The behaviour of wood ant foragers at the individual cohort and colony levels in the exploitation of carbohydrate food provided in nature by aphid aggregations

by

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A Thesis submitted for the Degree of
Doctor of Philosophy

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May 1998

To

Gordon MacKenzie

whose hopes and dreams towards the

polygynous behaviour of social insects:

no longer with us to share these findings.

Acknowledgements

I would like to thank Dr. Derek Cosens for his valuable guidance, keen interest, stimulating discussions and personal attention given to me throughout my research carrier.

Profs. David Saunders and Aubrey Manning are also acknowledged for fruitful discussions and suggestions during the course of this research.

My sincere thanks go to Dr. S. Samita for helping me with statistical analysis of the data and Ms. Julie Anderson for assisting some part of my research.

Grateful acknowledgements is made of the Soroptimist Trust, Sidney Perry Foundation, Laura Ashley Foundation (through the Churches Commission on Overseas Students Fund), Newby Trust, Roger and Sarah Bacroft Clark Charitable Trust and Edinburgh University Hardship Fund, for their financial support.

My very special thanks go to Mrs. Helen Howell for her support and understanding.

Finally heartiest thanks go to my husband Dr. Chandralal Hewage for invaluable assistance given throughout this study.

Declaration

This thesis is submitted in partial fulfilment of the requirements of the Degree of Doctor of Philosophy. It contains an account of my own research work performed at the Ashworth Laboratories, ICAPB, University of Edinburgh under the supervision of Dr. Derek Cosens. Unless otherwise stated, the work described is original and has not been previously submitted, in whole or in part, for any degree at this or any other university.

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This is to certify that this thesis contains the results of the research work undertaken by the candidate, Sagarika C. P. Hewage, under my supervision. The work described is original and has not been previously submitted, in whole or in part, for any degree at this or any other university.

Dr. Derek Cosens
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The Abstract

Aspects of the behaviour of the wood ant *Formica aquilonia* were studied in the laboratory and under natural conditions in Loch Ard Forest, Aberfoyle, Scotland. In this study the main effort was towards an understanding of how the foraging population is structured and controlled.

As the preferred food site of the foragers is often the first located site: maximisation of the net energetic yield of the colony as a whole may conflict with the optimal foraging as measured at the individual level. Site allegiance is a constant property of certain individuals within the colony's foraging population. A key component of the foraging system is a mechanism whereby a colony keeps a large proportion of its forager force distributed on the most profitable food sites whilst it members show strong site allegiance. Wood ants discriminate food sources without making comparisons among honeydew sources. Naive foragers show transient behaviours in their foraging repertory more often than veteran, allegiant foragers. This behaviourally flexibility of naive foragers is used to trace novel food sites likely to occur in the habitat. It is represented in this study by the small number of foragers recruited daily. By this recruiting of uncommitted foragers to the foraging population *F. aquilonia* colonies are able to overcome inherent inertia associated with site allegiance.

Although significant differences may be observed at the foragers' level of activity, there are no sub-populations operating at day and night time. The gradual declining activity observed when the colony was subjected to a 17.5:6.5 light:dark cycle does not began immediately after the light out. The rhythmicity was poor in constant dark and complete arhythmicity in constant light suggesting that these rhythms are entrained by light:dark cycles.

There was no evidence found to support that *F. aquilonia* foragers depend on chemical cues to orientate to carbohydrate food sources: mainly honeydew provided by aphids. Evidence was found to support dependence on visual cues and spatial memory for this orientation.

It was found that foragers may be predisposed toward developing search persistence depending upon the type and frequency of food contacted. This study clearly showed that search accuracy is significantly increased as a function of repeated reinforcement with carbohydrate food and the target distance for carbohydrate food searching is significantly short compared to protein food.

It was observed that individual foragers make decisions so to maximise the net rate of reward during a foraging bout. This goal was achieved to a large extent by minimising time spent at the aggregation through a relay system.

Table of Contents

Chapter 1

Chapter 2

Daily foraging activity and social structure within the colony

Chapter 3

Behaviour of the foraging population with respect to food quality

Chapter 4

How do the workers of *Formica aquilonia* orientate to food sources?

Chapter 5

Part One

Distribution of carbohydrate and protein food in the habitat and the wood ants' searching behaviour

Part Two

Recruitment to protein food

Chapter 6

Time and energy budgets of wood ants

Chapter 7

List of Figures

Colour Plates

List of Tables

Glossary, Abbreviations and Symbols

budding	colony multiplication by the departure of a relatively small force of workers from the main nest, accompanied by one or more queens
callow	newly eclosed adult workers
deployment	the sending out of foragers to a food site by the colony
foray	complete journey to a food site and back to the nest
foray interval	interval between two forays
foray frequency	number of forays made by an experienced forager during the experimental period
honeydew	a sugar rich fluid derived from the phloem sap of plants and passed as excrement through the guts of sap-feeding aphids
high raters	foragers which make a high number of forays
kinopsis	alarm communication or recruitment mediated by the sight of movement
low raters	foragers which make a low number of forays
naive	inexperienced (foragers)
polyethism	division of labour among colony members
recruitment	first time appearance of inexperience foragers at food site
replete	an individual forager whose crop is distended with liquid food
route fidelity	foragers' adherence to a particular route among several
site allegiance	foragers' adherence to a particular food site
trophallaxis	mouth to mouth food exchange
veterans	experienced foragers

ANOVA	analysis of variance	min	minute
ARS	area restricted searching	ml	millilitre
C	centigrade	mm	millimetre
CCTV	closed circuit television	MS	mean of squares
CHO	carbohydrate food	N	number of data
cm	centimetre	NS	not significant
D	dark	P	probability factor / significant level
df	degrees of freedom	PRO	protein
F	f value	s	second
FO	final orientation of wood ants	S	significant
g	gram	SD	standard deviation
h	hour	SE	standard error
ha	hectare	SFZ	spatial fidelity zones
IGT	Initial giving up time	SS	sum of squares
IO	initial orientation of wood ants	t	t-test value
kcal	kilocalorie	W	watt
L	light	w/v	weight/volume ratio
LD	light/dark	x^2	Chi squared value
m	metre		

CHAPTER 1

Introduction

1.1 Taxonomic status of wood ants

The ant *Formica aquilonia* is a member of the *Formica rufa* group which consists of the mound building wood ants. According to Douwes (1979) this group comprises five or six ecologically and morphologically very similar species: *Formica rufa* LINNAEUS, *Formica polyctena* FÖRSTER, *Formica aquilonia* YARROW, *Formica lugubris* ZETTERSTEDT, *Formica pratensis* RETZIUS, and *Formica nigricans* EMERY. *F. rufa* is used as the 'type' and is characterised by short, hairy maxillary palps, the 5th and 6th segments of which are not longer than the 2nd; workers are bicoloured; the frontal triangle shiny; and the eyes of males hairy (Yarrow, 1954). There is disagreement about the taxonomic status of *F. nigricans* and *F. pratensis*: *F. pratensis* is probably an ecomorph of *F. nigricans* (Seifert, 1992) and occurs in Britain locally in the county of Dorset.

There are two species of wood ant found in Scotland: *F. lugubris* and *F. aquilonia*; specimens of which are often quite difficult to distinguish. *F. lugubris* is considered to be larger, and hairier than *F. aquilonia* particularly behind the head and on the mesonotum, gena, and abdomen. Within Britain *F. lugubris* occurs throughout Northern England, where it may be sympatric with *F. rufa,* and in Scotland in the drier uplands; while *F. aquilonia* only occurs in Scotland in the wetter areas of the West Coast. *F. lugubris* has been found in both monogynous and polygynous communities. In comparison *F. aquilonia* has been found in polygynous communities only (Urbani & Collingwood, 1976; Rosengren & Pamilo, 1983).

1.2 Applied Ecology

F. aquilonia has a monomorphic worker caste. The nest-builders construct mound nests with conifer needles and other materials from the forest floor detritus, and during July prefer the dense woody flowers of conifers probably because they hold water and form a moist layer in the thatch protecting nests from the drying effects of sun and wind (Horstmann, 1974). The mound nests are angled in the direction of the incident sunlight to maximise a heat absorption surface at the edge of the tree canopy. These nests are connected to others by fixed 'internest' trails and the resulting polydomous, 'unicolonial' complexes can remain stable over many years, such that the nests reach heights and diameters of several feet and the trails become visibly worn into the ground. The trails, typically 30-40 cm wide, are used by individuals travelling between nests (internest trails) within the colony and by foragers to gain access to forage sites (foraging trails). The 'unicolonial nest complexes' are probably derived by a 'budding' process where workers and queen(s) leave the main nest and construct a subsidiary nest nearby. This budding process is possible owing to the polygynous nature of the colonies (Pamilo, 1981). Marking experiments show that ants move freely, via the internest trails, between nests that are sometimes 70 m apart. Members of *F. rufa* group have long been known to exist in mutualistic relationships with aphid species (Homoptera) (Way, 1963). These aphids produce sugary exudates or 'honeydew' on which the ants feed, and in return the aphids benefit by the efficient removal of their sugary excreta, an accumulation of which is liable to render them susceptible to attack from sooty moulds, often proving fatal due to interference with the opening of the anal valve (Way, 1963). In addition the aphids may receive some protection from predators although this is unconfirmed in many cases (O'Dowd & Catchpole, 1983). Elton (1932) described how ants at aphid aggregations guard the aphids from predators; and Holt (1955) claimed that the attendence of foraging ants reduces the number of aphid predators - although he records no direct observations of ant-predator interactions. Wood ants take a variety of foods which are in order of importance: honeydew from aphids (62%), insect prey (33%), sap and resin (4.5%), fungi and carrion (0.3%), seeds (0.2%) (Sudd, 1970); the proportion of protein food varies during the year (Wellenstein, 1952; Stradling, 1978): this variability probably reflects the availability of resources. Sap is important early in the year when aphids are not abundant (Wellenstein, 1952), and honeydew is collected more in late summer than in spring (Vowels, 1955). Like other ants, wood ants are known to be opportunistic in their capture of prey items: they select the different prey according to abundance (Skinner & Whittaker, 1981). However, the abundance of a prey does not make specific workers exploiters of that productive food source (Horstmann, 1972). Nonetheless the wood ants, as predators, together do retard the growth of populations of forest insect pests. But their influence also depends upon the size of the community: the number of mounds per unit area of the forest (Rosengren *et al.*, 1979). Both *F. lugubris* and *F. aquilonia* have been observed to be useful agents against forest pests in sub-alpine and alpine forests (Pavan, 1959). Wellenstein (1959) observed 'green islands' in forests elsewhere defoliated by *Panolis flammea*, and also found that the 'green islands' were areas within which wood ants foraged. According to his survey, 76% of researchers assigned a positive value to the ants against forest pests, while 24% regarded the overall effect of the *F. rufa* group to be at best neutral because of the relatively low percentage of harmful insects in their diet and at worst detrimental because their use of honeydew leads to a high parasitic burden for certain trees.

