3 of the 6 nests tested and between years for Nest One. The changes between dates did not follow any particular pattern so whatever controlled this change must also have varied unpredictably. Foragers' mean distances were greater in 1985 than in 1986 (for Nest One) and this was surely a reflection on the fact that foray durations were longer in the former year.

Itis possible that the shifts in mean distances were caused by changes in total food distribution. Of course the distance of the aphid clusters did not change between dates, and only changed very slightly between years for Nest One (210 cm in 1985; 200cm in 1986). However the distribution of scavenge items may well have changed (this was not assessed). It is easy to envisage recruitment as the mechanism involved in changing distance distribution in response to food finds at different distances but no evidence was gathered to support this notion.

The distance distribution of food resources may also have changed for the three nests where there was no change in foraging distance between dates, but such a change may have been masked by the great proportion of ant tending aphids.

This complication also applies to the nests where changes were found. There would be value in repeating this sample for another year, to see whether another change in foraging distance distribution occured. Such study might also incorporate the effects of altering the location of food sources by manipulating aphid- infested pot plants, so that the significance of this factor could be assessed more thoroughly.

The change in foragers' mean distance from the nest could have been caused by some environmental factor, e.g. temperature, which was greater on some dates than others or in one or other year (on sampling days at least). On the warmer occassions, say, the forays may be longer and the ants could then travel further from their nest. The effect of environmental factors on the duration of foraging trips was not investigated. [This may provide an interesting avenue for further study.]

The internal condition of the colony might also influence distance distribution. Changes in the demand for food could determine various foraging paramaters including the duration of forays.

However food distribution changes, mediated by recruitment, remains the most likely mechanism.

There was no evidence of individual specializing in foraging at particular distances, just as there was no indication of directional specialism. The absence of distance specialism was confirmed by the finding that no ants were consistently closer to or further from the nest during their foraging trips than other foragers, thus confirming that ants spend some part of their foraging trip at all distances from the nest. At the very least they will spend some time close to the nest as they travel out to further distances.

Therefore this ant does not display what Dobrzanski (1958) has termed a "secondary partitioning" of the foraging area. It is probable that among ***Myrmicine*** ants site fidelity and secondary partitioning are not common for Dobrzanska (1976) found that foragers of ***M. laevinodis*** did not return consistently to the same locations. Nor did foragers of ***M. scabrinodis*** (Dobrzanska, 1958).

These observations also show that the allocation of foraging effort in ***M. rubra*** differs from that in ***C. bicolor***, and from ***Neoponera apicalis*** both of which species display individual foraging. Harkness (1977) reported that ***C. bicolor*** individuals searched consistantly in a restricted area, i.e. restricted by both direction and distance. Fresneau

(1985) has shown that the total foraging area used by colonies of *N. apicalis* is made up as a mosaic of areas to which individuals are faithful over many foraging trips.

11.3 OPTIMAL PATCH USE.

It is certainly the case that foraging effort was restricted to certain patches of the area around each nest, this being seen as a clumping of directions in every case and also aggregation by distance for half of the nests.

MacArthur and Pianka's (1966) consideration of the number of types of patches of different quality that should be included in the itinary of an optimal forager is of no value here for each nest only uses one patch. Of course there may be sub-patches within the area receiving a disproportionate amount of foraging effort but this was not established.

Nor does this patch use pattern lend itself to comparison with the predictions of foraging models such as Charnov's (1976) Marginal Value Theorem. This is because the resources in the patch are not necessarily depleted by the attentions of foragers. Certainly the aphid clusters are non-depleting, for the aphids will continue with honeydew production for as long as the plants' sap flows. Indeed the patch might be considered to increase its value as a food resource if the aphids are well husbanded by the visiting foragers. Aphid clusters could only be considered as depleting patches if the ants were to harvest aphids (as prey) at a greater rate than they can be replaced - but there were no aphids in the booty collected from returning foragers.

Therefore it would seem that the aphid-tending portion of the forager-force displayed optimal patch exploitation. Charnov's prediction that foragers should leave a patch when the reward rate fall below a marginal threshold value is not contradicted by the aphid-tenders. As the reward rate remained high, because the patch was non-depleting, there didn't come a time when reward rate fell; so these foragers remained in the same patch.

Of course the honeydew from aphid clusters only provided part of the ants' diet. It was probable that the other sources of food, scavenged and prey items, were presumably depleted as they are exploited. It is also likely that new patches of (scavenge and prey) food resources were constantly, but unpredictably, cropping up. It seemed to be the case that the same patches contained both depleting and non-depleting food sources for aphid-tending ants and scavengers were found to forage over the same area.

The behaviour of the scavengers may also have been optimal. It would be optimal behaviour if the changes in the distance at which ants hunted reflected changing food distribution as new patches were discovered or old ones were depleted.

Similarily the finding that on some dates individual'smean bearings were not all clumped together shows that the directional clumping of foraging effort can also vary. Again these changes could reflect changing resource distributions.

Recruitment can readily be interpreted as the mechanism effecting the shifts in distance and directional distributions, for information obtained by one forager on new food finds can quickly be transfered to others. Usually this transfer contains directional information; thus if food was found in the direction of the aphids the recruits would also travel in this distance, but to different distances as required. If the new food was found in another direction then the recruits would go in this direction - this could mean that all the individuals' mean bearings were no longer clumped (as on 18% of dates) or this variation could be swamped by the number of aphid-tenders going in the familiar direction of the aphid cluster.

Also if a forager was to find a small prey or scavenge item the recruitment response could be to increase the number of foragers leaving the nest in all directions (as no directional information is passed on, Cammaerts, 1977, 1978). Such bearings of such recruits would be different from each other (as on that 18% of dates).

Moveover, Cammaerts has shown than recruitment information in ***M. rubra*** can include qualitative details of the food discovered. This will allow the match between foraging and food distributions to be further fine tuned as higher quality resources will attract more recruits. Thus the distribution of foraging effort could come to reflect the relative qualities of different resource patches and so patch use could be optimized.

The three nests where no changes on distance distribution were observed do not negate this suggestion of optimal behaviour. They too could have been foraging optimally, within their own particular circumstances. It could have been that for these nests the relative values of different parts of the patch remained constant over the period of observation, i.e. perhaps there were no major changes in the distribution of food. Or variations in scavenger distribution was swamped by the consistancy of the great number of aphid-tenders.

This serves to highlight once more the difficulty of trying to determine what an optimal pattern might be when no census of food availability had been made. Indeed without knowing what the pattern of food availability was like it is only possible to speculate as to what the optimal foraging distribution might be like. It seem unrealistic to expect to determine the overall distribution of food for a generalist foraging ant like ***M. rubra***. To have determined the locations of the main aphid clusters is probably as much as one can do.

11.4 OPTIMAL CENTRAL PLACE FORAGING.

In most cases the behaviour of the ants which tended aphids was that expected from an optimal central place forager; they utilized the closest aphid source to their nest. Thus they minimized the time and energetic costs of foraging and maximized the rate at which reward was returned to the central place - more round trips are possible over a shorter distance.

However, Nest Five proved to be an exception for there were at least two aphid clusters closer to the nest than the one which they did exploit. Now these other sources were being used by foragers from other nests so perhaps the nest was competitively excluded. The influence of competition is certainly seen in other species for Harrison and Gentry (1981) have shown that in ***Pogonomyrmex badius*** the directions of foraging column were determined by the foraging columns of neighbours; if one colony relocated its nest and/or foraging columns then its neighbours also shifted their foraging column to exploit any space vacated. Nest Five might have been operating optimally within the new constraint of having to avoid competition.

Alternately the use of different aphid clusters by different nest might have been a sign of cooperation between colony fragments. Many of the "nests" were probably fragments of the same colony, each one exploiting the food sources, certainly the honeydew sources, closest to it. Thus the colony was able to exploit food sources that were quite distant from each other without incurring extra foraging costs. This pattern has also been found in the green tree ant ***Oecophylla smaragdina*** by Holldobler (1983).

There was some evidence that the colonies among the rosebushes forage from several central places, and did indeed shift their central place, in order to better exploit different food sources.

Another way to manage the problems of central place foraging in an optimal manner is to shift the central place rather than the distribution of foraging effort about the same central place. Thus a distant food source becomes a proximate one.

However the evidence of the one occassion when an actual shift occured in 1986 would seem to indicate that the minimization of foraging distance is not a major determinant in nest location. Nests One and Three were observed to exploit the same groups of aphids. Foraging from Nest Three began to tail off as foraging from Nest One recommenced after a Summer recess (from June 13 until September); it did seem that this was the same colony undergoing a relocation. Now whatever factor initiated this relocation (as the Summer progressed Nest One, in the brickface, would have experienced a different regime of insolation), but it is certainly the case that the relocation increased foraging costs for the ants tending the aphids.

This shift is in contrast to Ayre's (1969) finding that under laboratory conditions ants of ***Myrmica americana*** are influenced by the location of food in determining where to locate their nest. They chose the nest site which would minimize their foraging distances.

The ants which did not tended aphids but still tended to hunt in the sector containing the aphid-bearing plants do not fit the expected optimal pattern for central place foragers nearly so neatly. These ants could have hunted closer to the nest by spreading out in all directions from the nest. Had thay done so they would have reduced their searching costs (by not having so far to travel to forage and not having so far to return food) without compromising the density of foraging effort per unit area.

Thus the foraging pattern of these scavengers would have been sub-optimal if food was evenly spread over the foraging area. However, given the uneven distribution of vegetation (especially after weeding) it is probable that the distribution of other food sources (excluding for the moment honeydew, which certainly had a clumped distribution) was not even either. So it might also be the case that the non-aphid tending foragers displayed an optimal distribution of foraging effort around the nest. Again the lack of a very detailed knowledge of total food distribution hinders a more thorough and more definite assessment.

Also recruitment must be mentioned as a mechanism which provides colonies with a facility to alter their spatial foraging allocation in response to the distribution of food. Thus the distribution of foragers can change within short periods of time, and can, moreover, be shaped to reflect the distribution of food.

Regardless of how effective recruitment can be in matching foraging effort and food distributions it is limited by the ability of the recruiter to find the food sources in the first place. If the first foragers do not search effectively then potential resources would not be detected, or may be depleted by competitors coming across the resource first. Therefore even the possession of a very efficient recruitment strategy does not exclude the optimal forager from having an effective searching strategy.

12. DISCUSSION OF FORAGING MOVEMENT

Information was gathered on foraging movement pattern on various time scales ranging from seconds, in the case of the early laboratory observations, to 30 second chunks of entire foraging trips in the field which lasted for several minutes. The various methodologies required in order to obtain this range of information meant that somewhat different movement parameters were determined at each level of detail. It seems appropriate, therefore, to investigate the nature of the information obtained at each level of detail and to consider how the various parameters are interrelated, before turning to consider the biological and optimality implications of the information provided.

12.1 CHARACTERIZATION OF MOVEMENT.

The most profound difference in methodology was between that used in the first laboratory observations and that used subsequently. In the first laboratory observations the positions of ants were recorded at every instant as they moved along paths which were regarded as continuous with turns being noted as "points of inflection" in an otherwise smooth curve. In the remaining observations detail was lost as the ants' positions were only determined at regular time intervals and the position of these fixes was then used to calculate the movement parameters. "Turns" were recorded whenever consecutive segments were oriented in different directions. Thus the turns recorded are not actually those made by the ants, but they do serve as a measure of straightness. Obviously the former method gave a truer picture of the ants movements.

The three movement parameters calculated from the ants' paths in the first series of observations were clearly interrelated. Indeed one would not have expected independence, for it seems intuitive that the net distance covered would be greater if an ant were to change direction infrequently and then only by a small amount; and greatest if the ant did not change direction at all.

In view of this it is perhaps surprising that beeline distance and turn size were not found to be related. Coupled with the finding that turn size and turn frequency were negatively correlated, this suggests that some sort of self-regulatory mechanism is involved in movement, such that if an ant were to take more turns then each would be smaller, and vice versa. Within the range of turn sizes; 20' to 60', and with no bias to right or left, both combinations will evidently produce the same straightness index.

In the three series of observations where fixes were used the level of detail decreases as the time interval between fixes increases. The greatest shift in level of detail was from the second to the third series of laboratory observations, as the interval between fixes increased 10 or 15-fold from less than 1 to 10 seconds. In contrast the shift from the third laboratory observations to fieldwork only involved a three-fold increase.

A comparison of the change of direction parameters between the first and second series of laboratory observatons highlights how parameters can change with methodology for the number of turns recorded was greater in the second series whilst the size of the turns was greater in the first series. Presumably some of the large turns, as recorded in the first observations, were recorded as a couple of smaller turns in the second observations. Thus these parameters are not transferable from one series to the other. This also suggests that fixes of less than a second are too short for they "create" information not actually present in the ants' trails.

The speed of ants was only calculated from the second series of observations. Overall the speed of movement was about 1cm/sec (individuals ranged from 0.9-1.1cm/sec), with the consequence that there was often little difference in the parameters regardless of whether they were assessed per unit time or per unit distance. This measure must actually be an underestimation of the ants' speed over the ground because the use of fixes, albeit short ones, will have "cut the corners" off the actual path. In the third laboratory observations and in fieldwork the interval between fixes was much too long for a measure of speed to be calculated.

This speed of 1cm/sec might be transfered to the other series of observations. When this speed is extrapolated back to the first laboratory observations it becomes possible to convert straightness indices to "10 second movelengths". Such movelengths, averaging 8cm in 10 seconds (this was 8cm net in 10cm total) match well to the real 10 second movelengths recorded in the third series of observations. This agreement would suggest that the speeds of ants in each series of observation, and perhaps also the movements generally, were similar.

It is also possible to extend the 10 second movelengths of the third laboratory observations to create "30 second movelength" by considering the net displacement involved in three 10 second segments, where each changed by the mean direction. Thus three segments of 7cm, with a 52' change in direction between each would give a net displacement of 16.64cm (or 15.48cm if both changes were of the same handedness). This again provides a good fit for the mean 30 second movelength in the field was 14.58cm, and suggests that the same small scale movement pattern was also used in the field.

One must be wary in transfering small scale parameters to longer observations because the extrapolations were not tested. There are many differnces between the situation in the laboratory and that in the field, where the ants were in an unpredictable environment with uneven terrain, changing weather conditions, and where the presence of plants provided a third vertical dimension not encountered in the laboratory, which might influence movement pattern. However, observation did suggest (subjectively) that the small scale pattern in the field was very similar to that recorded in the laboratory.

The match between extrapolated and actual movelengths might suggest that movelengths in the laboratory were not restricted by the limitations of space in the 50x50cm arena. However, this extrapolation was done from an average 10 second movelength; individual ants' mean movelengths varied greatly and this could be a reflection of how often the ants "bounced" off the sides of the arena. Similarily the size of direction changes at fixes varied greatly between ants; again this could be explained as a consequence of space restrictions.

Space restrictions in this nest arena certainly seem to have affected the directionality of the ants. They travelled consistently in the same direction between .5-1 second fixes, and over half of the ants trailed in the field were highly directed, but no such directionality was found on the intermediate scale. Moreover, all the ants travelled in very similar directions at the beginings of their forays, but became more dispersed thereafter. Again this suggests that the size of the nest arena imposed a restriction upon the ants outward movement. This restriction could also explain why the size of direction changes, another measure of straightness, varied between the individual ants.

Thus the movement pattern on a very short time scale can be summarized by the parameters determined in the first and second series of laboratory observations; ants travelled at a rate of approximately 1cm/sec, changed direction on average every 1.5 seconds, with these turns being mostly in the range 20'-60', but overall the ants travelled consistently in the same direction for periods of 10 seconds.

The extrapolations of small scale straightness indices to 10 second movelengths and the extrapolation of these to 30 second movelength suggests that this same small scale pattern is also used in the field over extended timeperiods.

Movements made by ants in the field were very variable. As an overall average ants moved a net displacement of 14.58cm in a 30 second period. For over half of the forays every displacement was in a consistent direction.

The variability in movement parameters between individuals is shared by ***Cataglypsis bicolor***, for Schmid-Hempel (1984) reports great variability in the straightness index of foragers of this species between 30 second fixes. Some of this variation could be accounted for as differences between ants from different nests, or ants foraging on different days, and some of the variation could be linked to the conclusion of the trails. Yet there was still a residual amount of variation within each group of foragers, just as there was between individuals in the smaller scale laboratory studies.

12.2 FORAGING AND NON-FORAGING MOVEMENTS.

A major difference was observed between foraging and non-foraging movement patterns in the first series of laboratory observations between those movements which were similar to foraging movements witnessed elsewhere and those movements which were composed of many tight concentric loops.

Now had the concentric loops been analysed there would have been many more turns, mostly in the same direction. These turns would have been much larger and the straightness indices for these movements would have been greatly reduced, probably about 3-4 rather than 7-8. Such parameters could have been used to discriminate objectively between the "foraging" and "non- foraging" movements. The parameters for this set of movements would not have been interrelated in the same way as for foraging movements; turn frequency and size would have been positively related and the straightness indices would have changed with the other two parameters.

These non-foraging movements incorporate two of the four tactics identified by Bell (1990); looping and frequent turns, to retaining the mover within the same local area.

This non-foraging movement pattern does not sound unlike that reported by Holldobler and Taylor (1983) in ***Northomyrmecia macrops*** as foragers try to relocate their nest opening on their return from a foray. They report that this ant experiences no difficulty in returning to within 5-20cm of the nest, but if the sourrounding soil and leaf litter has been artifically disturbed, then they move in "searching loops" with a radius of 10-20cm until they finally locate the entrance. These searching loops and the concentric loops reported here both ensure that the ants remains within the same local area.

The difference detected between "foraging" and "non-foraging" movements of "foragers" and "carriers" in the second laboratory observations may or may not represent a biological difference. The only parameter to vary significantly between the two groups was the number of turns; as noted above (#10.1) the number of turns was only poorly related to the actual turns made by the ant (as detected in the first series of observations). So it is possible that the statistical difference has no biological meaning. However, the same error was introduced for both groups so the discrepancy between the groups may relate to a real difference in small scale movement pattern.

All of the movements recorded in the field (and most likely in the third laboratory observations as well) can be considered as "foraging" movements. There is a small possiblity that some of the movements were not actually foraging movements (just as it is an approximation to equate all "outdoor" activity to be "foraging" activity) but the fact that the trails had to be followed for five fixes, 2.30 minutes in the field, before they could be analysed virtually eliminates this possibility.

12.3 MOVEMENTS OF APHID-TENDERS AND SCAVENGERS.

Some ants in the field travelled to permanent food sources whilst others traversed the surrounding terrain. The movement pattern of the "aphid-tenders" could be separated from those of the "scavengers". The aphid-tenders tended to be less variable in their mean movelengths than scavengers. Indeed the movelengths of aphid-tenders were fairly consistent between nests suggesting that this reduced range of movelengths is part of a common movement pattern for aphid-tenders.

Similarily the aphid-tenders were more consistent in their mean movedirection, and a slightly greater proportion were found to be consistently directed throughout their foray. This shows that most aphid-tenders do travel straight to their food source, but that some do reach the aphid bearing plant by a more circuitous route.

Some of the scavengers were directed, too, as they moved away from the nest, suggesting that they might also be travelling straight to known food sources in very different locations.

Movements of ants followed through a complete round-trip seemed to fit a third category - separate from both aphid-tenders and scavengers. Very few were recorded as being consistently directed throughout their trip, and their mean directions were extremely variable between round-trippers. This is only as one might expect, for the outward and inwards legs of their forays would be in opposite directions.

12.4 CHANGES WITH TIME INTO FORAY.

Generally speaking the ants did not change their movement pattern with time into their foraging run. There was only one exception to this, Nest One in 1985; foragers from this nest had shorter movelengths later in their foraging run, indicating that their searching became more area restricted with time elapsed. Foraging trips from this nest were of longer duration than from the other nests. This means that foragers from Nest One had more opportunity to change their movement pattern, and, also that there was a greater likelihood that any such change would have been detected by statistical tests.

It is possible that movements made by foragers from the other nests would have changed after the same period, but too few trails were followed for long enough for such extended comparisons to be made.

Foragers from Nest One had a greater potential to get further away from their starting place than foragers from any of the other nests. It is possible that in doing so they reached the boundaries of their foraging territory (I do not suggest how such boundaries might be defined) and so had to change their movement pattern accordingly.

The mechanism of having shorter movelengths later in the foraging trip is shared by some other ants. For instance, Harkness and Isham (1988) have shown that in ***Messor wasmanni*** the early movements of foragers as they go out in a column are highly directed and have movelengths of about 1m in 30 seconds whereas later on they reduce their movelengths to about 25cm (directionality is also reduced).

Similarily the mechanism of having shorter movelengths later is surely shared by the ants which are reported to "travel straight to an area they know well before searching this area intenively". Fresneau (1985) describes how individual foragers of ***Neoponera apicalis*** travel out from their nest along very stable, precise high directionality trajectories, before searching with low directionality looping movements over areas that each one is familiar with. Similar changes in movement have been reported for ***Pogonomyrmex badius*** (Harrison and Gentry, 1981), and for ***Myrmecocystus mimicus*** (Holldobler, 1981).

Now in order for 30 second movelengths to change the small scale movement pattern must also change. Reduced movelength could be caused by reduced straightness indices, more stops, longer stops, more turns, larger turns, etc.. Such measurements were not made in the field, but changes in small scale foraging movements were found in laboratory observations. The finding that turn size in the second laboratory observations increased with time elapsed is consistent with the large scale decrease in large scale movelength detected for Nest One in 1985. Of course this change occured over a period of about a minute whereas the changes observed in the field took 5 minutes or more so it might not be appropriate to equate these changes.

Speed also changed with time elapsed into the foraging run on a small scale but as this change was of an acceleration followed by a deceleration it does not help to explain the change found in the field.

12.5 MOVEMENT PATTERN INFLUENCES FORAGING SUCCESS.

In the first series of observations no comparison was possible between individuals because individual "ownership" of 10cm path segments was not established. Nonetheless there were important differences between the trails which ultimately led to food and those which did not. The trails which were successful at this food distribution contained significantly fewer turns (these turns being slightly larger, but not significantly so).

Straightness index did not vary with successfulness so this result cannot really be equated to Schmid-Hempel's (1984) finding that in ***Cataglypsis bicolor*** successful foragers travelled straighter than unsuccessful ones (clumping index r=0.56 v 0.42). In both cases success and movement were clearly interrelated.

The differences between the movement parameters of ants under different pre-treatments were also very interesting, particularily as the withholding of water caused the movements to become more like those of the successful ants (fewer larger turns). Thus the reaction to an environmental stress was a change which increased the probability that this stress would be relieved.

In the field, too, it was apparent that different movement patterns afforded different success rates. The aphid-tenders, all of which were successful (by definition), were found to have movement patterns with more similar movelengths (often a band in the middle of the total range for that nest) and more consistent movedirections than the scavengers.

Yet it was not the case that success was restricted totally to the aphid-tenders. Observations of ants returning to the nest revealed that many carried prey items (although in none of the 249 trails followed did an ant come across a large solid food item). Also many ants were observed to stop during their forays; it is possible that they could have been picking up some sort of food before continuing on their foray. This behaviour of "resting" during foraging trips was also reported for *C. bicolor* by Harkness and Maroudas (1985). It was not possible to compare the movements of successful scavengers with unsuccessful because "success" could not be clearly defined.

The movement parameters of the scavengers were very variable and there was no indication of any separation which could be attributed to successful and unsuccessful scavengers. Many of the scavengers moved consistently in the same direction throughout their foray, though not necessarily in the direction of the aphids, suggesting that they might also be travelling straight to known food sources. Overall the variation in parameters between scavengers, and even between scavengers from the same nest, suggests that some individuals engage in more area-restricted searching than others. Of course it was not established whether such individuals were consistent between foraging trips.

The variation between individuals from the same nest, coupled with the variation between aphid-tenders and scavengers is strongly reminiscent of the variations between individual foragers found in the laboratory. As in the laboratory some parts of the range of movement parameters turned out to be more successful, so too in the field different movement patterns afforded different success rates (at least in encountering aphid clusters).

12.6 OPTIMALITY OF FORAGING MOVEMENTS.

The finding that some parts of the range of foraging movements were associated with different success levels does not mean that these successful movements are the only optimal ones. Rather the entire range of foraging movements can be interpreted as being part of a larger optimal strategy. Indeed the non-foraging movements might also have been optimized.

The apparent differences between foraging and non-foraging movement patterns would seem to be the result of different selection pressures acting on different aspects of the "movement" component of the phenotype.

The non-foraging movements observed in the first laboratory observations, with their low straightness indices, frequent large turns and tendency to turn repeatedly in the same direction, provide a good strategy for keeping the ants near to their starting position. This strategy would seem to be an optimal one for ants which are required to remain near to their nest.

Now it was not established whether the ants which took these different kinds of paths did so consistently. Therefore it could not be discerned whether the different kinds of movements were made by different groups of ants. If indeed there were separate groups of workers it is possible that the difference reflected an age polyethism such that the non-foraging movements were made by younger workers and the "foraging" movements were made by the older workers.

Natural selection would favour colonies wherein younger workers had mechanisms to prevent them from going away from the nest but where older workers forage at greater distances. If this were to be the case then both patterns would be optimal, albeit for different criteria.

The distinction between scavengers and aphid-tenders also reflects optimal patterns. The aphid-tenders certainly use an optimal method for they go very directly to the aphids, and so do not waste time or energy exploring other areas. The similarity in the movelengths of aphid-tenders between nests further suggests that all were doing the same optimal thing. One would suspect that to use longer movelengths would be a further advantage, as the ants would reach their target all the sooner. There must be some restriction limiting movelength for these aphid-tenders. Perhaps the nature of the terrain leading to the aphid clusters imposed this restriction. Or maybe the ants were following a pheromone trail to the aphids (some of the ants may have been recruits) and that some time was consumed as the ants "sniffed-out" this trail. Again there may have been some extra cost associatedwith greater speed.

And again it was not established whether the ants which took these different kinds of paths did so consistently. Therefore it could not be discerned whether the different kinds of movements were made by different groups of ants.

If these different movements did belong to separate groups of foragers it is possible that the difference reflected an further age polyethism. Perhaps younger foragers (all foragers are old workers) travelled directly to aphids whereas older foragers (the very oldest workers) searched for prey and scavenge items by making more circuitous movements.

The differences in movement between nests and between different dates for the same nest may represent differences in the relative amounts of foraging being directed towards aphid-tending and towards scavenging. Or they may be due to temporal and spatial differences in the distribution scavenge and prey items (the reliable distribution of aphids was known to be constant) where the foragers' search strategies were modified accordingly.

Certainly the distribution of food is known to affect foraging behaviour in many species with recruitment being well established as a mechanism which alters the distribution of foragers and changes their movement pattern. The foragers which travelled straight to aphid-bearing plants, and perhaps also those scavengers which displayed high levels of directionality, may well have been recruited.

It is also possible that the differences between nests could be due to local features, e.g. topographic or built environment, in a particular area (perhaps in the same manner as 10 second movelengths were affected by space restrictions in the laboratory) but this seems improbable because there were also differences in the same parameters between dates.

The range of movement parameters found for the scavenging foragers would suggest that there was not one distinct foraging movement pattern, optimal or otherwise. However, it must be remembered that selection pressure does not act upon the individual forager but upon the colony as a whole, and it will favour colonies where the forager force is better able to find and retrieve food. As the overall distribution of food is unpredictable and unreliable (certainly in evolutionary time!) the best strategy to achieve this objective could be for foragers to move in a range of different ways, especially if each part of that movement range is suited to locating food at different distributions.

The benefit of having a forager movement repertoire is enhanced where there is a degree of flexibility allowing foragers to change their pattern in response to their particular conditions. That different parts of the range of movement patterns afford different success rates was demonstrated by comparing the trails which led ultimately to food with those which did not, and by comparing the movements of aphid-tenders with scavengers. Flexibility in the face of different conditions was demonstrated by comparing the movements of ants from nests which had or had not been watered. Thus the ants demonstrated two important facets of an optimal movement pattern.

Now thirsty ants had no "experience" of success or failure with the experimental set-up of target food locations. However, they had experienced a period of environmental stress. Perhaps this corresponds to a period of failure, and that it causes the ants to shift their movement pattern to a "lower density food search mode". Apart from their response to recruitment signals I know of no reference to whether ants change movement pattern due to environmental stress.

However, such changes do occur in other insects, for example, Jones (1977) reports that caterpillars of the cabbage white butterfly (***Pieres rapae***) alters its movement pattern as its degree of hunger increases.

The decrease in turn frequency which occured when the ants were placed under environmental stress could mean that the foragers will move out of an unrewarding patch, in which case they would be responding optimally according to the rules of Charnov's (1976) Marginal Value Theorem.

It would be interesting to know if any other parameters such as speed, for instance, displayed any of the same flexibility in response to changing conditions, and whether such changes had any influence on success rate.

The variability within the scavengers trails, and the observations that their movement pattern changed between dates, is in keeping with the behaviour proposed for "risk sensitive" optimal foragers, e.g. Caraco (1980). Rather than for all foragers to employ the same method, even though this method might be very successful with some particular food distributions, and a bonanza reward would be incurred if this particular distribution was present, it would be better for the forager force to employ a variety of methods so as to ensure that some will be successful in locating food under any prevailing circumstance. The mechanism of recruitment can serve to enhance the reward from any distribution once the food sources have been found and reported.

Now scavengers should not go too far from their central place, for the extra costs involved in travelling to and from food sources increases with the distance. A mechanism to avoid travelling too far was only found for one nest. Nest One in 1985 would seem to have been the only one behaving optimally in this respect. The other nests did not appear to, but it is possible that because forays from these nests were generally shorter that variation with time elapsed went undetected.

Alternatively it could have been the case that no "retaining" mechanism was found because these nests had exhausted food sources closer to the nest, and so were compelled to travel further. If the resources nearby had been exhausted due to the action of previous foragers then it would be appropriate for foragoers to travel further. This seems to be what happens in the case of ***Neoponera apicalis***, for Fresneau (1985) discovered that foragers which searched further from the nest were more likely to return with food. This is probably the case for all ants (at least as far as non-renewable food is concerned).

At the same time the paths of foragers should not be too directed for as both Cody's (1971) and Pykes's (1978) computer simulations have demonstrated, a greater search efficiency is obtained if directionality was between 0.6 and 0.8, or less than 1.0 respectively. This tendency to have paths which are less than perfectly straight (a directionality of 1.0 would be absolutely straight) is exacerbated for central place foragers.

Thus as central place foragers, it would ill-serve the colony if foragers were to search too far from the nest. As the area searched is related to path length (plus a "detection range" on either side) then having a less straight path would mean that more searching is done closer to the nest.

It is notable therefore that whilst foragers' straightness indices were much greater than those of the non-foragers they fell well short of being absolutely straight. Indeed the values of 7-8 found in the laboratory fit very well with the predictions of Cody's and Pyke's models, especially if allowance is made for the fast that ants are central place foragers, to give a most efficient search.

13 GENERAL DISCUSSION.

In the foregoing sections I have discussed food choice, the temporal and spatial distributions of foraging effort and foraging movements as if they were separate independent behaviours. It is more accurate however to view these as inseparable components contributing to a fully integrated whole.

Yet even foraging behaviour is only one component of the biology of an ant colony. As such, foraging behaviour will be influenced by the other components of colonial life. Nor is foraging behaviour independent of external environmental factors, such as theavailabilityof food resources.

In this section I now consider how these various components fit together to describe foraging behaviour in its totality. I also consider how foraging behaviour is affected by influences from within the colony, and by recruitment, as this influence pervades every aspect of foraging. I also discuss the importance of those external factors, including resource availability, which impinge upon foraging behaviour. Finally I consider the optimality of ***Myrmica rubra*** foraging behaviour.