In addition to their feeding behaviour, wood ants affect the forest in several other ways. For example, their excavations aerate the soil and it has been observed that trees are extremely viable and make rapid growth in the proximity of the wood ant mounds due to the addition of organic materials to the soil. Furthermore, as agents for seed transport and plant establishment they are of special importance in areas where the soil is subject to active erosion (Gösswald, 1951).

However, wood ants do enhance the populations of various species of aphids from which they obtain honeydew. The presence of large numbers of aphids feeding on the phloem sap must surely impose a considerable energy and nutritional drain upon a tree. Hence there is discussion as to whether interactions of this sort resulting in an increased parasite burden outweigh the benefits of protection against defoliating insect pest outbreaks (Rosengren & Sundström, 1987). According to Dixon (1971) any aphid effect causing a reduction of timber production is not due to the energy and nutritional drain, but probably to what the aphids put into the plant (host alteration). The environmental heterogeneity can cause interactions to be beneficial to plants under certain circumstances and harmful to plants under others (Ito & Higashi, 1991). Nonetheless, the total benefit should be reflected in the reproductive fitness of the plant rather than its vegetative fitness (Whittaker & Warrington, 1985).

In recent years the mature forest plantations of Scotland have been clear-felled; a technique where by all the trees of a stand are cut at once. The land may then be replanted. These modern practices in forestry are known to weaken wood ant populations and to increase the previously modest risk of damage by insect pests in Fennoscandinavian forests (Ehnström *et al.*, 1974). Moreover, such disruptions to the habitat have resulted in a dramatic decline in wood ant populations even in some cases to complete eradication. In mainland Europe wood ants have been actively conserved for many years. In 1880 a German law imposed a month's jail sentence, or hundred Mark fine, on anyone disrupting nests or killing wood ants (Donisthorpe, 1927). Recent grand scale defoliation of timber crops in Scotland by pine beauty moth caterpillars has awakened British interest in the conservation of the wood ant. The Forestry Commission's felling policy aimed at protecting the wood ants has been implemented for the last few years: mature spruce and silver birch local to the nests and forming the trophic area are left standing in order to maintain a honeydew source for the ants (Forestry Commision Bulletin, 1987). This policy has been partially successful in countering the effect of clear-felling, but reductions in colony size still tend to occur and the ultimate reasons for the decline are not clear. Wood ants inhabit the forests not because of the prey but rather the aphids which provide their major food source: honeydew. Hence every aspect of their success depends on interactions between the colony's food harvesters (foragers) and the honeydew producers (aphids). Understanding how the foraging population is structured and controlled, will facilitate the development of woodland management practices that favour wood ant communities. The behaviour of wood ants has been the subject of many studies although little work has been undertaken with *F. aquilonia* (Rosengren, 1977a,b; Cosens & Toussaint, 1985, 1986; Lamb & Ollason, 1993, 1994a,b). There are, however, a number of generalisations which can be made about the *F. rufa* group as a whole.

1.3 General habits of social insects

Social insects like ants evolved from solitary, carnivorous, wasp-like insects: whereby the mother came to remain with her offspring, feeding and tending them throughout their development. At a later stage mature individuals reared by the mother, remained with her and assist her in maintenance of the nest, care of further brood, and foraging. Eventually the full caste system arose, in which the colony's queen and the males are maintained solely for reproduction purposes, while workers take on all the other duties of the colony. The efficient running of the colony would be disrupted if workers ceased their normal duties in order to court, mate or lay eggs: specialisation of function within a society undoubtedly leads to more efficient organisation. So it is understandable why natural selection has acted to suppress the reproductive behaviour of workers. The distinction between queen and workers can be explained on the basis that workers are equipped with nervous connections for sexual behaviour but they lack the drive which would motivate it. If this is so then one must distinguish between the various sub-drives of the reproductive instinct corresponding to courtship, mating, egg-laying, nest-building, care of young, care of nest, and foraging. In an established colony of a species such as *F. aquilonia* the first three are present in the queen, the last four in the workers (Wilson, 1971; Hölldobler & Wilson, 1990). The total behavioural repertory of an individual worker is relatively simple since she needs to operate only with 'rules of thumb' where each rule (task) is easily handled by the individual. The decisions of individual foragers are based on local stimuli that may contain relatively small amounts of information (Krebs & McCleary, 1984), so each action is performed with limited precision. Yet when the actions of the foraging group are put together, the behaviour that emerges is more precise in execution. In addition, foragers exhibit moment to moment behavioural flexibility: when the needs of the colony demand it, they can switch to a new behavioural repertoire (Hölldobler & Wilson, 1990). There are many activities which are casually related to stimuli from the members of the colony. These stimuli are of a simply tactile nature and being fairly unspecific could be given by larvae and/or callows. They cause an 'excited' (agitated) responses which requires specific thresholds for many activities. The subsequent behaviour of the worker, such as foraging, nest-building and defending, is determined by the stimuli it later encounters (Vowels, 1955). It is easy to conceptualise insect colonies as analogues of simple machines and to invent ways by which worker behaviour might be modified to increase work and reproductive efficiency. But the encompassing and far more complex problem (of which efficiency is part) is that of adaptation, and adaptation implies a permissible optimum by which colony fitness can be measured. It is the optimum or goal in machine-oriented terminology (Wilson, 1966). Some complex aspects of insect behaviour are innate performed with little experience, other behaviours are learnt and altered according to experience, such as foraging (Johnson, 1991) and nest-mate recognition (Errard, 1994). However, insect learning capabilities are often limited to occurring within certain modalities. Within these modalities genetically pre-determined templates dictate that certain things are learnt more easily than others, and as a consequence learning can be inflexible (Menzel, 1972). In contrast to this apparent inflexibility, when a honeybees' food source is consistently moved by an experimenter, the bees are able to correctly anticipate where it is going to be next (Gould & Gould, 1982). This anticipatory behaviour is not so easily explained by the action of a genetic template manipulating the behaviour of its courier, and hints at the occurrence of more complex processing. One might assume invertebrates, like ants, with small brains (0.1 mm^3: Vowles, 1965) should behave stereotypically and exhibit rudimentary plasticity, however, workers of *Formica incerta* learn to navigate around a six point maze only 2 or 3 times slower than laboratory rats (Schneirla, 1946)! The current picture emerging of insect learning envisages species specific preparedness for neural processing of certain associations. The ant learning capabilities include habituation, associative learning (the acquisition of a previously meaningless stimulus with a reward) and more complex processing (Hölldobler & Wilson, 1990).

1.4 Foraging behaviour

A mound nest may harbour hundreds of thousands of workers, but only some of them are foragers. The percentage of foragers in the colony varies across species, Kruk-de Bruin *et al.* (1977) obtained a mean value of 24.8% (n=17, SD 15.9) for *F. polyctena*. The theory of adaptive demography predicts that the proportion of workers allocated to foraging should differ among populations in different ecological circumstances (Hölldobler & Wilson, 1990). The range obtained by Kruk-de Bruin *et* *al.* was indeed large: 4.5 to 57.5% of the workers. A worker's shift from another task to foraging is related to the perception of social stimuli carrying information about the current nutritional status of a nest and/or the activities of other colony members (Vowels, 1955). Foraging behaviour is a major component of colony fitness, often co-ordinated through communication and has two interlocking components: firstly, the search for food and secondly, retrieval of food items. The retrieval of food items is often accompanied by the recruitment of nestmates and the avoidance or defeat of enemies. Several factors affect the onset of foraging behaviour; the completion of physiological processes related to cuticular sclerotisation and acquisition of sensory receptor competence may be required before foraging can begin (Hölldobler & Wilson, 1990). However maturational, social or perceptual abilities may be associated with the onset of foraging. The mechanism of specialisation may be a learning process that permits a forager to identify qualitative properties of food and to quickly fix on a specific foraging task. This specialisation may increase the net rate of energy returned to the colony. Ants do not as a rule smell food from a distance of more than few millimetres and they are not attracted to traps baited with food away from the foraging range (Walker, 1957). Wood ants, which have rather good eye sight, are attracted to moving prey from distances up to 9 or 10 cm only (Stäger, 1931). The path of an ant through the foraging range seems to be decided by two things. Firstly in many species, individual ants repeatedly return to the same spot as long as they continue to find food there; secondly in some species, an ant which has found food can direct its nestmates there too. According to Sudd (1970) wood ants do not seem to be able to direct other ants to food sources, except from a very short distance. Resource related learning may also be involved in the persistence of route fidelity and memory shown in *Formica spp.* (Ökland, 1934; Dobrzanska, 1958; Rosengren, 1977a; Cosens & Toussaint 1985, 1986). At the colony level, learning may underlie a competitor recognition system and may mediate community interactions. An ant colony is a reproductive strategy based on the trade-off between maintenance and sexuality. Foragers harvest energy and transform these resources to kin biomass (nest workers). The foragers' joint activity represents a tropic machinery, a foraging system, the ergonomic efficiency of which is measurable by the net energetic yield of the colony as a whole (Oster & Wilson, 1978). If the colony is the effective unit, then foraging behaviour has been shaped by natural selection and its characteristics should be predicted by optimum foraging theory. Most of the foraging models predict that animals will choose the available foraging strategy that maximises some measure of energetic gain. However, the number of strategies available to an animal depends in part on constraints inherent in the behavioural capacity of that animal (Fewell, 1990). Hence certain types of efficiency at the individual level may play a large part in determining successful interactions at the community level within the woodland habitat. The theory of ecological competition usually assumes that different species depend upon limiting resources used in common. Over generations, then, individuals in a population may be pushed towards maximising their use of resources. Natural selection will favour those species most efficient in using energy, and evolution will proceed in 'such direction' as to maximise the total energy flux through the system compatible with the constraints (Lotka, 1922a cited by Taylor, 1978). Since the phenotypes we observe in nature derive from genotypes that are the result of natural selection, we expect the various components of fitness to have been combined to approach a maximum for some measure of total fitness. So it is apparent that a facet expected a priori to be maximised, is linked to a conflicting component in such a way that the latter is minimised. The total energetic yield of the colony will affect the fitness of mother queen(s) and workers in the same way and is thus of common interest to all parties (Oster & Wilson, 1978). Do the foragers tend to concentrate searching in areas of high food density or quality or both? Each forager is part of a larger community, and any behavioural adjustments by a foraging animal will affect its interactions with other elements within that community. These interactions can then be the source of important evolutionary pressures. The changes in foraging behaviour as a function of the spatial and temporal distributions of food will affect foraging efficiency. Recognition of this aspect of foraging behaviour has led to the development of optimal foraging theories. An important component of foraging theory deals with the relation between variation in food sources and the animal's capacity to alter its foraging response (Schoener, 1971; Houston *et al.*, 1988; Ollason, 1980, 1987; Lamb & Ollason, 1993). If different behavioural patterns result in different foraging efficiencies, then natural selection should favour those individuals which show the most efficient behaviours. While this approach is open to severe criticisms, it has the advantage of providing a method for generating clear predictions about patterns of foraging behaviour in particular situations. For example, optimal foraging theories have been used to make predictions about diet composition (MacArthur & Pianka, 1966). According to the Lamb and Ollason (1993) *Formica aquilonia* foragers, collecting sucrose from paired laboratory sites distribute themselves as predicted by 'ideal free distribution'. The 'ideal free distribution' will operate if each forager in the population moves among feeding sites according to decisions tending to maximise its rate of intake of food (Ollason, 1987). Adoption of 'ideal free distribution' implies that each forager uses a rule of this kind, and maximises its current rate of feeding by moving to more profitable sites. However Lamb and Ollason (1994a) later modified the application of 'ideal free distribution' theory to the wood ant foraging system since not all foragers were observed to behave as predicted. The demonstration of systematic patterns of foraging behaviour in response to these kinds of variables raises questions about the physiological and behavioural mechanisms that produce these patterns. For example, the predictions of many optimal foraging models depend upon the forager possessing a considerable amount of information about its food. Differences in ability to learn and remember food characteristics could produce differing patterns of food selection. Furthermore, the parameters of the learning and discriminatory processes of foragers will affect the rate and course of the evolution. A worker can increase its fitness by being a more efficient helper (West-Eberhard, 1978). The long time-lag between foraging and transformation of harvested resources to genetic gains suggests, like long colony longevity, that foraging should be examined as a long-term trade-off between instant resource exploitation, resource monopolisation and improvements of future resource availability. The source of uncertainty in the analysis of ant foraging systems is society's integrated nature. In this study foraging is considered as one facet of a multidimensional life history pattern, connecting resource structure and breeding structure. Hence it is clear that the study of foraging behaviour raises multifaceted and multidisciplinary questions that will require the application of different methodological and conceptual perspectives before complete understanding can be achieved.