13.1 FORAGING FOR THE WHOLE COLONY.

It is very much the case that foragers act not tosatisfy their own individual needs but for the benefit of the entire colony. Thus it would be wrong to consider the actions of each forager separately for each one contributes, in its own particular way, to the same whole. Rather it is necessary to consider how the sum of the various individuals' different contributions benefits the colony.

It was abundantly clear from these experiments and observations that, whilst the many foragers are all part of the same team and contribute to the same end, the forager-force was notsimply a collection of ants all doing the same thing. There would seem to be many ways to forage, and different individuals do use different methods.

Presumably all of the foragers, regardless of their individually different foraging practices, made some contribution to the colony's success. And the existence of this range of practices allowed thegreatestoverall contribution tobemade.

Such differences between foragers were widespread; some left the nest in groups while other left singly, movement pattern varied between individuals (with some moving straighter than others as they went to aphid clusters rather than in search of scavenge items), and, whilst most foragers focussed their search effortin a narrow sector from the nest there were always a few individuals from each nest which searched in other directions.

Such individual differences might also allow different types and sources of food to be exploited simultaneously. Thus the clustering found in both the spatial and temporal distribution of foraging activity and the very directed foraging paths of many ants could allow the efficient exploitation of food from known locations. At the same time the individuals which left the nest singly and followed tortuous paths to explore other parts of the surrounding terrain could uncover new sources of food, and possible different types of food.

In the same way the variety of field movements includes patterns which are more effective for different resource distributions. It was certainly the case with the small scale movements observed in the laboratory that some movement patterns were more successful that others at that particular food distribution. Where food distribution is unknown it might be best to use a variety of mechanisms to ensure that at least some foragers are successful. Then, once the resources are located, recruitment can be used to exploit them efficiently.

The flexibility of foraging movements seen in the laboratory, if it also occurs in the field, will allow the overall foraging movement pattern to reflect the overall food distribution changes.

Alternately the individual differences in foraging behaviour might reflect the experiences of each individual. This was found to be the case in ***Cataglypsis bicolor*** (Harkness, 1977, Schmid- Hempel, 1984) where individuals were liable to return to the site of previous success and to employ a very area-restricted movement pattern at this site, or may indicate an age specific polyethism within the forager force.

However I was unable to give individual foragers permanent marks so that they could be distinguished on subsequent forays. Thus it was impossible to say whether each individual did the same things over and over again.

Therefore one could not discern, for instance, whether the ants which were trailed to aphid clusters tended aphids on every trip, in which case they would probably have used the same movement pattern on each foray. Therefore the suggestions that individual differences in foraging practices represented idiosyncratic or age- or experience-based shifts in behaviour must remain just speculation.

13.2 FORAGERS' RESPONSIVENESS TO INTERNAL INFLUENCES.

It seems apparent that for the forager-force to be best able to achieve the objective of satisfying all the colony's dietary needs the foragers should be able to detect the colony's changing requirements and to be able to respond appropriately.

There are many internal influences which could conceivably influence foraging behaviour. The demand for food, and the demand for different types of food, might be determined by the total colony population, the age structure of workers and brood and their physiological state. These factors will also have a bearing on the availability of workers to indulge in foraging activity (remember that many workers are required to tend to the queen and to care for her brood). However, as these variables were not assessed, one can only speculate as to how these influences might have been effected. However, it does seem that any effect they might have had was minimal.

For instance, the decline in foraging activity from July onwards at the Doorstep Nest can hardly be related to decreasing food requirements for most of the broods demands would have continued until Autumn. Nor was it likely that the decline represented a cohort of brood reaching the pupation stage - these would have pupated into workers, increasing the food demands again, and eventually making more workers available to forage.

Of course complete brood cycles require two years in ***M. rubra*** in colonies with full brood, queen and worker compliments. Thus it might have been inappropriate to expect to see such changes reflected in foraging behaviour within the period of any of these observations.

It was possible that changing demands for different types of food might have altered the proportions of foragers going to aphids and going in search of scavenge items.

Similarly changing demands could also explain the differences in the movement pattern and in the general spatial distribution (mainly distance distribution) of foraging effort between dates. But this seems unlikely for these changes did not follow any particular pattern. It seems more likely that these changes merely reflected changes in resource distribution.

The only real evidence that the conditions experienced by the colony influenced foraging behaviour was the finding that foraging movement pattern changed when the colony had endured a period of water stress. In this case the withholding of water affected every member of the colony fragment, including the foragers. In this case, therefore, there is no suggestion that the particular conditions experienced by one group, such as the brood or the queen, are communicated to the foragers.

13.3 RECRUITMENT PERVADES ALL ASPECTS OF FORAGING.

Recruitment behaviour as described by Cammaerts (1977, 1978) was not recorded during these observations. Occasionally one witnessed what might be interpreted as "invitation" behaviour as some ants moved excitedly between fellow workers at a nest entrance. Such observations were made most frequently during observations of traffic at the Doorstep Nest entrance, and could involve either foragers returning from forays as they encountered nestmates or could involve groups of foragers exiting from the nest.

Yet the influence of recruitment could be discerned in the majority of the observations and experiments. The most obvious effect was in regulating the exits of foragers from the nest.

That recruitment should cause bursts of foragers to leave field nests seems to be slightly incongruous in view of the fact that most of the foragers were going to collect honeydew from established aphid clusters. These would not represent a "new" food source - so why should ants recruit to it?

One possible explanation is that honeydew was only one of the resources being harvested, albeit a major one. Recruitment events could have occurred as other food sources were discovered.

Another explanation is that the quality or availability of the honeydew may have been variable in time, due to environmental influences perhaps. Recruitment might have marked changes in the quality of this resource.

A third explanation might be that a recruitment signal is required every day, or even before each foray, to cause the majority of foragers (perhaps the younger ones in particular) to leave the nest to start foraging.

The asymmetrical distribution of foraging effort around the nest can also be explained as a recruitment effect. When the first scavengers locate food they will recruit nestmates to exploit it. Then the recruited ants will also forage in the same area as the first successful scavengers. Where the food found is from a permanent and reliable source, such as an aphid cluster, there could occur recurring recruitment events which would have the effect of saturating this area with foragers.

It is well established that foraging movements are controlled by recruitment signals in cases where the recruiter lays a pheromone trail to guide her recruits. The paths of individuals leading to plants with aphid clusters tended to be straighter than others, and more similar to each other, so it may well be the case that these foragers were being influenced by recruitment signals. Yet not all of the ants which travelled straight went to aphids; it is possible that they were following recruitment trails to other food sources. The difference in movement parameters between dates could be a consequence of different amounts of recruitment on each date, with this in turn being dependent on the variable success of scavengers.

Recruitment might also play a role in determining whether foragers would be aphid-tenders or scavengers. If this separation is a permanent one, or at least a long-lived one, it could be dependent upon whether naive foragers were first recruited to collect honeydew or to retrieve scavenge or prey items. If the separation is not permanent then it could depend on whether each individual is recruited to either type of food before it begins each sortie, or indeed whether it receives no recruitment information at all.

If the later was the case then recruitment would also play an important role in diet selection for it would influence the numbers of foragers going out to collect different types of food as well as the proportion going out to search for new food sources.

Recruitment certainly played a leading role in the laboratory food choice trials. The disruption caused by the action of removing lids from the nest boxes (in order to introduce the test foods to the colony fragment) meant that many foragers left the nest area and went to the food sources. Thereafter the rate of build-up of foragers at the droplets recruitment was taking place.

The extent of the recruitment build-up varied with the food sources available. It did not happen with pure water or with the weakest sugar solutions, and it was more obvious with fructose and sucrose solutions than with equimolar glucose solutions. This shows that ***M. rubra*** is able to convey information about the relative quality of resources, and is in direct agreement with the findings of Cammaerts (1977, 1978) in this respect.

13.4 EXTERNAL ENVIRONMENTAL INFLUENCES ON FORAGING BEHAVIOUR.

Just as foragers should be sensitive to the needs of the colony and are responsive to recruitment communication from nestmates, they will also be influenced by external environmental factors. As poikiothermic animals, ants are bound to be sensitive to changing climatic conditions. It was obvious that foragers changed their behaviour in the light of prevailing environmental conditions and, particularily, in response to changes in resource availability.

Temperature and light intensity were found to be significantly positively correlated with the amount of foraging activity. However this influence was only a weak one for large ranges were required before any effect on activity rate could be discerned. Perhaps temperature would have a greater influence in some critical range, such as that found at the onset of foraging in Spring or at the end of foraging in Autumn, but this was not investigated.

Temperature and light intensity, along with humidity, will influence the rate of honeydew production. This would mean that the quality of this resource varies with environmenatal conditions, and so could induce different recruitment effects from time to time. This could alter the proportion of foragers going to the aphids at different times - but the differences found between dates probably has more to do with the difficulties involved in following individual foragers.

Temperature might effect foraging movements; warmer ants will certainly move faster, but this seems an improbable explanation for the differences found in foraging movement pattern between dates.

Physical features of the terrain in the rose-gardensurely affected the distribution of food and of foragers. However the spatial restriction of foraging activity was greater than that imposed by the location of buildings and tarmac pathways. This restriction on foraging distribution probably had more to do with food distribution.

The main external factor to influence foraging behaviour was undoubtably food availability. This was most clearly evidenced with the spatial distribution of foraging effort which was aggregated in the area with the greatest resources. Recruitment surely combined with individual foragers' experience of success to match foraging effort to food distribution.

Recruitment also mediated the other effects of resource availability. The temporal pattern of foraging activity was strongly shaped by recruitment in response to changes in resource availability and quality.

Similarly the movements of foragers in the field were also controlled by recruitment responses to food distribution and availability; the movements of recruited foragers was different from those of "independent" foragers and the movements of ants exploiting clustered food (honeydew) differed from that of ther foragers scavenging for more widely dispersed items.

Also the variations found in movement pattern between dates could have been caused by the different distribution of various types of food around each nest and on separate dates.

Resource availability could also affect small scale foraging movements, for these were found to change to a more successful mode with the colony's experience of water stress. A period of starvation, as would be caused by low resource availability, would be expected to have a similar influence.

Resource availability also influenced food choice, although in this case recruitment is not implicated as an intermediary. Diet choice trials demonstrated clearly that the food selected by foragers depended on the total availability of foods of different quality. At times of poor resource availability the foragers selected the best food from the poor range available, but when resource availability was enhanced these previously preferred foods were rejected in favour of better ones.

Although recruitment is not involved in the selection of a prefered food from the range available it would have an important influence on the total quantity of each food returned. The finding that the rate of forager build-up varies between different sugars and between different concentrations of sugar solutions, is supported by Cammaerts' (1977, 1978) demonstration of graded recruitment in *M. rubra* and would indicate that more of the better food would be collected at times of rich resource availability, due to enhanced recruitment, than would be the case when only poor resources were available.

13.5 THE OPTIMALITY OF *M. RUBRA* FORAGING BEHAVIOUR.

Myrmica rubra is indeed an optimal forager. It operates to maximize its rate of benefit gain and at the same time to minimize its time expentiture per ration of food; this is seen most clearly in the food choice experiments, but was also indicated by other components of foraging behaviour.

The manner in which resource patches are exploited conforms well to the predictions of optimal foraging theory. The relationship between foraging behaviour and distance from the central place is probably optimal as well but a more definite definition is confounded by the fact that the total distribution of resources over the surrounding area was not known.

13.5.1 BENEFIT MAXIMIZATION AND TIME MINIMIZATION.

The foraging behaviour of ***M. rubra*** includes aspects which can be interpreted to fit both benefit maximization and time minimization, according to the models developed by MacArthur and Pianka and Emlen and their followers (see #1.2 above). Overall though, it would seem that ants fit better as benefit maximizers for there is no evidence or indication that foragers would stop foraging when a certain amount of food has been collected.

The practice of maintaining aphids to ensure a reliable supply of honeydew (and also occasionally of aphids!) is one behaviour which fits both types of models. It increases the gross benefit returned to the colony by ensuring that foragers will be successful whilst keeping down costs by allowing foragers to travel straight to the food supply without wasting time and energy searching independently. It also serves to decrease the foraging time required to obtain a fixed ration of food.

Recruitment also serves as both an benefit maximization and a time minimization mechanism. The total amount of time spent foraging (by the colony as a whole) might be minimized by having a few individual foragers spending a lot of their time searching whilst the majority remain in the nest, either "on call" or performing other duties. Only when the first foragers have found food will this reserve of foragers go out to retrieve it. And recruited ants are many times more likely to find food that those searching independently. Overall this might reduce the amount of time actually spent foraging for a fixed amount of food to be returned.

It would certainly seem to be the case that the ants were always able to recruit nestmates to food finds - allocating more individuals is theeusocial equivalent of a solitary animal devoting more time to a task - and so are able to increase the benefit returned.

A further benefit of recruitment is the fact that more foragers are recruited when the food source is of greater quality. Thus more beneficial foods are returned in a shorter time that would be the case without recruitment, further reducing the time spent foraging for a fixed ration.

This is not to say that this amount will necessarily be collected in the shortest elapsed time since of the onset of the foraging bout. Yet this could also be the case if the pattern of a few searching ants followed by recruitment was quicker than for all the ants to search independently and then for each one to exploit any food it found individually.

The behaviour revealed by the food choice experiments sits easily with both types of model, for by collecting the more energy rich sugar solutions the foragers ensure that the benefit accrued on each trip is maximized and also that more energy would be returned per unit time. The behaviour of collecting the less favoured sugar after the first one has been exhausted also fits in with both types of model, but the implication that the colony's energetic demands are not readily sated would suggest that benefit maximization is the dominant influence.

Of course the finding that amino acid was preferredto sugar demonstrated that that the benefit obtained is not just calorific - there was also an amino acid requirement to be met. The observation that the ants spent more or less the same number of ant-minutes collecting amino acid solution, regardless of whether this was in competition with sugar or with water, suggests that the amino acid requirement is fairly easily sated.

This knocks any time minimization suggestion. If they were to minimize the time spend foraging for a fixed ration of amino acid then all the available foragers should have exploited the amino acid resource from the begining until it was exhausted. Only when they amino acid source was exhausted, or when the required ration was obtained, should the foragers have shifted to harvesting the carbohydrate resource (rather as they had done in shifting from fructose or sucrose to equimolar glucose solutions).

The finding that ants would collect the best food from any range, regardless of the overall quality, is also in keeping with optimality predictions. When only poor food is available the ants took the "best of the bad lot", but when a better range of food was available the previously preferred items were rejected. This optimal behaviour may also explain whey some booty items appear to be of low nutritional quality and also, perhaps, why there was no clear size preferences displayed in relation to solid food baits.

The foraging movements revealed in this study pose something of a difficulty for optimal interpretation. The finding that, on a small scale, some ants use less successful methods that others begs the question, why didn't all the ants use the more successful method?

The probable answer to this was that the foragers did not"know" what the food distribution was like; hence by employing foragers with a variety of methods the colony ensured that some would be successful at the actual food distribution. Then recruitment could be used to exploit this find efficiently.

Similarily the differences between individual foragers in field- scale movement pattern might serve to ensure that some will be successful no matter what the food distribution is.

Also the differences in movement pattern between individuals might be an optimizing mechanism if the differences meant that some foragers researched areas where they had experiencedsuccess on an previous foray (presuming that this also indicates a likelihood of further success) but this was not investigated.

13.5.2 CENTRAL PLACE FORAGING.

It was very difficult to assess what significance the fact that antsarecentral place foragers had on the optimality of the foraging decisions made. This was because the overall distribution of food resources was unknown.

Optimal foraging theory predicts that the closer of two otherwise identical patches should be exploited preferentially in order to maximize the rate of reward returned to the central place. This prediction was not always met because foragers from one nest did not exploit the nearest aphids to their nest. This apparent non- conformity might be explained if one considers the separate nests to be colony fragments. It could be that the total sum of the distance from aphids to central places for all of the colony fragments was being kept to a minimum.

The fact that foraging effort drops off with distance from the nest is generally in keeping with optimal foraging predictions, but the fact that it does not tail off as quickly as might be expected (as in a random exponential distribution) would suggest that foragers travel further than they might have to.

However, if it was the case that food availability increases with distance, and none of the aphid clusters were very close, then this could be an optimal distribution.

Yet optimality theory suggests that there should be a limit to just how far a forager should travel away from the nest, for both time and energy costs will increase with distance. It was in keeping with this that foragers from one nest (the Doorstep Nest, Nest One) should change their movement pattern with time, and distance, away from the nest. This change was to a more area- restricted search - thus restricting further outward movement. It was notable that the foragers from the only nest where this trend was detected travelled for longer, and further, than for any of the other nests.

13.5.3 PATCH USE.

It was difficult to interpret the observed pattern of patch use in M. rubra because most foragers harvest food from a non- depleting patch. Given that there was a permanent and reliable source of honeydew the ants would be behaving optimally if they did not desert this (unless a better food source became available). The foragers obviously met this prediction.

Similarily foragers in the laboratory did not desert the patch of their favourite food (leaving aside those few individuals who accepted the "wrong" food). Only when the preferred food patch was exhausted did they switch to a second choice. This is also in keeping with optimal patch use models.

However when the choice was between sugar and amino acid the ants harvested from both patches. It could be that the food in both patches, although obviously different, was of equal value to the ants. Thus the ants could still have been behaving optimally in exploiting two patches of equal quality simultaneously, rather than suboptimally if one or other patch was of poorer quality.

Of course ants in the field had more than one type of food to choose from, and therefore more than one food distribution pattern. It seemed, however, that patches rich in other resources overlapped with the aphid patches. The fact that foraging distance, though not foraging direction, changed between days can be explained as scavenging foragers shifting their attentions from one patch to another. If these shifts reflected changing distributions of (patches of) scavenge or prey items then these foragers would indeed be behaving optimally.

Now on some dates (less than 20%) the individual foragers were not strictly clumped in the sector with aphids. On these occassions the foragers were obviously not restricted to the patches with aphids suggesting that either larger or different or more diffuse patches were being used or that a smaller proportion of foragers were tending aphids on these dates. However, as none of the foragers trailed found food items it cannot be determined whether these other patches were any more rewarding.

There may have been more shifts between resource patches but these could have been missed as it may have been difficult to detect changes in scavenger distribition because of the damping effect of large numbers of foragers going to the aphid clusters.

The difference in movement pattern between dates might also reflect shifts in scavenge patches (again with the movements of aphid tenders damping these fluctuations).

Some individual foragers restricted their foraging to reduced area by having short movelengths and low directionality (at least on that foray) whilst other covered larger patches (although there did not seem to be any secondary partioning of the foraging area between indiviuals). This could be an optimizing mechanism if the foragers were returning to thoroughly re-search an area which was liable to be rewarding (perhaps because the forager had experienced success there previously). This optimizing effect of area-restricted searching could apply to the variation with time into the foray, between individuals, between dates and between nests.

Of course recruitment also has a powerful effect in determining whichpatches are exploited. And it is surely an optimizing mechanism in this respect for foragers will only be recruited to patches where food is present, and indeed more foragers will be recruited to better quality patches.

Therefore it can be stated in conclusion that the foraging behaviour of individual workers and also of the collective forager-force of ***M. rubra***, as illucidated in this study, contains many features which clearly serve to maximize the rate of benefit gain for the colony.

There are several other aspects which can equally be interpreted as optimal behaviour if one is prepared to make reasonable assumptions about the distribution of food resources.

This optimality is attained by allowing individuals to do different things yet at the same time keeping all individuals working as part of an effective, integrated unit.

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IUSSI = International Union for the Study of Social Insects

APPENDIX ONE

CIRCULAR STATISTICS.

Several of the parameters contained in the mean movement and mean position vectors are "circular" statistics which cannot be calculated or analysed in the conventional manner (as "linear" statictics). Similarly the directions measured from observations of movements in the laboratory are also circular variables and so need the same special treatment.

Circular variables are restricted to the range 0' to 360' whereas conventional "linear" variables can range from 0 to infinity (or minus infinity). This unusual feature is because of the way angles "wrap around"; an angle of 430' is the same as an angle of 90'.

This Appendix outlines how the various components of the mean movement and mean position vector are calculated and how they can be analysed. The circular variables used in the laboratory studies are determined in the same way as the relevant part of the mean movement vector.

Cain (1989) found that very few authors used circular statistics when it would have been appropriate to do so (he did a literature survey of articles published between 1980 and 1989 in the journals Ecology, Ecological Entomology, Journal of Ecology and Oecologia).

CALCULATION OF THE "MEAN MOVEMENT VECTOR".

The mean movement vector contains eight elements to describe each ants movements. These relate to the "movelength" and "movedirection" of the intercepts joining 30 second fixes, as can be seen in Figure A1.1. In this hypothetical example the ants travels for four minutes, hence there are eight "snap-shot" fixes of its position.

The first two elements of the mean movement vector are mean of the net distance "moved" between 30 second fixes and the standard deviation of the ant's actual movelengths about this mean. The mean movelength and its standard deviation are linear variables and are

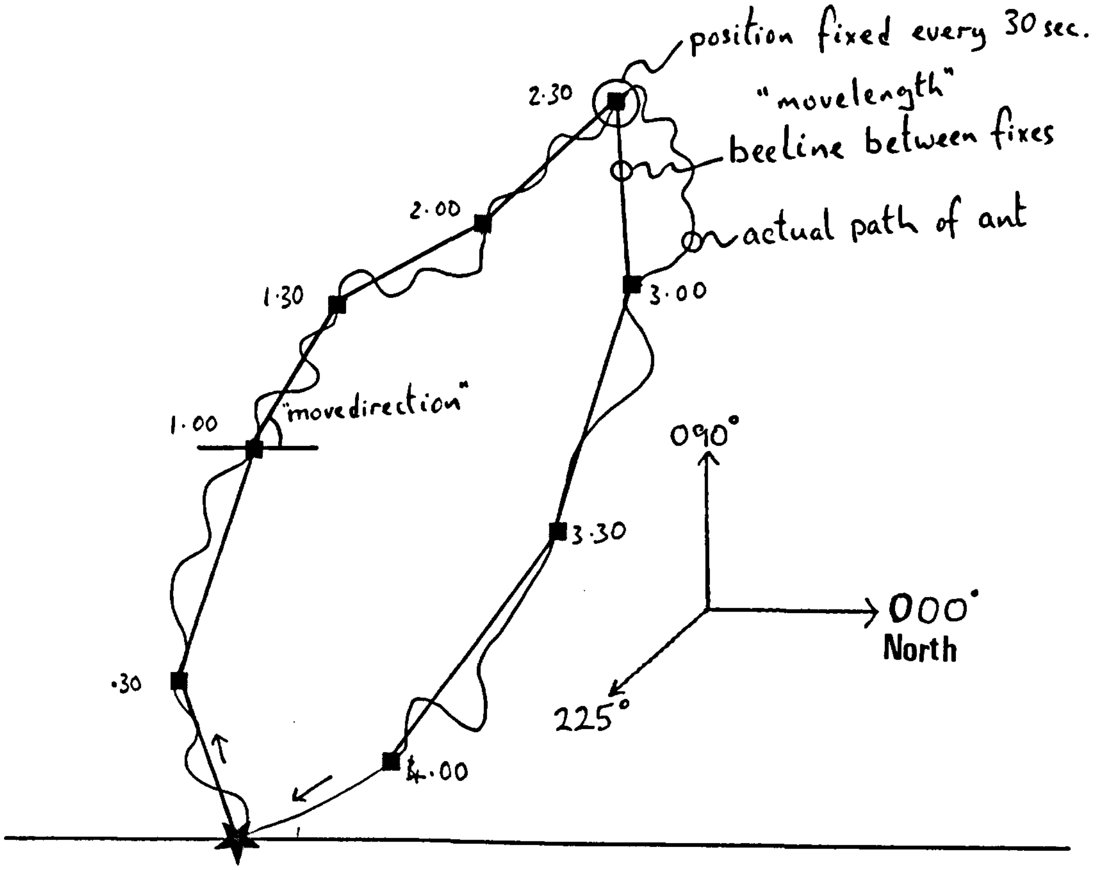

Figure A1.1. Demonstration of how a continuous path is broken down in straight line segments joining the locations of an ant at fixed time intervals. For each segement a movelength is determined as the beeline distance between two fixes. The movedirection is the direction of any fix from the previous one; all movedirections are measured from the North-South axis as shown.

calculated in the conventional manner. In the example shown in Figure A1.1 the mean movelength is 28.20cm with a standard deviation of 5.08cm (n=8).

The movedirection from one fix to the next requires more complicated analysis because it is a "circular variable" rather than a "linear" one. [This is also the case with the directions measured for ants followed in the laboratory.] This "circular" variable can still be summarized as a mean and the deviation of the sample about this meandirection.

The mean movedirection, Q, of a sample of movedirections q1, q2, q3 ... qn is calculated using the formula:-

Eqn. A1.1 $$Q = \tan^{-1}\left(\frac{\Sigma \sin q_i}{\Sigma \cos q_i}\right)$$

as demonstrated by Batschelet (1981). In the case of the path shown in Figure A1.1 the mean movedirection is 47.64 degrees. [This equation was also used to calculate mean movedirections for the ants followed in the third series of laboratory observations.]

The variation of the movedirections between each fix about this mean can be given in two ways. These are the "angular deviation" and the "mean vector length", r. These were calculated for field movements and for the third series of laboratory movements. The angular deviation uses the mean vector length in its calculation, as is seen in equation A1.2. The mean vector length can be calculated from the formula in equation A1.3.

Eqn A1.2 $$s\ (\text{degrees}) = \frac{180^\circ}{\pi}\left[2(1-r)\right]^{1/2}$$

Eqn A1.3 $$r = \left(\frac{\Sigma \cos q_i}{n_i} + \frac{\Sigma \sin q_i}{n_i}\right)^{1/2}$$

The main advantage of the angular deviation is that, like the standard deviation of linear statistics, it can be used in a descriptive manner to display how the sample of circular variables varies about the mean. The mean movedirection plus or minus one angular deviation should encompass 68.26% of the sample.

In our example the angular deviation is 73.3 degrees. Thus we can summarize that 68% of the sample of movedirections fell within 73.3' of the mean movedirections, i.e. in the range 334.34' to 120.94'. The "mean vector length" is primarily a statistical measure of the distribution of the sample movedirections around the mean movedirection. As the use of the term "length" in this context can lead to confusion when one is also discussing real distances I propose to replace the term with "clumping index" and so break with the terminology of Batschelet. The "clumping index" has no units and can only vary from 0 to 1. A value of r=1 would indicate that all the sample movedirections coincided exactly with the mean movedirection, i.e. perfect clumping, as would be found if the ant walked absolutely straight. A value of r=0 would indicate a perfectly random distribution.

The great advantage of the clumping index is that it can easily be used as a statistical test of whether the level of clumping of sample movedirections represents a significant departure from random (by using the"Rayleigh" test, see below). The level of significance of the "clumping index" is the sixth element of the mean movement vector. In this example the clumping index, r=0.1817, shows that the 8 sample moveangles are not significantly clumped around the mean movedirection. Thus the movement of this particular ant can be summarized by these six elements; it travels 28.2cm (+/-5.08cm) between 30 second fixes, though not all moves are consistently in the same direction(r=0.1817,n.s.).

A mean movement vector may be calculated for the entire foraging trip or for any portion of the foray, e.g. for the first three minutes of the outward phase (say). If one were just to consider the first five moves of this ant on the outward leg of its journey then a different picture would appear. During its outward movements the ant travelled 25.59 +/-4.17cm between fixes; each step was significantly clumped around the mean movedirection of 64.36 degrees (a.d.=30.83') for the clumping index was 0.8552, which with n=5 gives a significance level of p<0.002.

In the laboratory studies the difference in direction between consecutive steps is assessed. In the terminology of Batschelet this measure is the "angular distance" but as this term might be confusing here the term "size of turn" will be used instead. If two consecutive steps are in exactly the same direction then the "size of the turn" between them will obviously be zero. To illustrate with the example shown in Figure A1.1 the sizes of the turns were 49.4, 8.12, 37.08, 135.0, 18.44 and 15.26. Although the size can only vary in magnitude from 0 to 180 degrees it is not a circular variable (see Batschelet for proof) and so the conventional linear methods of analyses are appropriate. The mean size of turn in this example is 40.28 +/-44.1. Note than n=7; the number of turns is one less than the number of straight line segments. These sizes of turns are a measure of straightness; the straighter the paths of the ant, or at least the straighter the line of fixes, then the smaller the mean turn size will be.

CALCULATION OF THE "MEAN POSITION VECTOR".

The mean position vector is calculated from the distance and bearing of the ant from the nest at each fix. The polar coordinates (i.e. giving distance and bearing from the nest) of each fix can be seen in Figure A1.2.

The first two elememts of the mean position vector are the mean distance of the ant (or more strictly of the fixes) from the nest and the standard deviation about this mean. This distance is a linear variable and so the mean and standard deviation are calculated in the conventional manner. In the example in the figure the mean distance from the nest was 62.17cm with a standard deviation of 31.14cm.

The bearings of the fixes from the nest are circular variables. The mean bearing, and the angular deviation of sample bearings about this mean, are calculated using the formulae given in equations A1.1 to A1.3. The only difference from the calculation of the mean movement vector is that bearings from the nest are used instead of movedirections. The mean of the eight bearings in our example (121, 92, 83.5, 77, 64, 55.6, 46.5 and 29) is 70.92 degrees.

Again there are two measures of the statistical distribution of sample bearings about the means, the angular deviation which is akin to the standard deviation of samples of linear variables and the clumping index which can be used in a Rayleigh test of the significance of

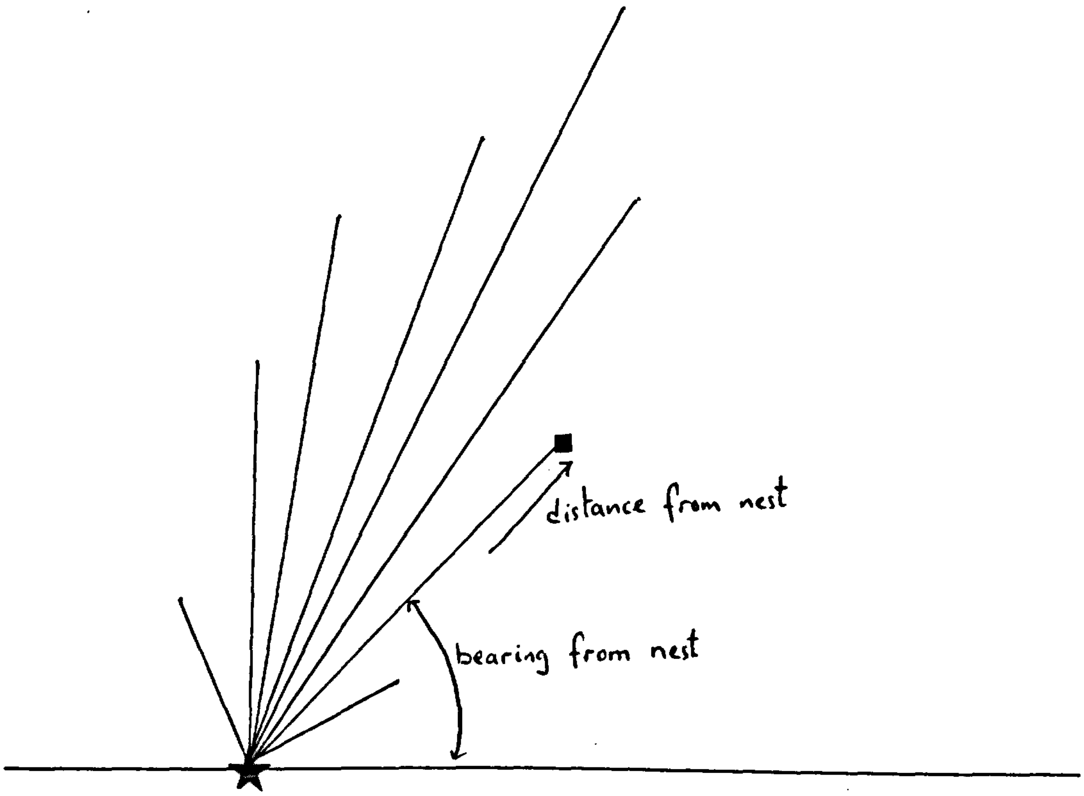

Figure A1.2. Demonstration of the parameters measured to calculate the mean position vector. The distance and bearing of each fix from the nest are determined. N.B. For the mean position vector the bearing of each fix from the nest is used, rather than the direction from the previous fix.

the clumping about the mean. This level of significance is the sixth element of the mean position vector.