1.5 Foraging strategies

It is well known to many ant-keepers that the greater the number of young, the greater the foraging activity of a colony. According to Schneirla (1933) when eggs are present the workers of Army ants (*Eciton*) forage sporadically and individually collect nectar and there is no subsequent regurgitation (food exchange) in the nest. However, when brood is present the foraging becomes marked and continuous, and workers bring back insect booty which they deposit among the larvae. When pupation occurs the foraging again becomes sporadic and individual. The foraging strategy of an ant species is likely to reflect the kind of food gathered and its distribution: clumped/dispersed; predictable/unpredictable; persistent/non-persistent; stable/unstable (Rosengren & Sundström, 1987). This may be constrained by other life history parameters: territorialism/nonterritorialism; long/short colony longevity; long/short time lag in allocating resources to sexual brood. A colony must therefore spatially organise its foraging strategy to harvest food efficiently and to minimise competition. This is accomplished through individual and colony wide foraging. The wood ants exploit the self-renewing sources of 'honeydew' provided by aphid aggregations, and hence belong to an ecological category of animals that defend a specific area (trophic zone) which provides spatially fixed point sources within a stable habitat. In addition they collect insect booty scattered throughout the territory. The stability of aphid aggregations in climax woodlands is remarkable both within and between years (Skinner, 1980a & b) and has favoured a dogged approach unlike the opportunistic approach associated with more ephemeral food sources which often involve the use of chemical trails to guide foragers. Wood ants' route fidelity and site allegiance based on topographic imprinting, leads to a partitioning of the foraging territory among individual foragers. The site allegiance and route fidelity could be a predictive strategy correlating past and future rewards and hence representing an adaptation to a spatially stable resource structure (Rosengren, 1971; Cosens & Toussaint, 1985, 1986). However, the operational unit is not the individual forager but the colony as a whole. So at the colony level of organisation, site allegiance could also be a probabilistic tactic for dispersal of foraging effort resulting in branching routes and permanently occupied sites within a known tropic zone. The demographic structure of the worker force implies that a reserve of spatially unbiased potential foragers is available within the mound nest ready to be recruited to profitable areas. This reserve of 'opportunistically' behaving potential recruits adds, especially in spring and early summer, an element of plasticity to the system, thus counter balancing the 'inertia' resulting from spatially conservative veteran foragers (Rosengren, 1986). The colony-level foraging strategy is not necessarily an extension of the behaviour of individuals (Oster & Wilson 1978; Pasteels *et al.*, 1987). It is possible, therefore, for the colony to use strategies which compensate for limits on individual responses. When examining the foraging strategies of social insects it is important to consider behavioural changes both at the level of the individual and the colony. The efficiency of a particular foraging strategy is affected by the foraging rate that the individual ants might achieve and by the energetic efficiency of that particular strategy. A flexible foraging system would allow the colony to switch strategies in response to the discovery of a preferred food source. The mechanisms for switching in response to such variables must occur at the level of the individual. It is unknown which subset of the foraging population will respond to a new resource, however, information on resource quality and accessibility is used in switching decisions. Little is known of the memory capability of ants in regard to food choice; a few studies (Rosengren, 1971; Rosengren & Pamilo, 1983; Cosens & Toussaint, 1985, 1986) show they have the ability to store information and use it for foraging decisions. Should foragers have knowledge of resource availability, how are the preferences of individuals summed to yield a colony-wide pattern of choice? The role of these factors in the implementation of a foraging strategy is poorly understood, albeit that the social organisation may influence spatial patterns of search and therefore resource assessment (Hölldobler & Wilson, 1990). Laboratory research under carefully controlled conditions generally not possible in the field is necessary to reach conclusions about foraging patterns and interactions.

Wood ant foragers acquire information about their colony's nutritional status by the ease with which they find internal nest workers ready to accept their crop loads within the nest (Cosens & Toussaint, 1985), rather than by evaluating directly such variables as, for example, growth rates determining their colony's food situation. Although waiting time to unload conveys crucial information about the wood ant colony's nutritional status (food reserves), it has not been moulded by natural selection to serve this purpose (Seeley, 1989). Unlike the 'signals' which are evolved specifically to convey information, this 'cue' conveys information as an automatic outcome because a replete forager cannot redeploy until she has passed on her load - so the foraging population will decline appropriately. Typically a wood ant colony is aware each day of about a dozen or more potential food sources: each with its own level of profitability determined by such variables as distance from the colony, abundance and the quality of the food. In order to gather its food efficiently a colony must deploy its foragers among the food patches in accordance with their profitabilities. In the case of the honey bee there are two competing hypotheses as to how each forager assesses a nectar source's profitability (Seeley *et al.*, 1991): 1) each forager judges by itself the profitability of a nectar source; 2) each forager is given this information by receiving food in the nest. A honey bee forager arriving at the hive after a successful foray can stimulate its hive mates to resume their visits to a known, previously exploited food source without dancing (Von Frisch, 1965). Trophallaxis is the mouth to mouth food exchange between individuals of the same or different castes in social insect colonies (Wheeler, 1923). Observations of trophallactic behaviour during recruitment suggest that information about the profitability of a food source could be encoded in some parameters of this food-exchange behaviour (Lindauer, 1948, 1954; Nûñez, 1970; Seeley, 1986; Seeley *et al.*, 1991). Although observations as above have not been documented in wood ants, transferring information about food sources to other foragers (Cosens & Toussaint, 1986) and nest mates could be a significant outcome of wood ant trophallactic contacts.

To reach goals, such as food or a nest site, ants can basically employ two systems: 1) trail-laying and trail-following; 2) use of visual cues. As far as the latter is concerned an important role is played by celestial cues and path integration (Hölldobler & Wilson, 1990). Wood ants, for instance, visit 65 species of aphids and may travel 100 m on their routes to them (Wellestein, 1952). Considering that tended aphids can be up to 100 horizontal metres from the nearest nest and several vertical metres up a tree, the forays represent a considerable orientation ability by wood ants. Journeys to aphid aggregations are in fact guided by the same kinds of navigation as the ants use in hunting (Sudd, 1970). Rosengren (1971) studying *F. rufa* and *F. polyctena*, both close relatives of *F. lugubris* and *F. aquilonia*, marked foragers on different foraging trails and demonstrated that individuals show strong preferences for a particular route, that is they show route fidelity. This tendency of individuals to consistently use one route almost exclusively occurs throughout the season and increases as the season progresses. It is possible that there is a relationship between the route fidelity observed by Rosengren (1971) and tendency to return to a particular aphid aggregation. The strong site allegiance and consequential route fidelity that results are typical of wood ant veteran foragers. Route fidelity does not reduce significantly over time; it persists through hibernation in those members of the foraging population that survive to the next season when they pass on knowledge of routes to novice foragers (Rosengren, 1971, 1977a). This perpetuation of the 'topographic tradition' each spring is based largely upon remembering visual cues provided from tree configurations and canopy patterns. Winter tree-felling near a foraging route disorientates foragers and leads to their abandonment of the route, even though the 'worn' path is discernible in the moss cover (Rosengren & Pamilo, 1983). This suggests that tactile and olfactory cues are unimportant for wood ant orientation, at least in this context (Rosengren & Pamilo, 1983). Yet route fidelity also persists during the dark nights when visual cues are unavailable; this fact led Rosengren (1977b) to hypothesise that routes are marked with faecal deposits which may 'smell' differently on each route according to the food source at the end of the route. Cues other than olfactory ones, such as the position of the moon, may be used in nocturnal navigation. Since the continuation of foraging throughout the cloudy nights provided temperature is sufficiently warm to permit activity in *F. rufa* and *F. polyctena* (Rosengren, 1977b) and *F. aquilonia* (Personal observations) suggests that non-visual cues can also be memorised by the foragers (Vowels, 1954a & b; Dumpert, 1981; Cosens & Toussaint, 1985, 1986). Wood ant trail-laying for directional recruitment, although denied by some authors (Dobrzanska, 1958; Cosens & Toussaint, 1985, 1986), has been reported in foragers of starved laboratory colonies (Beugnon & Fourcassie, 1988; Fourcassie & Beugnon, 1988; Lamb & Ollason 1994b). The experiments performed by Rosengren and Fortelius (1986a) had shown that olfactory cues, probably identical with scent markings are idiosyncratic orstreue during dark period and these olfactory orientating cues, which in the main are switched off in the presence of visual cues, may be stored in the memory. Elgret and Rosengren (1977) found that workers of *Formicoxenus nitidulus* follow the 'scent trails' of their wood ant host, more precisely than the wood ant workers: this observation implies a relative unimportance of scent trails to the wood ants. It is known that wood ants do have gravitational sense organs in their neck and are capable of time compensated sun compass orientation during the daytime: they are also capable of remembering the location of food sites relative to their nests by using co-ordinates (Vector Orientation) (Jander, 1963). So it is possible that wood ants are aware of the spatial position of their goals and this kind of navigation could also be used on dark nights (Cosens & Toussaint, 1985).