In this example the angular deviation is 36.32' and the clumping index is 0.8945. For a sample of 8 bearings, this clumping index represents significant clumping ($p<0.001$). All the information given by the elements of the mean position vector can be used to provide a summary of the area searched by the ant during its foray. Thus the ant in the figure can be summarized as having spent most of its time clumped in an arc between 34.60' and 107.24', and between 31.03cm and 93.31cm from the nest.

ANALYSIS OF THE MOVEMENT PARAMETERS.

Once the mean movement and mean position vectors have been established it is possible to compare the movements and spatial distributions of different ants. Analyses can also be performed to compare between different groups of ants (grouped by date, nest or year). It is also possible to compare the movements of ants at different times into their forays. The movelength and the size of turns are linear variables so there are no particular constraints on the tests used to analyse them. The situation is more complicated for the distance from the nest element of the mean position vector for, whilst it is also a linear variable, it is not drawn from an independent sample. This complication arises because the distance at any fix will be influenced by the distance at the previous fix. For example, if the ant is far away at one fix then it is likely that it will also be far away at the next fix, after only 30 seconds. Therefore it is neccessary when analysing the distances of the ants from their nest that this anomaly is taken into consideration. This can be achieved by ranking the data and using non-parametric tests.

Friedman analyses of variance tests (Sokal and Rohlf, 1969) were used to compare distances from the nest between individual ants. These tests do not use the mean distance at all. Rather they compare the distance of the ants from the nest at the same time intervals. The distance from the nest at each time interval is ranked for all the ants, and then the ranks are summed for each ant. The null hypothesis was that no ants would forage consistently closer or further from the nest than their colleagues and so each ant would score the same sum of ranks.

Kruskall-Wallis tests (Sokal and Rohlf, 1969) were used to compare between groups of ants e.g. to compare those from one nest with another. In these tests the mean distance of each ant from the nest was used. These were ranked for all the ants from all the groups, then the sum of the ranks for each group are calculated. The null hypothesis was that the sum of the ranks for each group should be the same.

The Rayleigh test was widely used to determine whether samples of movedirections and of bearings from the nest were significantly clumped about their respective means. Batschelet (1981) describes the Rayleigh test as being by far the most frequently used circular one-sample test. This is surely because the test statistic is easily calculated. The test statistic is the clumping index, r, the calculation of which has already been demonstrated. If the distribution of sample bearings is not random then the clumping index will be large. The only other information needed to determine whether this distribution is random, in addition to the size of r, is to know the sample size. Levels of significance can be read from a table (Table H in Batschelet (1981)) for the appropriate clumping index and sample size. The main restriction of the Rayleigh test is that it requires that the sample contains at least five directions or bearings.

Rayleigh tests were used in the first instance to determine if the movedirections of all the 30 second steps was significantly clumped around the mean moveangle for each individual ant, i.e. if the ant consistently travelled in the same direction and whether the bearing from the nest were significantly clumped for each individual, i.e. if the ant was consistently found in any particular direction. One great convenience of circular statistics is that it is legitimate to use the mean of means. Thus the same method which was used to compare the sample of movedirections and bearings for each individual ant can be used to compare different ants with each other. This is legitimate only if the movedirections between fixes or the bearings of each fix are significantly clumped for each individual ant. Again the prerequisite of the Rayleigh test that there must be at least five data in the sample to be analysed applies.

This permitted Rayleigh tests to be used again to compare between different foragers (once it had been established that for each individual there was a significant clumping of movedirections or bearing). In these comparisons a new mean (a grand mean) and a new clumping index would be calculated (in exactly the same way as the first means were calculated, equations A1.1and A1.3). This grand clumping index could then be used in a Rayleigh test to investigate the distribution of mean movedirections and bearing (of individual ants) about the grand mean (of all the ants from that date, nest or year).

Moreover it is legitimate to use the grand mean movedirections and bearings to calculate further means. Again this involves the calculation of a new angular deviation and a new "clumping index", which again can be used in a Rayleigh test. This allows different groups of ants to be compared, for instance comparing the movements of ants foraging from different nests or comparing the spatial distribution of foraging effort on different dates.

Sometimes, however, a Rayleigh test is not appropriate, such as when there are less than five ants' paths with significant clumping of the sample movedirection around their mean movedirection. In such instances a circular chi-squared test or a Mardia-Watson-Wheeler test might be used.

The "circular chi-squared" test is very similar to its linear counterpart and tests whether different samples have the same distribution. The most noticable difference is that in the circular version the expected frequency in a group need be four or more, not five as in the linear test.

The "Mardia-Watson-Wheeler" test can compare the distribution of movedirections or bearing in different samples. It makes the assumption that the sample populations have a continuous circular distribution from 0' to 360'. All the movedirections or bearings from all the samples are ranked, then the ranks for each sample are summed. The null hypothesis, that there is no difference between the samples, suggests that the sum of the ranks should be the same for each sample.

12/8/85 4 items
1 aphid; 1 woodlouse (head end only); 1 fly; 1 insect thorax with legs.

14/8/85 14 items
1 insect thorax with wing; 1 insect wing (as previous); 1 insect thorax with legs; 2 legs (not pair); 3 pupae; 1 springtail; 1 seed-head; 1 worm; 3 other items.

15/8/85 3 items
1 caterpillar, a (hoverfly?) thorax; 1 piece rubble.

21/8/85 18 items
2 hoverflies; 1 gnat; 1 fly; 3 insect legs; 1 pupa; 1 aphis; 1 birch seed; 1 earwig abdomen; 1 woodlouse; 4 insect heads (2 same, 1 with antennae and mouthparts, 1 shell); 2 other items.

28/8/85 25 items
2 beetles, 3 woodlice; 1 caterpillar; 2 worms; 1 springtail; 1 spider; 2 aphids; 1 insect thorax with wing); 1 insect head; 1 antenna; 1 insect leg; 2 hollow tubes (perhaps insect legs or antennae?); 2 very small slugs(?); 1 seed coat; 4 other items(1 egg, 1 plant epidermis).

30/8/85 11 items
2 pieces of woodlice; 1 fly (wings not fully unfurled); 1 caterpillar; 1 bug; 1 plant cuticle; 2 pieces of moss; 3 other items.

4/9/85 8 items
1 hoverfly; 2 other flies; 1 springtail; 1 caterpillar, 1 piece woodlouse;1 insect leg, 1 insect thorax and abdomen.

9/9/85 14 items
2 small flies, 1 aphid; 1 piece moss; 1 insect wing; 3 cranefly legs; 6 pieces of leg or antennae.

12/9/85 2 items
1 piece woodlouse; 1 piece of insect abdomen.

16/9/85 6 items
1 woodlouse (front end only), 1 aphid; 1 seed; 1 insect leg; 1 shell of head and thorax; 1 other item (looked like tissue paper).

17/9/85 10 items
1 fly; 2 heads of flies; 1 aphid; 1 centipede; 1 caterpillar; 3 leg or antennal pieces; 1 amorphous globular item.

Appendix 2. Food items taken from foragers returning to Nest One (in 1985) at Wrotham Field Centre.

DATE	TIME	EXITS	ENTRANCES	MEAN	No.	SITE	SITE	SITE	SITE	SITE	SITE
		per 10 mins		TEMP	MINS	1	2	3	4	5	6
13-Jun	11.30	19	13	29.34	10	28.2	23.1	32.8	34.6		28.0
13-Jun	12.00	10	16	31.44	10	30.9	27.0	34.4	35.7		29.2
13-Jun	12.30	17	19	33.44	10	33.1	30.6	35.0	37.6		30.9
13-Jun	13.00	14	10	34.50	10	34.8	32.8	35.5	38.2		31.2
13-Jun	13.30	13	15	34.08	10	34.7	33.7	34.3	37.1		30.6
13-Jun	14.00	36	33	31.48	10	31.2	28.9	30.3	39.4		27.6
13-Jun	15.00	9	23	29.72	10	31.7	30.0	31.1	27.5		28.3
13-Jun	15.30	30	34	33.74	10	32.6	29.6	30.2	39.5		36.8
13-Jun	16.00	21	25	30.38	10	33.6	29.9	31.1	31.7		25.6
18-Sep	11.00	5	7	18.13	10	16.5	25.8	22.2	22.2	11.2	10.9
18-Sep	12.00	3	8	20.07	10	17.4	21.5	20.1	16.8	20.4	24.2
18-Sep	13.00	6	6	21.97	6	22.2	24.0	21.5	18.1	21.8	24.2
18-Sep	14.00	12	10	14.80	7	15.4	15.3	14.4	14.0	15.6	14.1
18-Sep	15.00	7	14	19.50	7	19.2	22.6	21.4	17.0	20.5	16.3
18-Sep	16.00	10	12	17.98	4	17.5	25.7	17.3	15.1	17.6	14.7
18-Sep	17.00	17	12	15.75	5	15.1	23.7	13.9	13.9	14.7	13.2
18-Sep	18.00	6	17	13.07	6	14.8	12.7	12.8	13.1	13.2	11.8
19-Sep	11.00	7	10	11.27	1	11.1	11.3	11.1	11.4	11.1	11.6
19-Sep	12.00	2	6	14.65	1	14.5	14.5	14.4	14.5	14.4	15.6
19-Sep	13.00	8	13	17.00	1	17.2	16.8	15.6	16.4	18.0	18.0
19-Sep	14.00	13	18	22.18	1	25.0	21.0	22.0	20.4	25.0	19.7
19-Sep	15.00	9	20	20.32	8	23.6	19.0	21.0	19.2	20.9	18.2
03-Oct	11.00	2	2	15.70	10	15.7					
03-Oct	14.00	1	3	31.30	10	31.3					
03-Oct	16.00	2	0	27.70	10	27.7					
03-Oct	17.00	1	2	25.50	10	25.5					

Appendix 3. Soil surface temperatures recorded at six sites around the Doostep Nest (Nest One) in the rosebeds at Wrotham Field Centre in 1986. The temperature at each recording site is given as the median of the n minutes recordings made during the 10 minute period.

DATE	TIME	EXITS	ENTRANCES	MEAN	SITE	SITE	SITE	SITE	SITE	SITE
		per 10 mins		L.I.	1	2	3	4	5	6
13-Jun	11.30	19	13	12.12	13.6	4.4	15.0	15.4	10.3	14.1
13-Jun	12.00	10	16	12.45	13.8	7.6	14.6	14.2	10.5	14.0
13-Jun	12.30	17	19	14.32	14.9	13.8	15.0	14.8	12.5	15.0
13-Jun	13.00	14	10	13.99	14.8	13.3	14.5	14.2	12.4	14.8
13-Jun	13.30	13	15	14.10	14.8	13.1	14.0	13.6	13.5	15.7
13-Jun	14.00	36	33	9.02	9.6	8.3	9.1	8.1	8.8	10.2
13-Jun	15.00	9	23	7.21	8.2	6.0	6.7	6.6	6.8	9.1
13-Jun	15.30	30	34	9.44	11.7	9.2	10.1	8.6	8.0	9.1
13-Jun	16.00	21	25	8.97	11.4	8.6	9.6	9.0	5.7	9.6
18-Sep	11.00	5	7	3.70	4.2	3.8	3.8	3.3	4.1	3.2
18-Sep	12.00	3	8	6.90	4.8	14.3	9.0	6.8	2.7	3.9
18-Sep	13.00	6	6	11.98	12.9	9.5	10.8	9.0	15.0	14.7
18-Sep	14.00	12	10	3.13	3.0	3.0	3.3	3.0	3.0	3.5
18-Sep	15.00	7	14	8.40	10.5	8.0	8.9	6.6	11.4	5.1
18-Sep	16.00	10	12	3.93	4.5	3.8	3.8	3.8	4.2	3.6
18-Sep	17.00	17	12	3.68	4.1	3.6	3.5	3.6	3.8	3.6
18-Sep	18.00	6	17	4.65	11.1	3.3	3.2	3.9	3.3	3.2
19-Sep	11.00	7	10	3.38	2.9	3.2	3.8	3.5	3.5	3.6
19-Sep	12.00	2	6	4.28	4.0	5.9	2.7	4.7	2.8	5.6
19-Sep	13.00	8	13	5.87	5.9	6.4	6.2	4.7	6.2	5.8
19-Sep	14.00	13	18	11.20	14.9	12.0	13.5	8.4	10.5	8.0
19-Sep	15.00	9	20	3.80	3.8	4.2	3.9	3.3	3.9	3.8
03-Oct	11.00	2	2	3.70	3.7					
03-Oct	14.00	1	3	7.40	7.4					
03-Oct	16.00	2	0	4.80	4.8					
03-Oct	17.00	1	2	5.10	5.1					

Appendix 4. Light Intensity recorded on soil surface at six sites *around the Doostep Nest (Nest One) in the rosebeds at Wrotham* Field Centre in 1986. The temperature at each recording site is given as the median of the 2 or 3 recordings made during each 10 minute period.

APPENDIX FIVE

MEAN MOVEMENT VECTORS OF FORAGERS TRAILED AT WROTHAM

Data presented are nest, date, ant no., duration of trail (no. of fixes), outcome of trail (1=to aphids, 0=round trip) mean movelength between fixes (and standard deviation), mean movedirections between fixes (and angular deviation), clumping index and level of significance (5=p<0.001, 4=p<0.005, 3=p<0.01, 2=p<0.05, 1=p<0.1, 0=no significant clumping of individuals'movedirections).

NEST ONE 1985 65 ANTS					MOVELENGTH		MOVEDIRECTION		CLUMPING	
NEST	DATE	ANT	DURA	RESU	MEAN	S.D.	MEAN	A.D.	INDEX	SIGN
85.1	14-Aug	1	11		18.84	6.36	81.17	29.04	0.8716	5
85.1	14-Aug	2	9		14.9	12.65	115.04	54.73	0.5438	2
85.1	14-Aug	4	16		20.8	7.3	58.8	60.73	0.438	2
85.1	14-Aug	5	11		23.48	14.4	65.35	49.75	0.623	4
85.1	14-Aug	6	14	0	15.38	10.29	126.66	73.88	0.1687	0
85.1	15-Aug	1	11		20.15	13.7	87.86	38.57	0.776	5
85.1	15-Aug	2	6		12.83	8.89	87.03	33.34	0.831	5
85.1	21-Aug	1	21		16.52	8.84	87.11	70.65	0.2398	1
85.1	21-Aug	2	18		14.9	8.8	189.5	75.99	0.1204	0
85.1	21-Aug	3	7		24.59	19.88	80.9	20.9	0.933	5
85.1	21-Aug	4	7		23.6	17.04	75.44	32.17	0.843	5
85.1	21-Aug	5	26	0	30.87	23.43	317.77	77.31	0.0897	0
85.1	21-Aug	6	24		13.58	9.71	81.8	64.9	0.3581	3
85.1	21-Aug	7	9		21.38	14.91	76.8	14.09	0.9698	5
85.1	28-Aug	2	10		9.42	4.6	65.41	60.64	0.4399	2
85.1	28-Aug	3	10		16.58	12.65	102.43	15.99	0.961	5
85.1	28-Aug	4	16		12.62	8.4	81.95	51.41	0.5975	2
85.1	30-Aug	1	8	0	20.83	17.09	226.78	35.7	0.8059	3
85.1	30-Aug	4	6		15.12	9.12	97.72	57.18	0.6011	2
85.1	04-Sep	1	16		12.48	11.98	85.91	46.01	0.6776	5
85.1	04-Sep	2	19		11.93	11.18	66.06	54.54	0.547	4
85.1	04-Sep	3	12		16.98	10.1	103.79	39.58	0.7614	5
85.1	04-Sep	4	16		19.87	13.96	86.54	64.34	0.3964	2
85.1	04-Sep	5	26		12.32	11.4	101.66	58.95	0.4705	4
85.1	04-Sep	6	13		19.73	9.28	94.95	27.67	0.8884	5
85.1	04-Sep	7	8		21.74	13.2	78.7	24.21	0.9107	5
85.1	04-Sep	9	18		20.56	7.41	87.68	62.49	0.4052	3
85.1	04-Sep	10	26		10.17	9.69	94	46.47	0.6711	5
85.1	04-Sep	11	42		9	3.02	102.56	74.26	0.16	0
85.1	06-Sep	1	5		27.65	11.28	52.84	11.71	0.9791	5
85.1	06-Sep	2	13		17.09	8.88	84.52	47.85	0.6513	4
85.1	06-Sep	3	7		27.6	16.25	89.83	34.66	0.817	2
85.1	06-Sep	4	4		12.64	6.84	150.6	46.54	0.6702	n=4
85.1	06-Sep	5	9	0	73.78	14.29	204.93	73.78	0.1708	0
85.1	06-Sep	6	15		40.83	15.25	96.71	40.83	0.746	5
85.1	09-Sep	3	10	1	29.21	16.47	94.42	22.3	0.9269	5
85.1	09-Sep	4	7	1	29.27	18.12	79.95	21.91	0.9269	5
85.1	09-Sep	5	15		17.77	13.4	66.64	61.93	0.4159	2
85.1	09-Sep	6	8		27.92	12.34	91.24	10.72	0.9825	5
85.1	09-Sep	7	9		13.71	9.1	99.27	67.52	0.3057	0
85.1	12-Sep	1	14		12.19	13	91.19	50.16	0.6168	4
85.1	12-Sep	2	7		2.36	3.11	150.31	72.56	0.1982	0
85.1	12-Sep	3	10		3.97	5.56	3.51	63.19	0.3919	0
85.1	12-Sep	4	19	0	8.89	7.89	257.04	79.29	0.0424	0
85.1	16-Sep	1	22		9.32	5.85	76.53	31.45	0.8495	5
85.1	16-Sep	2	8		3.68	2.1	103.51	64.1	0.3742	0
85.1	16-Sep	3	7		26.26	14.9	60.73	18.44	0.9482	5
85.1	16-Sep	4	8		1.81	1.93	109.65	66.78	0.3208	0
85.1	16-Sep	5	10		22.94	8.69	123.53	30.21	0.8609	5
85.1	16-Sep	6	10		15.81	9.73	79.14	26.99	0.8891	5
85.1	16-Sep	7	7		4.74	3.75	78.22	42.51	0.7248	2
85.1	17-Sep	1	13		17.29	16.37	74.16	51.7	0.5929	5
85.1	17-Sep	3	11		16.2	11.7	72.28	66.77	0.3205	0
85.1	17-Sep	4	10		19.34	11.35	117.46	43.26	0.7149	2
85.1	17-Sep	6	6	0	55.11	62.69	75.9	67.1	0.3142	0
85.1	17-Sep	7	10	0	13.35	6.55	228.46	76.01	0.1201	0
85.1	17-Sep	15	11		19.38	11.93	73.61	22.33	0.924	5
85.1	17-Sep	16	17		17.99	10.018	111.1	47.56	0.6555	5
85.1	20-Sep	1	23		11.53	10.32	92	57.64	0.49398	5
85.1	20-Sep	2	9		6.17	7.69	64.27	59.23	0.4657	2
85.1	20-Sep	3	12		21.04	0.84	99.76	35.68	0.8061	5
85.1	20-Sep	4	11		15.64	14.18	63.25	51.43	0.5791	2
85.1	20-Sep	5	7	1	16.27	7.76	64.42	21.66	0.9285	5
85.1	20-Sep	6	20	0	22.28	12.9	152.08	77.83	0.0773	0
85.1	20-Sep	7	8	1	22.8	8.01	70.02	46.69	0.66796	2

NEST TWO 1985 38 ANTS					MOVELENGTH		MEAN	ANG.	CLUMPING	
NEST	DATE	ANT	DURA	RESU	MEAN	S.D.	DIRECTION	DEV.	INDEX	SIGN
85.2	28-Aug	4	13	1	18.7	9.68	232.82	71.85	0.2135	0
85.2	30-Aug	5	7	1	12.4	6.92	234.86	42.59	0.7238	2
85.2	30-Aug	6	11		11.56	11.13	348.26	68.19	0.2919	0
85.2	30-Aug	7	7		15.68	5.14	279.52	36.95	0.7921	3
85.2	04-Sep	13	12	1	6.51	9.17	248.7	49.39	0.6284	2
85.2	12-Sep	5	4	1	20.5	11.8	256	57	0.5057	n=4
85.2	12-Sep	6	5	0	10.998	4.83	191.55	73.99	0.1662	0
85.2	12-Sep	7	5	0	13.25	7.49	253.74	18.32	0.9489	5
85.2	12-Sep	8	12		8.44	6.02	259.12	58.41	0.4804	2
85.2	12-Sep	9	9		9.99	7.82	289.71	62.43	0.4064	0
85.2	12-Sep	10	7		11.27	6.16	273.29	47.54	0.6558	2
85.2	12-Sep	11	9	1	9.93	4.82	277.01	19.32	0.9432	5
85.2	16-Sep	9	10		7.14	4.07	213.09	40.67	0.7481	5
85.2	16-Sep	10	15	1	10.88	3.6	237.51	69.71	0.2598	0
85.2	17-Sep	10	7		7.76	4.49	151.56	52.27	0.5839	0
85.2	17-Sep	11	8	1	14.38	11.65	292.9	55.72	0.5271	0
85.2	17-Sep	13	4	1	18.78	6.74	250.76	22.49	0.9929	n=4
85.2	17-Sep	14	11	0	15.35	7.22	60.72	71.66	0.2179	0
85.2	20-Sep	8	6	1	14.35	7.5	254.31	45.1	0.6903	2
85.2	02-Oct	1	5	1	13.45	12.94	246.9	51.26	0.5998	2
85.2	02-Oct	2	8	1	10.01	5.39	235.16	43.77	0.7083	2
85.2	02-Oct	3	7	1	9.41	12.87	254.09	61.48	0.4243	0
85.2	02-Oct	4	7		15.3	3.19	136.89	71.37	0.2241	0
85.2	02-Oct	5	9	0	17.57	4.93	37.83	75.82	0.1245	0
85.2	07-Oct	1	6		12.38	4.54	255.5	45.69	0.6801	2
85.2	07-Oct	2	7		10.5	4.52	237.98	48.51	0.6414	2
85.2	07-Oct	3	8		1.03	1.32	265.71	76.26	0.1143	0
85.2	07-Oct	4	12		9.13	3.89	180.03	80.42	0.0148	0
85.2	09-Oct	1	7		4.09	6.71	245.13	64.25	0.3712	0
85.2	09-Oct	3	6	1	13.23	4.44	248.98	7.28	0.9919	5
85.2	09-Oct	4	10	1	9.25	5.42	245.34	45.62	0.683	5
85.2	09-Oct	6	6	1	11.97	8.27	250.97	14.48	0.9681	5
85.2	09-Oct	7	5		14.58	7.83	259.35	35.4	0.8091	2
85.2	09-Oct	9	9		8.14	4.01	237.08	27.27	0.887	5
85.2	09-Oct	10	7	1	11.85	5.51	263.77	36.92	0.7924	2
85.2	09-Oct	11	18		9.5	4.38	230.19	28.71	0.8745	5
85.2	09-Oct	14	6	1	14.39	2.78	251.67	22.76	0.91	5
85.2	09-Oct	15	5		10.49	5.49	111.6	76.24	0.1146	0

NEST ONE 1986 37 ANTS					MOVELENGTH		MEAN	ANG.	CLUMPING	
NEST	DATE	ANT	DURA	RESU	MEAN	S.D.	DIRECTION	DEV.	INDEX	SIGN
86.1	08-Sep	1	7	1	9.79	4.73	105.76	36.74	0.7944	3
86.1	08-Sep	2	9		23.25	8.97	92.91	51	0.6039	0
86.1	08-Sep	3	12		14.37	7.48	94.5	61.4	0.4259	0
86.1	08-Sep	4	12		49.67	43.58	189.94	59.97	0.4522	0
86.1	08-Sep	5	7		7.01	5.92	80.21	15.43	0.9368	5
86.1	08-Sep	6	10		4.99	5.37	61.94	75.85	0.1238	0
86.1	09-Sep	6	5		22.94	12.39	140.67	27.36	0.886	3
86.1	09-Sep	7	10		4.38	5.36	104.44	67.06	0.315	0
86.1	09-Sep	8	6	1	15.7	4.53	128.02	14.69	0.9671	4
86.1	09-Sep	9	3	1	17.52	8.52	92.37	14.45	0.9682	n=3
86.1	09-Sep	10	12		12.04	6.41	57.05	38.23	0.7774	5
86.1	09-Sep	11	5	1	21.74	15.05	124.14	22.19	0.925	3
86.1	09-Sep	12	7	1	27	12.22	80.28	9.75	0.9855	5
86.1	09-Sep	13	3	1	17.25	9.85	102.02	21.81	0.9276	n=3
86.1	09-Sep	14	11		16.36	4.84	45.25	45.49	0.6849	4
86.1	12-Sep	1	5		1.61	2.55	73.77	69.15	0.2718	0
86.1	12-Sep	2	7		12.56	8.46	79.98	60.18	0.4484	0
86.1	12-Sep	3	6		12.18	4.91	90.63	10.6	0.9829	5
86.1	12-Sep	4	10		20.56	10.13	131.13	48.73	0.6383	3
86.1	12-Sep	5	15	0	10.14	3.08	37.28	76.94	0.0984	0
86.1	12-Sep	6	9		34.61	32.11	111.82	42.89	0.7198	3
86.1	12-Sep	7	10		12.58	7.08	87	16.41	0.959	5
86.1	12-Sep	8	7		16.03	11.18	87.97	39.92	0.7573	2
86.1	12-Sep	9	5	1	11.63	8.24	83.06	39.09	0.7673	2
86.1	12-Sep	10	11	1	19.32	9.42	83.72	43.95	0.7058	4
86.1	12-Sep	11	5		7.84	2.12	114.22	43.07	0.7185	0
86.1	12-Sep	12	10		20.33	13.5	66.45	49.48	0.6276	2
86.1	12-Sep	13	8	1	22.21	12.75	272.21	26.81	0.8905	5
86.1	12-Sep	14	10		15.88	9.5	96.2	22.09	0.9257	5
86.1	12-Sep	15	6		1.82	2.01	80.08	59.24	0.4654	0
86.1	12-Sep	16	6		15.57	7.43	167.48	29.79	0.8648	3
86.1	16-Sep	7	5	1	11.52	6.74	116.89	36.92	0.7923	2
86.1	16-Sep	8	6		10.95	4.66	75.54	19.92	0.9396	5
86.1	16-Sep	9	6		3.55	2.43	179.4	44.39	0.6999	2
86.1	16-Sep	10	10	1	19.7	15.55	80.58	12.04	0.9779	5
86.1	16-Sep	11	5	1	11.71	6.66	100.22	19.92	0.9396	3
86.1	16-Sep	12	7	1	8.51	3.69	88.43	28.55	0.8758	2

NEST TWO 1986	47 ANTS				MOVELENGTH		MEAN	ANG.	CLUMPING	
NEST	DATE	ANT	DURA	RESU	MEAN	S.D.	DIRECTION	DEV.	INDEX	SIGN
86.2	05-Sep	1	10		13.6	23.32	56.07	52.23	0.5845	2
86.2	05-Sep	2	7		12.6	13.94	161.45	55.73	0.527	0
86.2	05-Sep	3	9		6.09	6.98	154.71	66.96	0.3172	0
86.2	05-Sep	4	3		6.74	9.47	79.16	77.33	0.0893	n=3
86.2	05-Sep	5	4		16.79	27.74	69.03	70.94	0.6047	n=4
86.2	05-Sep	6	6		25.12	36.32	119.17	49.84	0.6217	0
86.2	05-Sep	7	5		23.51	38.14	208.57	49.25	0.6306	0
86.2	05-Sep	8	8		41.85	20.59	179.24	55.5	0.5309	0
86.2	05-Sep	9	6		5.43	6.06	163.94	53	0.5721	0
86.2	05-Sep	10	10		8.59	10.35	104.2	76.02	0.1199	0
86.2	05-Sep	11	5		19.84	27.03	64.22	50.19	0.6164	0
86.2	08-Sep	7	7		8.09	10.51	157.19	37.69	0.7837	3
86.2	08-Sep	8	5		6.51	7.48	259.66	42.44	0.7257	0
86.2	08-Sep	9	8		7.58	8.75	193.18	22.14	0.9253	5
86.2	08-Sep	10	10		7.33	8.95	152.85	34.9	0.8144	5
86.2	08-Sep	11	8		2.67	4.697	57.25	66.97	0.3169	0
86.2	08-Sep	12	5		5.13	6.22	145.99	66.85	0.3193	0
86.2	09-Sep	1	23		3.73	6.34	221.52	77.33	0.0892	0
86.2	09-Sep	2	5		2.23	3.07	104.44	52.65	0.5778	0
86.2	09-Sep	3	6		5.51	7.19	231.77	69.56	0.2631	0
86.2	09-Sep	4	5	0	5.83	7.52	121.74	67.98	0.2961	0
86.2	09-Sep	5	9		4.99	7.63	146.64	62.27	0.4095	0
86.2	16-Sep	1	6		3.64	4.68	168.23	19.27	0.9435	3
86.2	16-Sep	2	6		4.78	5.41	166.31	54.45	0.5485	0
86.2	16-Sep	3	5	1	6.04	7.56	205.49	38.08	0.8125	2
86.2	16-Sep	4	6	1	6.35	8.23	202.08	52	0.5881	0
86.2	16-Sep	5	10		1.96	4.2	226.49	66.17	0.3331	0
86.2	16-Sep	6	11		2.8	4.21	149.19	56.48	0.5141	0
86.2	16-Sep	13	22		5.44	6.67	153.59	77.42	0.0871	0
86.2	18-Sep	1	12	1	39.53	21.44	189.38	41.19	0.7416	5
86.2	18-Sep	2	5	1	14.13	16.65	202.15	25.91	0.8977	3
86.2	18-Sep	3	6	1	12.06	14.11	193.84	27.37	0.8859	2
86.2	18-Sep	4	19	1	6.63	7.56	189.74	63.16	0.3925	0
86.2	18-Sep	5	6	0	5.45	6.32	163.75	63.57	0.3845	0
86.2	18-Sep	6	8	1	9.9	11.69	193.88	34.73	0.8163	2
86.2	18-Sep	7	5		14.27	17.98	148	22.34	0.924	3
86.2	18-Sep	8	7	1	10.21	12.16	189.62	33.1	0.8331	5
86.2	18-Sep	9	7	0	9.39	11.83	117.47	70.83	0.236	0
86.2	18-Sep	10	5		11.13	15.63	169.52	17.54	0.9532	3
86.2	18-Sep	11	8	1	9.62	12.28	186.95	47.76	0.6526	2
86.2	18-Sep	12	7		5.08	7.57	169.96	47.92	0.6502	0
86.2	19-Sep	1	6		7.02	9.08	140.33	36.95	0.792	2
86.2	19-Sep	2	7	1	8.2	9.88	192.84	21.86	0.9272	5
86.2	19-Sep	3	22		8.2	8.98	279.7	46.19	0.675	5
86.2	19-Sep	4	7	1	10.12	11.32	186.96	21.76	0.9278	5
86.2	19-Sep	5	5	1	13.72	14.46	192.86	32.41	0.84	2
86.2	19-Sep	6	7	1	10.86	12.4	182.67	44.23	0.702	2