1.6 Aims of the project

The main objective of this study is to understand which behavioural aspects of *F. aquilonia* are susceptible to modern forestry practices used in Scotland that may cause the wood ant populations to decline. The project was tackled by investigating activitoies at the individual and colony levels, although all the complex behaviour of social insect colonies are implemented through the behaviour of individuals. The behaviour repertoire of social insects can be studied on two levels. Firstly, individuals might behave to maximise their rates of food intake, to avoid predators, or to minimise search time. Secondly, behaviour of individuals can be considered as a manifestation of its larger context, the society. In the first level of approach, an animal could move through the environment according to the theory of optimal foraging (Davidson, 1978; Ollason, 1980, 1987; Dresig, 1988; Bell, 1990; Lamb &

Ollason, 1993). In the second approach, an individual behaviour is examined in the light of its contribution to the entire colony growth and/or reproduction (Oster & Wilson, 1978; Seeley, 1985; Fewell, 1990). In this study, a major effort was made towards the second approach: asking how the behaviour of individuals outside the nest is affected by the social structure inside the nest. Although how the individual forager moves through its environment seeking to forage optimally was considered also.

The most obvious effect of clear-felling is the disappearence of tended aphid aggregations. In Chapter 2, providing two identical food sources to the laboratory colonies, the distribution and pattern of daily activity at both colony and individual levels and the foragers' response to a sudden accruing food-deficit is examined.

An efficient foraging system should be matched to the distribution of resources, including resources yet to be discovered. In Chapter 3 how this matching is accomplished at the colony level and by individual behaviour is examined. A topographic tradition based upon site and route fidelity produces a rewarding foraging effort in stable woodland canopies: but has a 'built-in' inertia for a response to changing circumstances. How have the wood ants overcome the inherent penalty: the dogged allegience to known locations within the habitat?

The site allegiance and consequential route fidelity of wood ants, based on visual cues, does not reduce significantly over time, and persists over hibernation in those foragers that survive to the next season (Rosengren, 1971). In Chapter 4 the recruitment and orientation ability of foragers is examined since the impairment of visual orientation cues is an immediate effect of timber felling in forest plantations.

Wood ant foragers attend aphids to gather honeydew excretions, and forage for prey: chiefly other arthropods. These resources differ in their distribution patterns: aphids are more or less fixed in their spatial locations and their carbohydrate excretions are consistent in quality and renewed at a predictable rate (Mittler, 1958; Sudd & Sudd, 1985). Insect prey items, by contrast, are unpredictable in time, space and size and are not renewed in a predictable manner. In Chapter 5 foraging behaviour is examined specifically to see whether the distribution of carbohydrate and protein foods within the habitat is reflected in the foragers' searching behaviour.

It is clear that energy is not the only constraint on an animal's foraging behaviour: physiological limitations, risk of predation, dietary requirements, competition, food handling ability and other necessary but non-foraging activities all have effect. Another important constraint is time. It is reasonable to assume that animals will treat time and energy as valuable resources and will budget accordingly. The efficient exploitation of available food is a vital requirement of all animals. How much food a forager can collect depends not only on how quickly it can find food but on how much time it has to spend finding and carrying to it nest. Wood ants often down-load (by trophallaxis) their gathered honeydew to nestmates they meet at the foot of the tree and on the foraging trails, so that it may be carried to the nest by a relay system. Whether the wood ants optimise their time budget by employing a relay method when they forage, and under what circumstances, is examined in Chapter 6. So far this type of approach (quantification of the degree of behavioural cohesion) to the wood ants' foraging system has not received any kind of attention.

Clearly these aims demand an investigation of behaviour as it occurs in the wild, therefore, the strategy adopted was to maintain the colony under as natural conditions as possible. The laboratory colonies were not restricted by plaster of Paris nests (Jander, 1957; Rosengren, 1971), rather the ants were placed on large tables, provided with food on another table and left to build a nest and obtain food in a self-directed manner. Once established, observations could be made in a controlled and semi-natural way. Of course, foraging behaviour is affected by a number of variables in addition to those studied here, such as metabolic rates, season of the year, temperature, humidity, colony size and the ecological context of the habitat.

1.7 General methods used in this study

The following sections describe general materials and methods used in this study; methods specific to a particular aim are described in the appropriate chapter. Six colonies: Colony 1, 2, 3, 4, 6 and 7 acquired from the Drumore Wood, Aberfoyle (OSMR: NS492984) were used in the experiments. Colony 1 (Fig. 1.1) was housed on two nest tables that were linked by a wooden bridge which also provided access to a foraging table (120 x 240 cm^2).

1.7.1 Experimental colonies and the foraging area

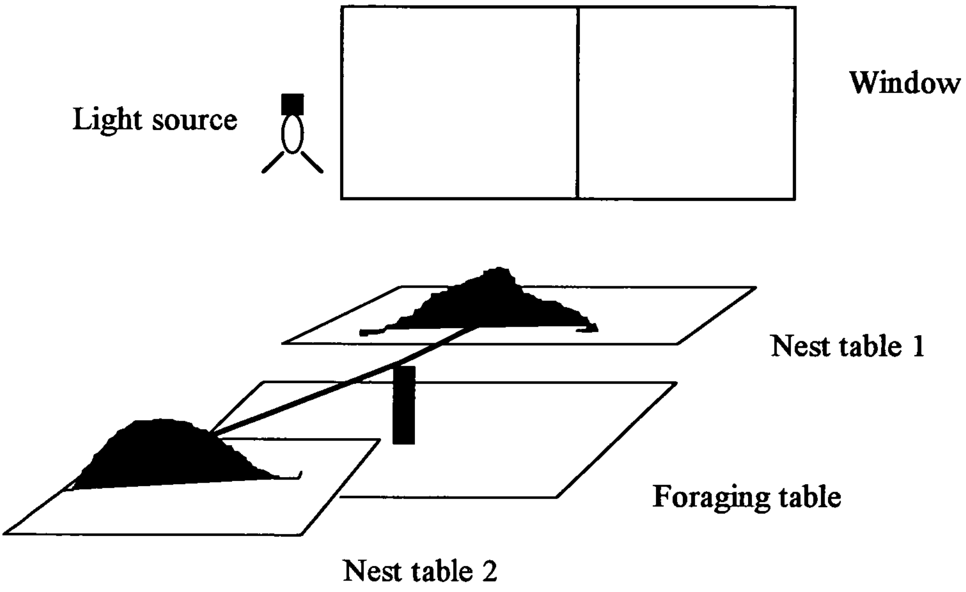


Figure 1.1: Colony 1 layout (not to scale)

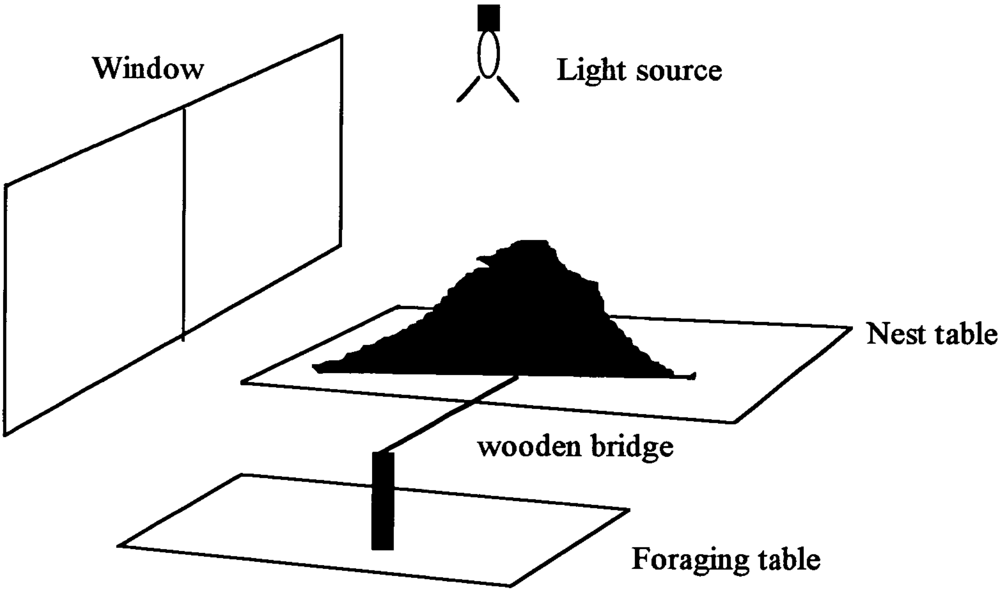


Figure 1.2: Colony 2 layout (not to scale)

Plate 1 The mound nest of *Formica aquilonia* in the field

Plate 2 The mound nest of *Formica aquilonia* in the laboratory

Plate 3 Colony 2 lay out in the laboratory

Plate 4 *Formica aquilonia* daughter nests resulted from budding

The nest and foraging tables were each surrounded by moats in order to retain the ants within the delineated areas and also to maintain humidity. Colonies 2, 3 and 4 (Fig. 1.2) were housed on one of the nest tables and its moats were drained to prevent loss of individuals by accidental drowning. In addition, aluminium walls 15 cm high and coated with Trappit barrier glue (a Green Garden Product) were placed around the foraging table to prevent the ants escaping and drowning in its moat.

1.7.2 The foraging table

Model tree trunks, made from larch wood 10 cm in diameter and of varying heights, were fitted with calibrated feeders; or model trees made from bark-stripped spruce trunks 6 cm in diameter and 60-70 cm in height, drilled to take doweling branches were used. The branches ended with a small square of hardboard onto which a 5 cm diameter Petri dish of sugar solution could be placed. The positions of the model trunks and trees on the foraging table were appropriate to the experimental design. For experiments in which several model trees were used, two of them were designated F1 and F2 and used with a food source on one branch, and an inaccessible control tree was used to measure the fluid loss from a similar food source due to evaporation alone.

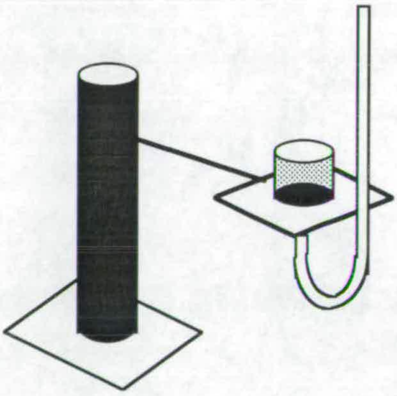


Figure 1.3 Feeding system

An unlimited supply of a 10% (w/v) solution of raw cane sugar (typical value of energy per 100g = 375 kcal.) was available in a Petri-dish, or in a dish connected by a plastic tube siphon to a pipette which acted as a gauge monitoring the amount of sugar solution taken by the foragers over time (Fig. 1.3). The wood ants' diet was supplemented once a week with protein in the form of blow fly larvae (*Calliphora* sp.). The live protein food was provided out-of-phase with the experimental procedures to cause minimal disruption of the foraging behaviour directed at the 'honeydew mimic' sites.

1.7.3 Environmental conditions in the laboratory

About 2 m above each nest a 250 W lamp provided a source of heat irradiation between 10.00-19.00h to mimic that from the sun. However incidental daylight was not excluded and this provided a gradual increase of the day-length in the later part of the study period. All recordings of data were against real time. Rainfall was provided at irregular, but frequent intervals by watering the whole system through a 'rose' fitment on a watering can (6-7 l).

1.7.4 Marking individual foragers

In order to identify foragers individually or to identify them as members of particular 'cohorts', all the foragers visiting a food dish were marked on their gaster and a femur of one leg with a small dot of cellulose paint (Carplan 'touch in' range, Automotive Chemicals Ltd.). This particular cellulose paint does not adversely affect the behaviour or longevity of the wood ants (Cosens, personal communication). Although the paint markings were probably groomed away sooner or later by other ants, markings on the very first segment of the gaster and femur remained for a reasonable period of two months and allowed individuals to be knowingly observed repeatedly. The marks were applied as quickly as possible after a forager began to feed, although marking caused some foragers to walk around nervously for a while and communicate excitedly with their sisters, the majority of them did not appear to be concerned at all. If the marking is carried out carefully whilst foragers are feeding at the dishes, little disturbance is caused, feeding bouts are not interrupted and very few mortalities result.

The colours used were unique for the site and some times also for the particular day of marking. Consequently each forager had a colour-code denoting where she had foraged since the study began. Many of the foragers were individually recognisable by unique colour combinations and shapes of the paint marks, affording information on individual behaviour and foray rates, how long foragers remained part of the foraging population, and whether foragers that had ceased foraging, ever resumed that activity at a later time.

1.7.5 Observational techniques and sampling methods

Observations were made on days spread through Spring, Summer, Autumn and Winter seasons. During each study day, observations were made between 9.00-17.00h or 9.30-16.00h. Two sampling methods were used (unless otherwise specified) throughout the study period: a) instantaneous 'scan' sampling and b) focal sampling (Altman, 1974).

a) Instantaneous 'scan' sampling: The number of ants foraging at each feeder was recorded every five minutes through the study period. This was broken down into counting the number of different coloured and unmarked individuals depending on the experiment performed. The five minutes interval was chosen to minimise the chances of either missing forays completely or counting a forager twice, because preliminary observations revealed that the average feeding time of an individual was 2.5 min (SD=0.35, N=47).

b) Focal sampling: Records against real time were made of each individually marked forager.

1.7.6 Amount of food collected

The amount of sugar solution collected was recorded at 30 min intervals, or at the end of the 24 h period, or at the end of an experimental period. Volumes were adjusted for evaporation.

1.7.7 Gaster volume measurement: load per foray

In order to obtain a more detailed picture of an individual's behaviour, a closed-circuit television camera and a video recorder were used to magnify the image of individuals feeding at sites on some experimental days. As an ant feeds its gaster becomes swollen, and measurements of the length and width before and after feeding may be obtained from the recordings (Fig. 1.4). Since the profile approximates to that of a regular ellipse, the increase in volume of the ellipsoidal gaster can be estimated from the following equation (Table 1.1; Cosens & Toussaint, 1986).

$$V_s = \pi/6 \times (L_a \times W_a^2 - L_b \times W_b^2)$$

V_s = volume of sugar solution; L = maximum length of gaster; W = maximum width of gaster; a = after feeding; b = before feeding.

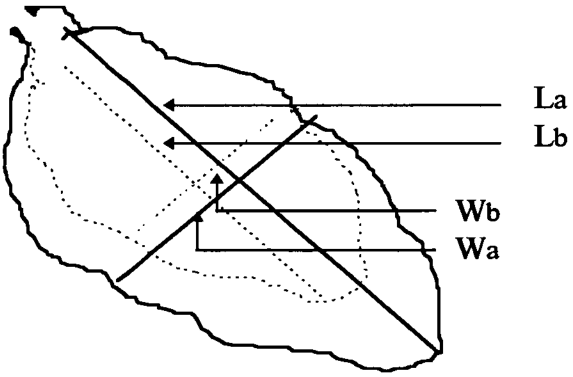


Figure 1.4: Gaster profile of an ant before and after feeding

Table 1.1: Comparative dimensions of replete and non-replete gasters

	Mean length (mm)	Mean width (mm)	$\pi(L \times W^2)/6$
Non replete	2.21 ± 0.075	1.37 ± 0.014	2.17
Replete	2.99 ± 0.016	1.52 ± 0.3	3.62

Deriving a mean factorial increase of 1.67 upon becoming replete
± = (SD) standard deviation; N=17.

CHAPTER 2

Daily foraging activity and social structure within the colony

2.1 Introduction

2.1.1 Elements of foraging behaviour

A colony of ants obtains food through the foraging behaviour of its workers. A mature wood ant colony, which may contain nearly one million workers and survive for at least 50 years, sends out about 30,000 foragers each day on cleared, permanent trunk trails (Gordon *et al.*, 1992). A major part of the diet of wood ants is provided by the honeydew excreted by aphid aggregations. However, one third of their diet consists of other invertebrates. Although wood ants typically select different prey according to abundance (Horstmann, 1972), Inozemster (1974) suggests that *F. rufa* selects prey by preference, choosing Lepidoptera and Coleoptera and avoiding Collembola, Orthoptera, Hemiptera, other Formicinae and Gastropoda and Aranaeae. At the end of March, workers begin to wander from the nest and re-establish foraging trails used during the previous years (Rosengren, 1977a,b). At this time of the year their diet is mainly prey items needed to feed developing sexuals, and because aphids are not yet present to provide honeydew. There is evidence that spring battles may break out between colonies of wood ants as they re-establish their foraging areas and because prey items are often in short supply (Elton, 1932). As 62% of food is from aphid honeydew then one might expect territories to be formed as the aphids appear in early to mid-May. Aphids reach their peak in mid June when wood ant colonies bud.

The motivation to forage may be a response to colony hunger. According to Vowles (1955), there may be three hunger sources to stimulate a prospective forager: the brood, the other adults of the colony and the forager's own viscera. In general it would be expected that foraging for the brood is a part of the major reproductive instinct, while foraging to satisfy personal hunger is a part of the major feeding instinct (Tinbergen, 1951). Certainly, it has been observed in ant colonies with no brood that foraging activity is very low. This observation might suggest that the response to personal hunger is of little importance when considering social foraging. The stimuli by which the larvae excite workers to forage are largely tactile. The writhing of the larvae brings them in contact with prospective foragers who receive sharp blows from heads: which cause workers to become 'excited' and some may then leave the nest in search of food (Vowles, 1955). The stimuli by which callows and successful foragers excite other workers are of a similar tactile nature to those given by the larvae (Barnes, 1941). The difference between these excitatory stimuli and those used for soliciting for food is that the latter are more gentle and of a caressing nature leading to regurgitation (trophallaxis). Trophallaxis is the mouth to mouth food exchange between individuals of the same or different castes in social insect colonies (Wheeler, 1923). Trophallactic contacts are frequently observed in wood ants: when two individuals participate, the 'donor' ant offers food regurgitated from its crop by opening wide its mandibles, the 'recipient' ant takes the offered food by protruding its labial tongue and placing it between the mouth parts of the donor. The association of ants with aphids for honeydew was first recorded by Huber (1810), cited by Vowels (1955). The manner in which honeydew is collected is also the subject of controversy. *F. rufa* is said to 'milk' the aphids by palpating the back of the aphid with the antennae in order to stimulate the aphid to excrete (Elton, 1932). However, according to Nixon (1951) the behaviour of the ant in collecting honeydew is little different from its behaviour in obtaining nectar from extra floral nectaries. It is possible that the caressing movements which the ant makes with its antennae to persuade the aphid to yield its excrement may resemble those used in soliciting larval secretions in the nest, and may be learned. Douglas and Sudd (1980) in a thorough behavioural analysis suggested that the long maxillary palps, rather than antennae, are used to 'tickle' the aphid. Way (1963) reporting findings of Nixon, suggested that the use of the palps is not to stimulate the aphids to excrete, but rather to collect excrement that has been produced. Way's suggestion was confirmed by Toussaint (1983) in his laboratory experiments.