NEST THREE 1986 25 ANTS					MOVELENGTH		MEAN	ANG.	CLUMPING	
NEST	DATE	ANT	DURA	RESU	MEAN	S.D.	MOVEDIREC	DEV.	INDEX	SIGN
86.3	14-Jul	1	9		9.44	3.84	71.93	76.35	0.1122	0
86.3	14-Jul	2	13	0	10.27	12.87	78.82	62.33	0.4082	0
86.3	14-Jul	3	7	10	29.01	42.65	76.6	70.81	0.2363	0
86.3	14-Jul	4	8	1	25.68	36.91	186.12	51.06	0.6029	2
86.3	14-Jul	5	7		26.44	33.94	174.77	71.79	0.2151	0
86.3	14-Jul	6	12		24.26	27.62	35.58	44.28	0.7014	5
86.3	14-Jul	7	4		20.63	26.07	112.26	52.25	0.5842	n=4
86.3	14-Jul	8	24		19.48	26.24	98.65	60.21	0.4478	2
86.3	14-Jul	9	5	1	46.85	41.83	225.52	62.42	0.4065	0
86.3	14-Jul	10	15		21.82	41.63	208.49	73.94	0.1674	0
86.3	14-Jul	11	3	1	35.72	45.25	45.64	21.13	0.932	n=3
86.3	14-Jul	12	7	1	26.37	33.66	112.28	73.65	0.1739	0
86.3	14-Jul	13	4		39.7	56.53	61.96	56.29	0.5174	n=4
86.3	14-Jul	14	6	0	12.65	22.4	211.22	37.12	0.7901	4
86.3	14-Jul	15	6		41.29	55.62	56.24	51.39	0.5978	0
86.3	15-Aug	1	5		55.36	48.97	81.28	60.48	0.4429	0
86.3	15-Aug	2	5	1	29.31	39.46	27.29	45.01	0.6914	0
86.3	15-Aug	3	7		19.94	31.39	79.11	39.41	0.7634	2
86.3	15-Aug	4	10		17.58	27.54	38.72	66.89	0.3186	0
86.3	15-Aug	5	18		9.23	22.54	210.423	73.08	0.1866	0
86.3	15-Aug	6	10		22.91	31.26	81.58	67.85	0.2987	0
86.3	15-Aug	7	14		15.01	21.98	118.12	75.67	0.1279	0
86.3	15-Aug	8	6		32.35	44.3	198.68	57.88	0.4897	0
86.3	15-Aug	9	6		20.81	29.48	29.46	37.92	0.781	2
86.3	15-Aug	10	6		19.34	31.15	165.92	66.08	0.3349	0

NEST FOUR 1986 19 ANTS

NEST	DATE	ANT	DURARESU		MOVELENGTH MEAN	S.D.	MEAN DIRECTION	ANG. DEV.	CLUMPING INDEX	SIGN
86.4	29-Sep	1	5		9.13	11.91	37.12	47.34	0.6587	0
86.4	29-Sep	2	4	1	16.7	13.53	0.97	63.63	0.3833	n=4
86.4	29-Sep	3	7		11.02	14.22	353.65	51.67	0.5934	0
86.4	29-Sep	4	5		14.91	18.58	30.19	41.03	0.7436	2
86.4	29-Sep	5	8		13.22	16.05	39.73	41.26	0.7408	3
86.4	29-Sep	6	8		31.67	31.74	43.19	66.38	0.3289	0
86.4	29-Sep	7	8		12.7	14.49	40.3	33.99	0.8241	4
86.4	29-Sep	8	11		7.61	9.69	15.65	38.98	0.7686	5
86.4	30-Sep	1	5		9.21	12.27	351.18	55.37	0.5331	0
86.4	30-Sep	2	10	1	15.62	17.98	26.49	37.64	0.7842	5
86.4	30-Sep	3	9		11.58	13.1	27.71	40.64	0.7484	4
86.4	30-Sep	4	9	1	12.1	14.17	3.37	37.4	0.787	4
86.4	30-Sep	5	9	1	10.8	12.82	345.01	40.22	0.7536	4
86.4	03-Oct	1	7		13.57	15.67	17.77	53.43	0.5652	0
86.4	03-Oct	2	10	0	18.15	24.87	300.37	69.12	0.2723	0
86.4	03-Oct	3	4		11.58	18.42	1.69	49.79	0.6224	n=4
86.4	03-Oct	4	4		39.18	19.24	101.72	53.16	0.5694	n=4
86.4	03-Oct	5	8	10	24.16	24.76	318.91	60.2	0.4481	0
86.4	03-Oct	6	5	1	28.97	28.18	23.04	39.81	0.7586	2

NESTS 5, 6 & 7

NEST	DATE	ANT	DURARESU		MOVELENGTH MEAN	S.D.	MEAN DIRECTION	ANG. DEV.	CLUMPING INDEX	SIGN
86.5	07-Jul	1	9	0	18.59	17.34	207.51	75.17	0.1393	0
86.5	07-Jul	2	9	1	17.88	20.93	90.41	46.21	0.6748	2
86.5	07-Jul	3	9	1	27.82	21.14	91.88	17.43	0.9537	5
86.5	07-Jul	4	16	1	15.04	17.7	85.81	27.41	0.8856	5
86.5	07-Jul	5	6	1	25.81	16.75	44.25	47.44	0.6573	0
86.6	20-Jun	1	4		7.92	12.08	161	13.9	0.9706	n=4
86.6	20-Jun	2	6		12.87	14.52	154.61	33.9	0.825	3
86.6	20-Jun	3	5	1	12.08	13.74	84.17	23.56	0.9155	2
86.6	20-Jun	4	3		11.24	14.23	132.83	22.52	0.9228	n=3
86.6	20-Jun	5	6		11.34	14.38	140.82	61.49	0.424	0
86.6	20-Jun	11	8		19.11	21.34	105.52	34.38	0.82	4
86.6	20-Jun	12	4		18.08	22.19	123.26	60.16	0.4487	n=4
86.6	20-Jun	13	7	1	10.94	13.53	94.56	50.16	0.6168	0
86.7	20-Jun	6	8		13.94	12.38	248.89	69.97	0.2544	0
86.7	20-Jun	10	5		29.87	24.19	252.51	52.76	0.567	0
86.7	20-Jun	7	9		11.31	16.33	356.56	67.24	0.3114	0
86.7	20-Jun	8	3		20.69	24.69	283.39	24.39	0.9094	n=3
86.7	20-Jun	9	6		12.19	15.32	274.22	26.29	0.8947	4

APPENDIX SIX

MEAN POSITION VECTORS OF FORAGERS TRAILED AT WROTHAM

Data presented are nest, date, ant no., duration of trail (no. of fixes), outcome of trail (1=to aphids, 0=round trip) mean distance of fixes from the nest (and standard deviation), mean bearing of fixes from the nest (and angular deviation), clumping index and level of significance (5=p<0.001, 4=p<0.005, 3=p<0.01, 2=p<0.05, 1=p<0.1, 0=no significant clumping of individuals'movedirections).

85.1	14-Aug	1	11		77.39	49.91	81.37	29.03	0.9922	5
85.1	14-Aug	2	9		92.13	32.31	90	5.995	0.9945	5
85.1	14-Aug	4	16		83.26	36.03	45	16.91	0.956	5
85.1	14-Aug	5	11		125.68	43.14	24.45	28.69	0.875	5
85.1	14-Aug	6	14	0	93.13	27.4	56.19	9.812	0.9863	5
85.1	15-Aug	1	11		124.45	57.7	85.9	4.39	0.997	5
85.1	15-Aug	2	6		38.84	27.05	82.12	3.22	0.998	5
85.1	21-Aug	1	21		118.5	43.63	81.04	6.15	0.994	5
85.1	21-Aug	2	18		91.44	47.42	92.39	20.4	0.937	5
85.1	21-Aug	3	7		90.62	54.95	85.54	9.19	0.987	5
85.1	21-Aug	4	7		86.76	56.4	73.44	7.35	0.992	5
85.1	21-Aug	5	26	0	157.27	70.49	325.35	39.47	0.7566	5
85.1	21-Aug	6	24		116.87	52.84	83.14	18.2	0.9496	5
85.1	21-Aug	7	9		128.2	50.56	68.2	6.74	0.9931	5
85.1	28-Aug	2	10		31.64	9.83	59.3	12.34	0.9768	5
85.1	28-Aug	3	10		70.64	48.23	95.85	3.08	0.9986	5
85.1	28-Aug	4	16		89.5	52.27	84.87	14.28	0.9689	5
85.1	30-Aug	1	8	0	70.76	61.5	218.34	29.33	0.869	5
85.1	30-Aug	4	6		41.02	17.53	132.4	35.03	0.8131	2
85.1	04-Sep	1	16		135.55	86.85	81.23	4.15	0.9974	5
85.1	04-Sep	2	19		143.11	41.61	84.66	2.2	0.9993	5
85.1	04-Sep	3	12		124.85	75.42	93.76	11.18	0.981	5
85.1	04-Sep	4	16		112.8	30.48	92.4	7.17	0.9922	5
85.1	04-Sep	5	26		155.53	61.18	91.61	4.9	0.9964	5
85.1	04-Sep	6	13		153.54	68.17	87.36	4.22	0.9973	5
85.1	04-Sep	7	8		84.58	57.85	87.48	4.01	0.9976	5
85.1	04-Sep	9	18		153.32	45.52	90.8	19.7	0.9714	5
85.1	04-Sep	10	26		164.67	61.87	76.76	3.01	0.9986	5
85.1	04-Sep	11	42		191.63	41.52	85.33	5.03	0.9962	5
85.1	06-Sep	1	5		71.86	50.51	49.52	9.09	0.9874	5
85.1	06-Sep	2	13		125.58	59.46	88.46	3.78	0.9978	5
85.1	06-Sep	3	7		106.46	57.99	86.26	4.12	0.9974	5
85.1	06-Sep	4	4		32.14	9.68	109.42	16.56	0.9582	n=4
85.1	06-Sep	5	9	0	21.6	15.7	39.55	28.11	0.8797	5
85.1	06-Sep	6	15		152.91	76.66	90.69	6.93	0.9929	5
85.1	09-Sep	3	10	1	179.12	84.9	90.91	4.23	0.9973	5
85.1	09-Sep	4	7	1	123.43	61.5	87.85	5.48	0.9954	5
85.1	09-Sep	5	15		124.52	53.4	88.26	7.31	0.9919	5
85.1	09-Sep	6	8		123.22	72.28	88.34	2.42	0.9991	5
85.1	09-Sep	7	9		52.83	19.55	77.64	6.5	0.9936	5
85.1	12-Sep	1	14		87.51	44.49	80.41	7.71	0.991	5
85.1	12-Sep	2	7		5.96	1.42	132.84	19.99	0.9392	5
85.1	12-Sep	3	10		31.53	8.99	2.05	2.13	0.9993	5
85.1	12-Sep	4	19	0	45.33	24.4	0.76	18.65	0.947	5
85.1	16-Sep	1	22		106.25	53.34	80.56	6.59	0.9934	5
85.1	16-Sep	2	8		13.21	3.5	45.86	19.47	0.9422	5
85.1	16-Sep	3	7		82.17	68.12	54.71	15.08	0.9654	5
85.1	16-Sep	4	8		9.21	1.96	84.95	6.56	0.9934	5
85.1	16-Sep	5	10		123.63	69.9	141.78	14.56	0.9677	5
85.1	16-Sep	6	10		73.12	51.44	80.72	14.79	0.9667	5
85.1	16-Sep	7	7		12.02	11.52	61.54	28.86	0.8732	5
85.1	17-Sep	1	13		139.61	62.69	60	5.41	0.9954	5
85.1	17-Sep	3	11		69.6	27.08	82.33	12.63	0.9757	5
85.1	17-Sep	4	10		92.43	41.85	93.998	7.62	0.9912	5
85.1	17-Sep	6	6	0	44.87	61.16	70.39	29.63	0.8663	5
85.1	17-Sep	7	10	0	23.67	15.75	41.998	40.05	0.7557	4
85.1	17-Sep	15	11		115.09	67.85	73.57	7.32	0.9918	5
85.1	17-Sep	16	17		131.94	53.65	76.75	7.65	0.9911	5
85.1	20-Sep	1	23		132.23	45.82	87.78	5.5	0.9954	5
85.1	20-Sep	2	9		44.65	14.6	73.6	6.14	0.9943	5
85.1	20-Sep	3	12		155.05	83.67	91.36	8.44	0.9892	5
85.1	20-Sep	4	11		18.53	55.6	84.3	1.94	0.9994	5
85.1	20-Sep	5	7	1	54.26	35.81	56.74	10.06	0.9846	5
85.1	20-Sep	6	20	0	66.88	46.41	73.71	33.58	0.8283	5
85.1	20-Sep	7	8	1	73.49	35.74	79.67	6.06	0.9944	5

NEST TWO 1985 38 ANTS					DISTANCE FROM NEST		BEARING FROM NEST			
NEST	DATE	ANT	DURA	RES.	MEAN	S.D.	BEARING	A.D.	C.I.	SIGN
85.2	28-Aug	4	13	1	33.74	20.11	269.23	54.97	0.5398	2
85.2	30-Aug	5	7	1	44.96	25.46	237.38	31.79	0.846	3
85.2	30-Aug	6	11		63.61	19.03	279.44	5.05	0.9961	5
85.2	30-Aug	7	7		56.64	24.25	257.89	19.46	0.7424	5
85.2	04-Sep	13	12	1	583.16	26.66	247.18	2.2	0.9993	5
85.2	12-Sep	5	4	1	39	29.65	264	54	0.5625	n=4
85.2	12-Sep	6	5	0	9.54	9.04	117	52.98	0.5725	0
85.2	12-Sep	7	5	0	46.08	15.21	243.55	3.99	0.9976	5
85.2	12-Sep	8	12		59.005	46.5	301.02	24.08	0.9917	5
85.2	12-Sep	9	9		45.43	23.91	275.61	4.39	0.9971	5
85.2	12-Sep	10	7		48.91	19.93	261.95	8.89	0.988	5
85.2	12-Sep	11	9	1	46.64	26.85	275.76	6.55	0.9935	5
85.2	16-Sep	9	10		39.94	17.69	201.96	8.15	0.9899	5
85.2	16-Sep	10	15	1	67.91	23.13	260.26	8.26	0.9896	5
85.2	17-Sep	10	7		17.06	10.38	128.97	33.76	0.8264	5
85.2	17-Sep	11	8	1	63.39	40.29	288.83	6.51	0.9936	5
85.2	17-Sep	13	4	1	50.64	18.18	242.3	6.2	0.9941	n=4
85.2	17-Sep	14	11	0	16.55	12.9	256.3	66.7	0.3223	0
85.2	20-Sep	8	6	1	42.12	24.48	261.91	42.41	0.726	2
85.2	02-Oct	1	5	1	52.59	22.23	246.8	0.91	0.99987	5
85.2	02-Oct	2	8	1	44.06	24.72	246.07	9.74	0.9855	5
85.2	02-Oct	3	7	1	55.27	19.24	251.71	1.92	0.9994	5
85.2	02-Oct	4	7		23.82	9.46	211.29	41.94	0.7321	2
85.2	02-Oct	5	9	0	30.11	13.86	262.9	24.92	0.9054	5
85.2	07-Oct	1	6		36.73	22.23	245.18	43.6	0.7104	2
85.2	07-Oct	2	7		35.65	20.9	235.48	41.91	0.7325	3
85.2	07-Oct	3	8		2.54	0.48	341.91	16.21	0.96	5
85.2	07-Oct	4	12		20.27	12.77	323	41.57	0.7368	5
85.2	09-Oct	1	7		22.78	7.92	256.24	6.31	0.9933	5
85.2	09-Oct	3	6	1	43.62	27.24	252.18	2.67	0.9989	5
85.2	09-Oct	4	10	1	46.97	21.04	252.11	13.63	0.9717	5
85.2	09-Oct	6	6	1	41.59	26.72	251.26	9.01	0.9876	5
85.2	09-Oct	7	5		39.51	25.15	266.99	32.33	0.8408	2
85.2	09-Oct	9	9		36.51	24.06	241.43	7.68	0.991	5
85.2	09-Oct	10	7	1	43.63	28.81	258.06	34.84	0.8151	4
85.2	09-Oct	11	18		90.55	46.25	224.91	6.13	0.9943	5
85.2	09-Oct	14	6	1	41.88	20.72	249.77	6.96	0.9926	5
85.2	09-Oct	15	5		10.53	4.99	110.01	29.34	0.8689	2