2.1.2 Daily cycles of foraging activity

Each ant species has a distinctive daily foraging schedule and a clear example of this is the remarkably precise changeover of ant species at dusk in the heath of South-western Australia (Wilson, 1971). Are such daily cycles based on circadian rhythms or are they guided hourly by changes in temperature and or other external stimuli? Circadian rhythms affecting foraging behaviour are widespread, but in many cases they can be overridden or at least frame-shifted by colony hunger and/or certain environmental changes (McClusky & Soong, 1979). The diel foraging rhythms in ants show that these patterns are influenced by exogenous factors, and the temporal pattern of activity is seen to be initiated by an endogenous pacemaker or biological clock - perhaps entrained by one or more environmental cues (Whitford & Ettershank, 1975). Endogenous timing mechanisms in ants were investigated by McClusky (1963) who found a circadian rhythm in emergence from a laboratory nest of *Iridomyrmex* and *Veromessor* males. The machine recordings of activity patterns of wood ants (Rosengren, 1977a) suggested that there is a connection between the light: dark cycle and collective activity patterns of workers, although this pattern faded in constant light. Activity patterns may also differ between different colonies of a species, each maintaining its own 'individual signature' (Rosengren & Fortelius, 1986a). However, DeBruyn & Kruk-De Bruin (1972) failed to demonstrate a foraging rhythm with *F. polyctena* in the laboratory under a light:dark regimen. North (1987) experimented with individuals of *F. rufa* and found that individuals which trained to a light:dark 18:6 h cycle become less active at lights-out although the decline of activity did not begin immediately which suggests an endogenous nature of the rhythm. However, individuals trained to a light:dark 12:12 h cycle had activity patterns which were less rhythmic and this may be explained by the failure of the biological clock to entrain to the short light period. Workers that had been entrained to a light:dark cycle and then transferred to constant light or constant darkness generally showed poor rhythmicity. So North suggested that continuous light or dark may suppress or stimulate locomotory activity. Wood ants forage continuously in nature, although foraging is temporarily inhibited by heavy rains and winter temperatures (in Argyll below 4°C, Cosens personal communication). This pattern of foraging activity enables the ant community to obtain a broader selection of prey than would be obtained from concentrated foraging at the same time each day.

2.1.3 Social structure within the colony

Social insects are able to regulate the environment of their nests but they rely heavily on the location and construction of the nest to achieve automatic microclimate regulation. In most ant species all stages of brood are kept in the warmest chambers where the temperature ranges between 25-40°C, but pupae are usually segregated into the drier parts. A more advanced form of microclimatic regulation has been attained by the small minority of ant species including wood ants, that build mounds. True mounds are most common in habitats subject to extremes of temperature and humidity; bogs, stream banks, coniferous woodlands and deserts. The outer crust like layer of the mound seems to reduce loss of heat and moisture. The shape of the mound itself exposes it to more sunlight and enhances warming on cool days. Thatching of the mound surface, a common feature, appears to reduce erosion of the crust by rain and perhaps also provides trapped air spaces that improve insulation. The mound is constantly in a state of flux as workers move material around to reinforce and repair the crust and interior (Cole, 1932).

Within an ant colony, co-ordinated groups conduct parallel, as opposed to serial, operations and hence make fewer mistakes, especially when labour is divided among specialists. That is if different cadres of workers in an ant colony simultaneously forage for food, feed the queen and remove her eggs to a safe place: they are more likely as a whole to complete the operation than if they perform the steps in repeated sequences in the manner of solitary insects (Herbers, 1981). The food supply to the colony is stabilised by the use of larvae and special adult forms to store reserves in the form of fat bodies; while defence, nest construction and foraging are accomplished by specialists. Within-colony spatial order has been predicted because it should enhance efficiency of function and in particular the division of labour (Seeley, 1985; Wilson, 1985; Tofts, 1993). Zakharov (1973) assumed that an ant colony may be divided into cohesive subgroups, each inhabiting a given sector of the nest and communicating with the habitat by a group-specific trunk route. The intranest sampling of field nests of *F. rufa* showed a weak but statistically significant site allegiance (Rosengren & Fortelius, 1986). Spatial fidelity zones (SFZ) have also been observed in colonies of *Leptothorax unifasciatus* which occur with partial overlap in a sequence from the colony centre to the colony periphery; yet no clear segregation of the basis of age was observed (Sendova-Franks & Franks, 1995). They earlier (Sendova-Franks & Franks, 1993) demonstrated that individual workers showed fidelity to particular zones within the nest. *L. unifasciatus* forms small colonies of some 500 workers in flat crevices in rocks, so they may be housed in transparent nests which have similar geometry in the laboratory allowing continuous observation of the spatial relations of all the ants. The division of labour in *L. unifasciautus* was found to be flexibly organised along the continuum of spatial fidelity zones where each worker performed the tasks within her own fidelity zone. However, adoption of a method as direct as that of Sendova-Franks and Franks (1995) is not feasible with *F. aquilonia* owing to their large individual and colony size: hence recording the synchronous activity and spatial positions of all the members of the colony is not possible.

According to Sudd (1970), based on Otto (1958), in *F. polyctena*, provided that the colony has a normal balance between young and old workers, the workers do not begin to forage until at least 40 days after eclosion. Although they have certain aspects of adult behaviour at this stage, such as adopting a correct curled position when nestmates carry them; they are treated more or less like pupae by their older sisters. They begin to take regurgitated food as early as the third day; other social activities like grooming neighbours, licking the brood begin between the 3rd and 6th days of emergence. During their service inside the nest workers engaged in brood care; delivering the queen of eggs; licking young larvae and regurgitating to them and feeding older ones with pieces of insects. When an ant reached the age of 40 days or more it began to spend a lot of its time in the nest entrance where it may be described as a 'watchman', although its behaviour is not like that of the guards in a honeybee colony. An ant's first excursion beyond the mound nest usually started when a replete forager returned to the nest and disturbed it sitting in the nest entrance. The change from intranidial to extranidial work occurred between the 45th and 80th days after eclosion when important changes are also occurring in its internal organs. Almost all the workers of *F. polyctena* caught outside the nest had degenerated ovaries, but a large proportion of those inside the nest had well developed ovaries. Also, during the move to a subsidiary nest, the ants which were being carried had ripe ovaries while the carriers had degenerate ones. The normal course of development of the ovaries is altered if the conditions in which the workers live are abnormal: in particular ovarian development depends on diet and the company of older workers. Young ants are not distributed among the various tasks inside the nest on the basis of age: instead some ants specialise in certain tasks and spend most of their time on them. However, specialists may be made: not born. Perhaps ants which happen to tend larvae at an early stage of their adult life become attached to this task more permanently, at least for as long as they work intranidially. Workers outside the nest show some specialisation too: some foragers are attached to honeydew collection, others to hunting (Kiil, 1934). *F. polyctena* workers can change from nursing to foraging or the reverse, if they are placed in groups all of the same age (Sudd, 1970; Kruk-de Bruin, *et al.*, 1977).

2.2 Objectives of the study

1 To determine the standard pattern of daily foraging activity on which the subsequent experimental studies were based, and how this pattern of activity is affected by light:dark cycles of different periods.

2 To identify and test the foragers allegiant to a particular food site.

3 To examine the turn-over rate of a foraging cohort: for how long does a forager continue at that task?

4 To examine how a forager and the cohort respond to a colony food deficit.

5 The mechanisms of food transferral from the forager to the rest of the colony are not yet fully understood. To examine to whom the foragers down-load: is it directly to larvae, to the nurse workers or to repairers and potential foragers? And to examine whether a particular forager always down-loads in a designated area within the mound nest (displaying an internal site allegiance and spatial fidelity zone)?

The 'observation nest' (Fig. 2.18a) was used to answer these questions.

2.3 Materials and Methods

2.3.1 Daily activity pattern

Colony 1 was used in these activity pattern experiments. Trees (F1 and F2), provided with an unlimited supply of 10% (w/v) solution of raw cane sugar, were placed on the foraging table (Fig. 1.1, but see also Plate 3). The foraging activity directed at each tree was assessed using instantaneous scan sampling (Chapter 1) and by recording the amount of food collected (correcting for evaporation) at 30 min intervals between 9.00-17.00 h. The same experimental procedure was performed with colour-marked foraging cohorts over 24 h periods, while recording ambient temperature (°C) and light intensity (W/m^2). Since these initial experiments demonstrated that foraging activity was not affected by the minor temperature variations within the laboratory, but was affected by light intensity, further experiments were carried out to investigate whether this foraging rhythm was endogenous or influenced by external factors. Colony 7 obtained from Aberfoyle and set up on nest table 1 (Chapter 1) was trained to a 17.5:6.5 light:dark cycle for 7 months at a constant temperature of 21°C. Initially 10% w/v sugar solution was supplied *ad libitum* and foraging activity at the food site was assessed every 5 mins continuously for 32 h. This procedure was repeated four times, each cycle being separated by the period 17.00 to 9.00 h every second day. Then the colony was subjected to constant dark for 7 days and foraging activity at the food site was assessed as before. Thereafter the colony was subjected to the 17.5:6.5 light:dark cycle for 7 days during which it reverted to the initial level and pattern of activity. Then foraging activity was assessed while subjecting the colony to constant light (1.2 W/m^2) as described earlier. This procedure was not continued with changing temperature as preliminary experiments did not show any relationship with the minor temperature variations occurring in the laboratory, although dramatic temperature variations could take place in field situations between day and night. Because of the irregularity present in the data sets visual characterisation of rhythmic components was not always feasible. There is no wholly appropriate method for analysing rhythms, although comparisons of different methods of analysis of circadian rhythms are given in Binkley (1976) and Enright (1981). Hence, to differentiate the activity patterns during the light and dark periods, the mean number of forays between light hours (9.00-21.00 h) and dark hours (21.00-9.00 h) were compared using the $\bar{x}^2$ test. On some experimental days, gaster profile data of foragers were obtained using CCTV and recorder to estimate factorial increase of gaster size with time and number of forays to the site.

2.3.1a Results and Discussion

Daily provisioning of an unlimited supply of 10% w/v raw cane sugar solution resulted in a predictable pattern of foraging activity. This pattern was typical for the known sites used by this particular Colony 1. There were essentially two components to this pattern of daily foraging activity displayed over several months of study: the increase in numbers of foragers at the sites during the initial observational period (co-insides with the initial light period of the particular experimental day) of 1-1.5 h; and the maximum number of foragers observed there in a five minute count ($\bar{x}$=30, SD=12.4, N=30 days), this number was sustained for the remainder of the observed part of the foraging day (Fig. 2.1). The tendency of individual foragers to exploit familiar resources is well documented in the literature (Otto, 1958; Rosengren, 1977b; Cosens & Toussaint, 1985, 1986). Indeed, at 'known sites' and under constant conditions this study has demonstrated that foragers collected the sugar solution in a highly predictable manner.

The tree F1 was placed on the foraging table and provisioned on 16.6.93: Day 1, followed by tree F2 on Day 3. Foragers found tree F1 at 11.33 h on Day 1, however, 10 days elapsed before they found tree F2 on Day 11 (Fig. 2.2). Although the two trees were identical and equidistant from the mound nest, the pattern of daily activity illustrates how the foraging population was not distributed at the two sites equally as predicted by optimum foraging models (Fig. 2.3). Instead, maximum and minimum levels of activity at tree F1 remained unchanged (compare Figs. 2.1 and 2.3) as before the discovery of tree F2. This could be explained by the fact that tree F2 was found by independent searchers from the colony as the demand for food grew as the season progressed. Because the foraging population was not marked during this time, it was not certain whether the foraging population at F2 was, indeed, different in whole or part from that at F1. The intensity of use of a particular site is governed by its productivity. But the wood ants' natural carbohydrate food sources are renewable and predictable: foragers from one generation to the next tend to repeatedly reuse a site. A forager's fidelity to a particular site and route means that new sites are not sought unless necessary (Cosens & Toussaint, 1985; Rosengren & Forteilus, 1986). Local patches may be ignored in preference to more distant, but known locations.

The physical distance to a foraging patch may not constrain its use, because travel time to a distant, known patch will be energetically less expensive than searching for new locations. Studies of *F. rufa* (Holt, 1955) have shown that in the spring time the foraging population is primarily made up of inexperienced foragers and a small number of veterans.

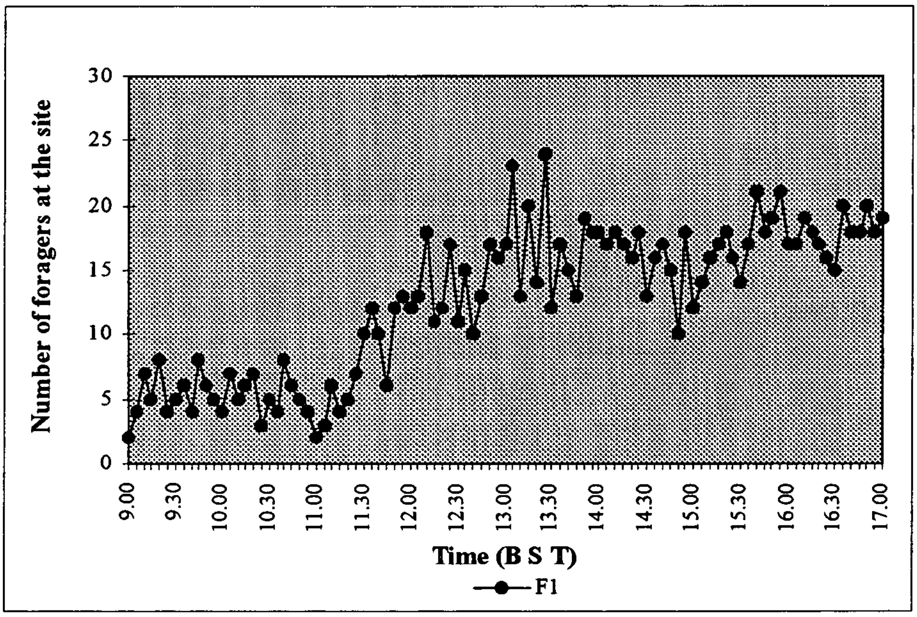


Figure 2.1 Daily foraging activity at tree F1 on 17.6 1993: before finding tree F2 described by counts of the foragers at 5 minute intervals, an index of the number of forays made to the site since foragers return repeatedly and foray intervals exceed 13 minutes.

At this time of the year the colony is initially disorganised and stressed, having just emerged from hibernation. This stress is compounded by the scarcity of food prior to the onset of summer. To utilise the available resources effectively the majority of foragers rapidly become slavishly faithful to one feeding site. As the season progresses and availability of food increases one might expect the rigorous site allegiance to wane, but for the majority of foragers it does not (Rosengren & Forteilus, 1986; Rosengren & Gordon, 1992). It has also been found that in wood ant colonies there is a group of idle individuals consisting presumably of young workers still without a definite task preference (Rosengren & Sundström, 1987). These young workers might function as a reserve to exploit sudden abundance's of food, as well as defending and patrolling the territory.

There were troughs and peaks in the pattern of daily foraging activity (Fig. 2.1), which may be due to random departure from the nest as the travelling time between nest and food site was relatively constant: $\bar{x}$=3.1 min, SD=1.01, N=43. These fluctuations in foraging activity could represent groups of foragers which were allegient to different 'spatial zones'. It was also observed that variation in the number of forays per forager (Figs. 2.5, 2.6, 2.7 & 2.8) was less than the variation between foragers (Fig. 2.4). Since most extranidial elements contributing to the foraging time were constant for all foragers (see Chapter 6, Table 6.2), the variations in the frequencies of forays were largely due to intranidial activities or distances which could relate to 'spatial fidelity zones' within the nest.

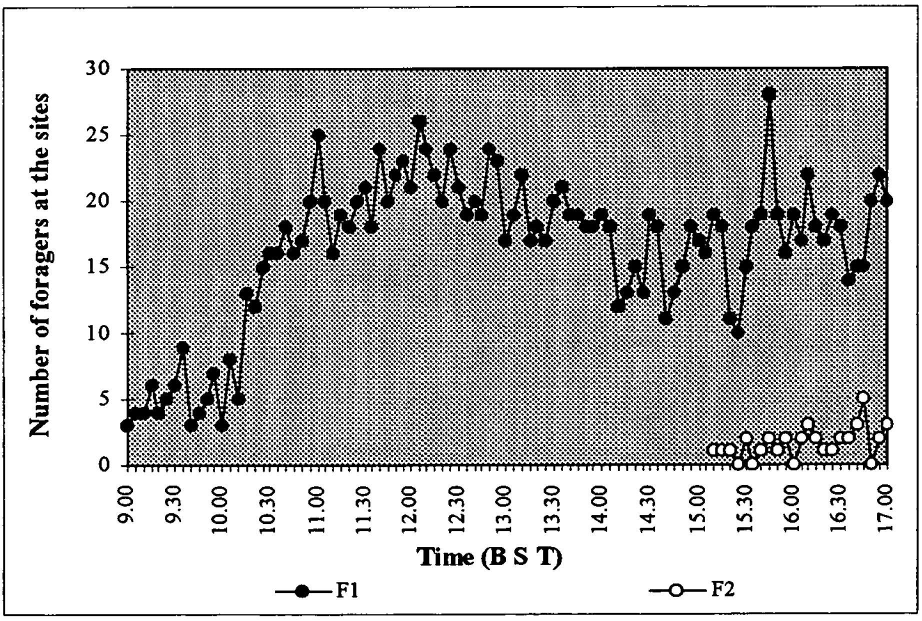


Figure 2.2 Foraging activity at tree F1 on 27.06.1993: described by counts of the foragers at 5 minute intervals, and the discovery and exploration of tree F2 at 15.10 h.

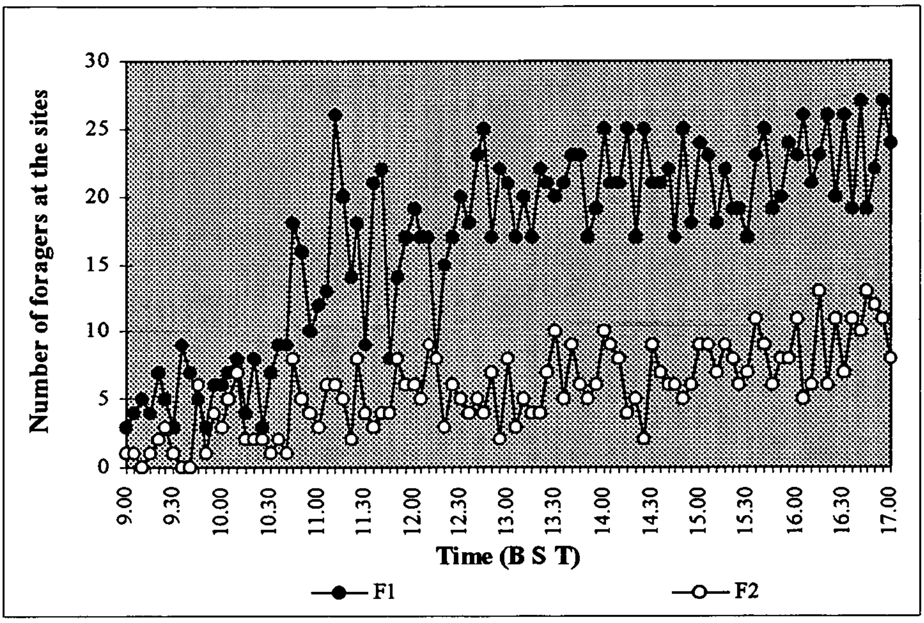


Figure 2.3 Activity at the two trees after the establishment of foraging populations at the two sites. Note that the foragers were not distributed equally and that tree F1 remained the major site.