NEST ONE 1986 37 ANTS					DISTANCE FROM NEST		BEARING FROM NEST			
NEST	DATE	ANT	DURARES.		MEAN	S.D.	BEARING	A.D.	C.I.	SIGN
86.1	08-Sep	1	7	1	28.16	19.9	104.61	20.52	0.9359	5
86.1	08-Sep	2	9		86.94	50.14	78.39	6.23	0.9941	5
86.1	08-Sep	3	12		57.51	34.06	89.99	24.01	0.9122	5
86.1	08-Sep	4	12		81.74	51.51	213.98	39.45	0.7629	5
86.1	08-Sep	5	7		18.64	15.82	75.61	8.18	0.9898	5
86.1	08-Sep	6	10		12.16	2.65	92.02	42.97	0.7188	4
86.1	09-Sep	6	5		65.21	39.72	156.09	15.75	0.9622	5
86.1	09-Sep	7	10		19.85	6.56	62.99	29.96	0.8633	5
86.1	09-Sep	8	6	1	48.52	31.62	124.52	7.47	0.9915	5
86.1	09-Sep	9	3	1	28.66	21.58	90.85	10.7	0.9826	5
86.1	09-Sep	10	12		50.56	32.16	46.32	12.997	0.9743	5
86.1	09-Sep	11	5	1	64.73	41.34	113.18	8.77	0.9883	5
86.1	09-Sep	12	7	1	99.9	69.94	76.06	3.88	0.9977	5
86.1	09-Sep	13	3	1	30.555	21.05	111.16	13.7	0.9714	5
86.1	09-Sep	14	11		81.51	40.51	36.16	19.25	0.9435	5
86.1	12-Sep	1	5		6.03	0.11	103.71	8.57	0.9888	5
86.1	12-Sep	2	7		45.11	37.91	102.16	21.02	0.9327	5
86.1	12-Sep	3	6		43.5	24.87	84.36	3.48	0.9982	5
86.1	12-Sep	4	10		78.33	51.14	132.76	17.71	0.9522	5
86.1	12-Sep	5	15	0	39.31	21.58	6.83	15.59	0.963	5
86.1	12-Sep	6	9		74.75	59.04	118.48	23.41	0.9165	5
86.1	12-Sep	7	10		57.94	44.78	92.6	5.68	0.9951	5
86.1	12-Sep	8	7		42.69	32.36	83.99	14.8	0.9666	5
86.1	12-Sep	9	5	1	28.84	22.62	87.02	37.7	0.7835	2
86.1	12-Sep	10	11	1	106.38	55.36	82.1	4.21	0.9973	5
86.1	12-Sep	11	5		19.18	10.86	102.34	16.25	0.9597	5
86.1	12-Sep	12	10		85.79	58.58	83	7.55	0.9913	5
86.1	12-Sep	13	8	1	96.16	58.88	273.11	21.3	0.9309	5
86.1	12-Sep	14	10		64.55	51.78	107.19	17.39	0.9539	5
86.1	12-Sep	15	6		7.73	2.85	75.63	8.62	0.9887	5
86.1	12-Sep	16	6		42.98	26.2	158.86	8.68	0.9885	5
86.1	16-Sep	7	5	1	27.8	17.03	115.52	16.37	0.9592	5
86.1	16-Sep	8	6		31.36	23.42	76.32	17.79	0.9518	5
86.1	16-Sep	9	6		13.93	6.11	164.9	7.27	0.993	5
86.1	16-Sep	10	10	1	103.93	75.72	83.32	3.48	0.9982	5
86.1	16-Sep	11	5	1	32.32	21.85	95.9	6.6	0.9934	5
86.1	16-Sep	12	7	1	29.61	18.28	86.4	7.53	0.9914	5

NEST TWO 1986 47 ANTS					DISTANCE FROM NEST		BEARING FROM NEST			
NEST	DATE	ANT	DURA	RES.	MEAN	S.D.	BEARING	A.D.	C.I.	SIGN
86.2	05-Sep	1	10		46.81	18.4	219.44	14.66	0.9673	5
86.2	05-Sep	2	7		27.53	15.73	141.47	28.01	0.8805	5
86.2	05-Sep	3	9		25.23	7.83	148.62	10.51	0.9832	5
86.2	05-Sep	4	3		11.51	1.31	112.72	30.87	0.8549	n=3
86.2	05-Sep	5	4		50.6	6.01	342.72	10.11	0.9844	5
86.2	05-Sep	6	6		123.2	26.81	97.73	5.31	0.9957	5
86.2	05-Sep	7	5		61.67	8.14	106.25	12.29	0.977	5
86.2	05-Sep	8	8		86.98	3.88	104.47	21.84	0.9274	5
86.2	05-Sep	9	6		16.52	6.17	181.63	11.75	0.989	5
86.2	05-Sep	10	10		23.85	12.89	55.16	47.86	0.6512	2
86.2	05-Sep	11	5		51.14	5.57	107.36	18.95	0.9453	5
86.2	08-Sep	7	7		33.73	14.84	174.42	7.45	0.9915	5
86.2	08-Sep	8	5		14.51	8.92	280.02	31.05	0.8532	2
86.2	08-Sep	9	8		27.5	19.79	182.02	5.78	0.9949	5
86.2	08-Sep	10	10		30.2	20.06	165.56	10.4	0.9835	5
86.2	08-Sep	11	8		14.25	6.14	76.74	38.22	0.7775	3
86.2	08-Sep	12	5		8.96	1.43	166.97	23.22	0.9179	5
86.2	09-Sep	1	23		18.22	8.55	253.93	42.89	0.7198	5
86.2	09-Sep	2	5		4.27	0.71	167.76	16.31	0.9594	5
86.2	09-Sep	3	6		4.45	2.65	145.27	54.63	0.5455	5
86.2	09-Sep	4	5	0	14.49	4.39	159.45	15.61	0.9659	5
86.2	09-Sep	5	9		12.58	6.51	98.9	43.13	0.7167	2
86.2	16-Sep	1	6		14.77	6.08	156.84	10.61	0.9829	5
86.2	16-Sep	2	6		14.53	7.03	152.85	14.996	0.9658	5
86.2	16-Sep	3	5	1	19.21	6.46	204.81	46.88	0.6653	1
86.2	16-Sep	4	6	1	19.7	6.28	182.62	44.79	0.6845	1
86.2	16-Sep	5	10		16.19	8.42	185.33	34.69	0.8168	5
86.2	16-Sep	6	11		22.51	111.3	138.4	3.48	0.9982	5
86.2	16-Sep	13	22		13.3	15.88	126.2	55.96	0.523	4
86.2	18-Sep	1	12	1	67.18	111.3	189.56	20.41	0.9366	5
86.2	18-Sep	2	5	1	45.05	15.88	181.1	9.74	0.9856	5
86.2	18-Sep	3	6	1	44.04	14.98	170.41	10.58	0.9829	5
86.2	18-Sep	4	19	1	42.54	14.38	232.68	23.71	0.9144	5
86.2	18-Sep	5	6	0	9.64	4.32	160.18	40.31	0.7525	2
86.2	18-Sep	6	8	1	43.2	17.7	170.47	8.58	0.9888	5
86.2	18-Sep	7	5		51.22	16.66	159.45	4.39	0.9971	5
86.2	18-Sep	8	7	1	40.93	14.37	171.73	9.39	0.9866	5
86.2	18-Sep	9	7	0	25.71	5.43	177.31	13.71	0.9714	5
86.2	18-Sep	10	5		40.88	11.88	157.39	5.46	0.9955	5
86.2	18-Sep	11	8	1	39.83	19.54	171.36	5.91	0.9947	5
86.2	18-Sep	12	7		22.34	4.95	174.92	5.52	0.9954	5
86.2	19-Sep	1	6		28.2	8.45	134.61	9.83	0.9853	5
86.2	19-Sep	2	7	1	25.46	18.08	180.58	10.76	0.9824	5
86.2	19-Sep	3	22		85.25	45.78	264.24	14.08	0.9698	5
86.2	19-Sep	4	7	1	31.96	19.38	177.85	12.03	0.9779	5
86.2	19-Sep	5	5	1	34.36	17.08	174.58	14.41	0.9284	5
86.2	19-Sep	6	7	1	33.26	13.51	150.9	19.14	0.9442	5

NEST THREE 1986 25 ANTS DISTANCE FROM NEST BEARING FROM NEST

NEST	DATE	ANT	DUR	ARES.	MEAN	S.D.	BEARING	A.D.	C.I.	SIGN
86.3	14-Jul	1	9		66.24	1.25	110.52	1.8	0.9995	5
86.3	14-Jul	2	13	0	34.74	14.44	115.95	31.29	0.8509	5
86.3	14-Jul	3	7	10	62.9	11.62	116.97	27.42	0.8854	5
86.3	14-Jul	4	8	1	50.38	24.03	312.9	37.79	0.7825	4
86.3	14-Jul	5	7		39.55	12.13	322.53	36.47	0.7974	3
86.3	14-Jul	6	12		86.79	46.06	21.99	16.4	0.959	5
86.3	14-Jul	7	4		50.51	10.31	146.66	11.51	0.9798	5
86.3	14-Jul	8	24		68.86	53.94	146.19	57.05	0.5042	4
86.3	14-Jul	9	5	1	41.84	17.47	271.9	53.77	0.5596	0
86.3	14-Jul	10	15		55.77	6.21	212.04	64.27	0.3709	0
86.3	14-Jul	11	3	1	69.75	27.6	35.25	8.63	0.9886	5
86.3	14-Jul	12	7	1	49.09	38.75	39.04	31.54	0.8485	5
86.3	14-Jul	13	4		56.98	24.78	195.26	27.41	0.8855	n=4
86.3	14-Jul	14	6	0	51.35	2.07	151.61	11.06	0.9814	5
86.3	14-Jul	15	6		63.61	24.53	68.36	32.07	0.8433	3
86.3	15-Aug	1	5		95.86	43.11	135.57	22.88	0.9203	5
86.3	15-Aug	2	5	1	59.82	6.65	93.62	28.89	0.8729	2
86.3	15-Aug	3	7		89.41	16.72	109.25	11.23	0.98908	5
86.3	15-Aug	4	10		63.22	6.9	114.23	23.25	0.9177	5
86.3	15-Aug	5	18		100.74	6.13	166.05	5.07	0.9961	5
86.3	15-Aug	6	10		66.8	9.36	115.1	25.03	0.8046	5
86.3	15-Aug	7	14		80.84	16.53	140.72	8.19	0.9898	5
86.3	15-Aug	8	6		96.27	11.32	159.05	10.04	0.9847	5
86.3	15-Aug	9	6		59.88	7.44	91.68	20.25	0.9375	5
86.3	15-Aug	10	6		71.28	5.71	132.55	6.78	0.993	5

NEST FOUR 1986 19 ANTS					DISTANCE FROM NEST		BEARING FROM NEST			
NEST	DATE	ANT	DURA	RES.	MEAN	S.D.	BEARING	A.D.	C.I.	SIGN
86.4	29-Sep	1	5		20.37	18.08	52.2	47.37	0.6582	0
86.4	29-Sep	2	4	1	15.23	11.73	70.47	65.11	0.3544	n=4
86.4	29-Sep	3	7		21.88	19.99	9.45	42.35	0.7267	2
86.4	29-Sep	4	5		49.9	35.04	37.69	46.8	0.6664	0
86.4	29-Sep	5	8		57.43	39.67	22.29	38.8	0.7706	3
86.4	29-Sep	6	8		54.67	32.09	75.86	41.18	0.7418	3
86.4	29-Sep	7	8		60.64	23.44	19.5	13.996	0.9702	5
86.4	29-Sep	8	11		52.99	21.13	21.57	7.81	0.9907	5
86.4	30-Sep	1	5		26.13	19.46	26.17	46.95	0.6638	0
86.4	30-Sep	2	10	1	67.73	34.06	24.62	13.71	0.9714	5
86.4	30-Sep	3	9		43.2	26.98	43.94	46.07	0.6767	2
86.4	30-Sep	4	9	1	56.85	35.92	346.72	36.98	0.7917	4
86.4	30-Sep	5	9	1	51.7	33.08	350.35	36.38	0.7984	4
86.4	03-Oct	1	7		38.57	24.44	35.18	40.71	0.7476	4
86.4	03-Oct	2	10	0	39.78	22.76	336.09	35.25	0.811	5
86.4	03-Oct	3	4		35.41	25.01	9.05	51.26	0.5998	n=4
86.4	03-Oct	4	4		73.24	40.24	44.87	41.62	0.7361	n=4
86.4	03-Oct	5	8	10	60.11	55.2	298.75	44.03	0.7047	2
86.4	03-Oct	6	5	1	63.29	37.95	27.53	16.13	0.9599	3

NEST FIVE 1986 5 ANTS					DISTANCE FROM NEST		BEARING FROM NEST			
NEST	DATE	ANT	DURA	RES.	MEAN	S.D.	BEARING	A.D.	C.I.	SIGN
86.5	07-Jul	1	9	0	32.26	22.39	20.88	39.34	0.7642	4
86.5	07-Jul	2	9	1	64.65	36.85	66.78	10.9	0.9819	5
86.5	07-Jul	3	9	1	141.99	79.22	81.21	7.7	0.991	5
86.5	07-Jul	4	16	1	116.94	76.63	76.92	10.61	0.983	5
86.5	07-Jul	5	6	1	72.68	20.02	23.9	5.65	0.9951	5

NEST SIX 1986 8 ANTS					DISTANCE FROM NEST		BEARING FROM NEST			
NEST	DATE	ANT	DURA	RES.	MEAN	S.D.	BEARING	A.D.	C.I.	SIGN
86.6	20-Jun	1	4		26.53	5.55	161.33	3.55	0.9981	n=4
86.6	20-Jun	2	6		34.39	18.2	186.61	26.84	0.8902	4
86.6	20-Jun	3	5	1	32.94	18.99	92.02	17.52	0.9533	5
86.6	20-Jun	4	3		24.2	7.8	150.39	8.74	0.9884	n=3
86.6	20-Jun	5	6		22.33	8.72	136.06	30.92	0.8544	5
86.6	20-Jun	11	8		80.11	37.45	115.79	5.94	0.9946	5
86.6	20-Jun	12	4		28.75	5.54	149.47	24.32	0.9099	n=4
86.6	20-Jun	13	7	1	30.71	15.47	80.47	19.84	0.94	5

NEST SEVEN 1986 5 ANTS					DISTANCE FROM NEST		BEARING FROM NEST			
NEST	DATE	ANT	DURA	RES.	MEAN	S.D.	BEARING	A.D.	C.I.	SIGN
86.7	20-Jun	6	8		70.79	8.14	101.51	2.02	0.9994	5
86.7	20-Jun	10	5		55.04	16.36	128.61	19.19	0.9439	5
86.7	20-Jun	7	9		52.17	7.91	279.62	6.7	0.9932	5
86.7	20-Jun	8	3		55.57	6.77	278.11	2.05	0.9994	n=3
86.7	20-Jun	9	6		44.36	14.92	286.5	6.39	0.9938	5