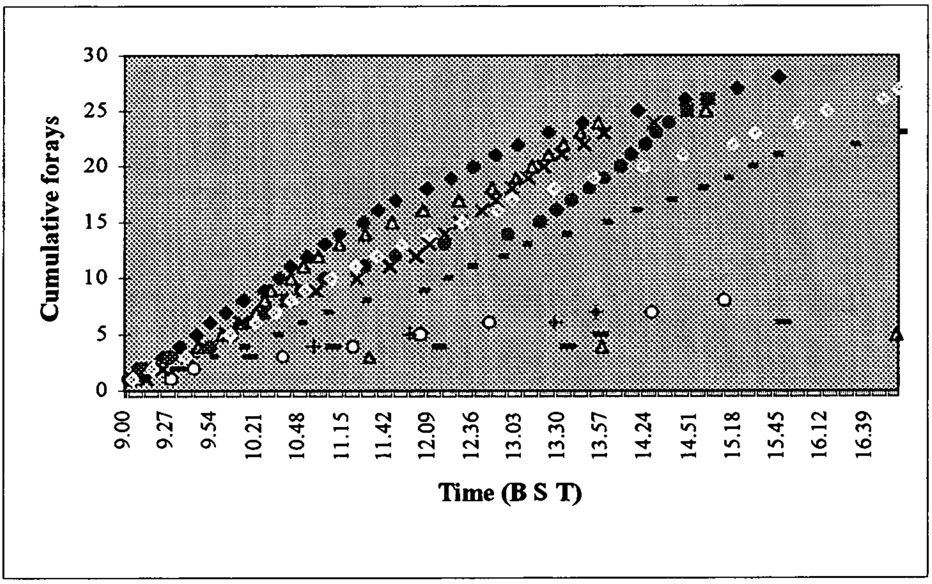


Figure 2.4 Foray profiles of the foraging population on one day, between 9.00-17.00 h. Foray frequencies of 10 uniquely marked individuals selected at random from the foraging population. Note that the foray frequencies are quite variable, and that interforay periods are relatively constant.

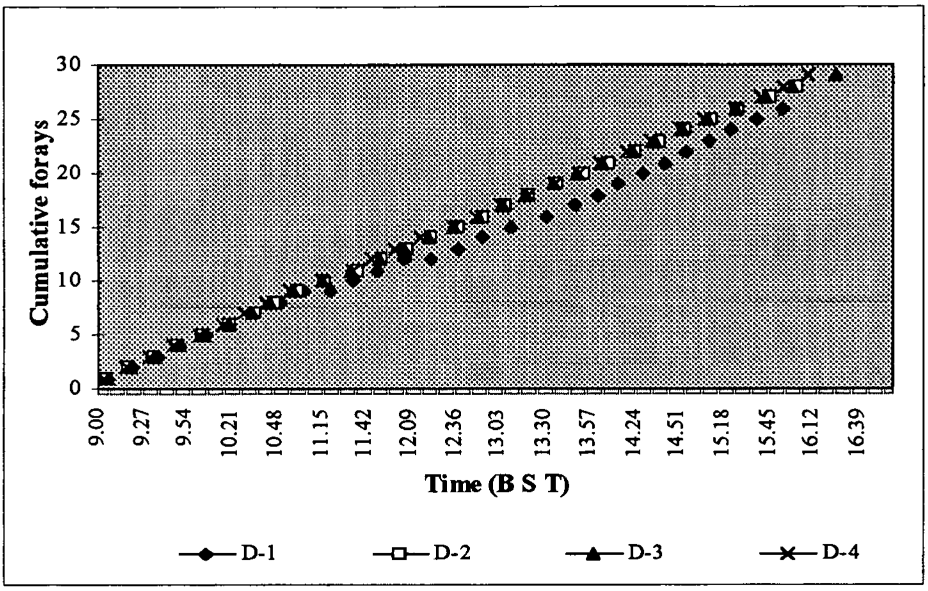


Figure 2.5 Foray frequencies recorded for single marked forager 'Wg' over four consecutive days. D-1 day1, D-2 day2, D-3 day3, D-4 day4

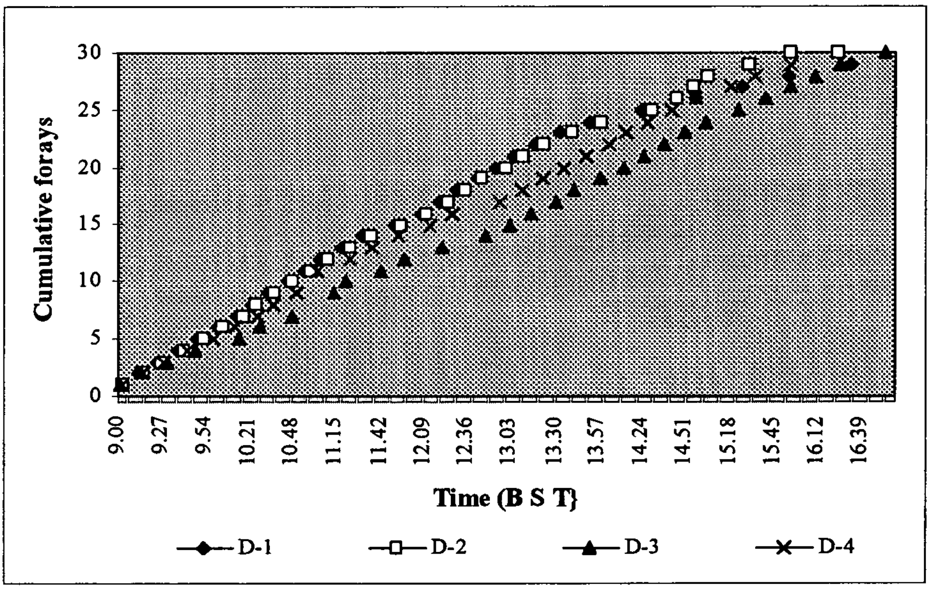


Figure 2.6 Foray frequencies recorded for single marked forager 'Wo' over four consecutive days. D-1 day1, D-2 day2, D-3 day3, D-4 day4

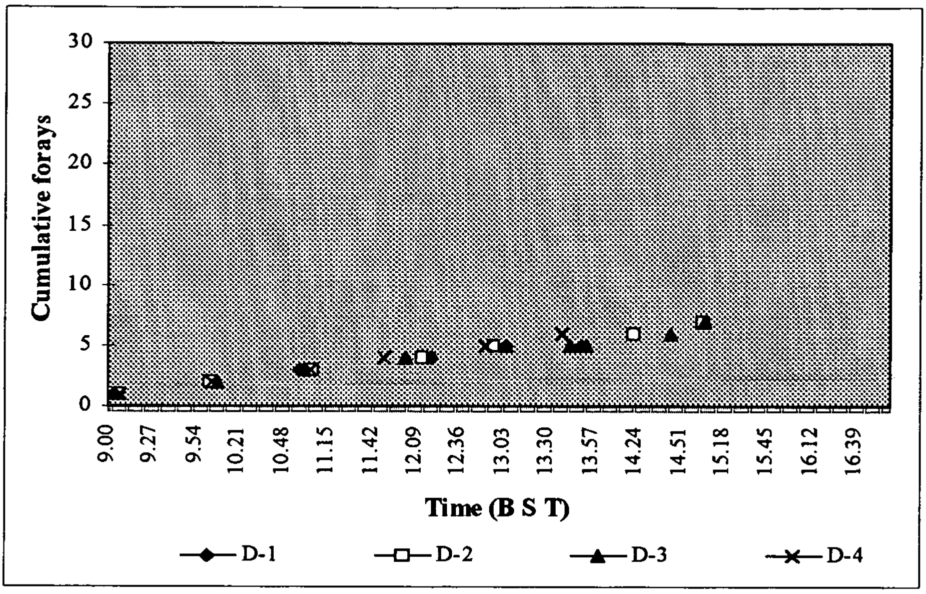


Figure 2.7 Foray frequencies recorded for single marked forager 'Wa' over four consecutive days. D-1 day1, D-2 day2, D-3 day3, D-4 day4

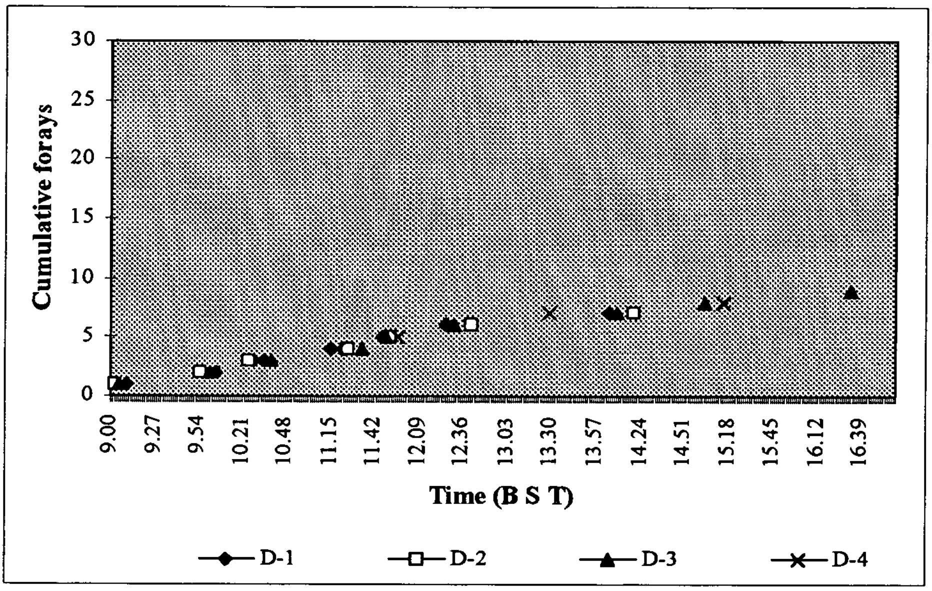


Figure 2.8 Foray frequencies recorded for single marked forager 'Wd' over four consecutive days. D-1 day1, D-2 day2, D-3 day3, D-4 day4

Within an experimental day, the foraging population at a particular tree was found to be a heterogeneous group comprising 'high raters': foragers that make a high number of forays (higher than 18: Wg, Fig. 2.5; Wo, Fig. 2.6), and 'low raters': foragers that make a low number of forays (lower than 7: Wa, Fig. 2.7; Wd, Fig. 2.8). These categories were selected from the foray frequencies of 47 individuals by dividing the foray frequencies into two sets: more or less than 10.

Then selecting within each set the commonest recorded frequency to characterise the set: 7 or less and 18 or more (Fig. 2.4). Foragers which made forays in between 7-18 were considered as at transitional stages from 'low raters' to 'high raters'. The onset and cessation times varied across the population, although these particular observations were based on randomly selected foragers that appeared at the trees between 9.00-10.00 h. When the performance of any one forager was compared across several foraging days, she was seen to maintain a similar foraging rate throughout the period (Figs. 2.5, 2.6, 2.7 & 2.8): this was particularly true of the high raters. In some low raters the frequency of forays tended to increase as the days progressed (transitional stages), although the majority of them maintained a constant performance. According to Cosens (personal communication) novel foragers when recruited to the foraging population make fewer forays compared to the veteran foragers of the same population.

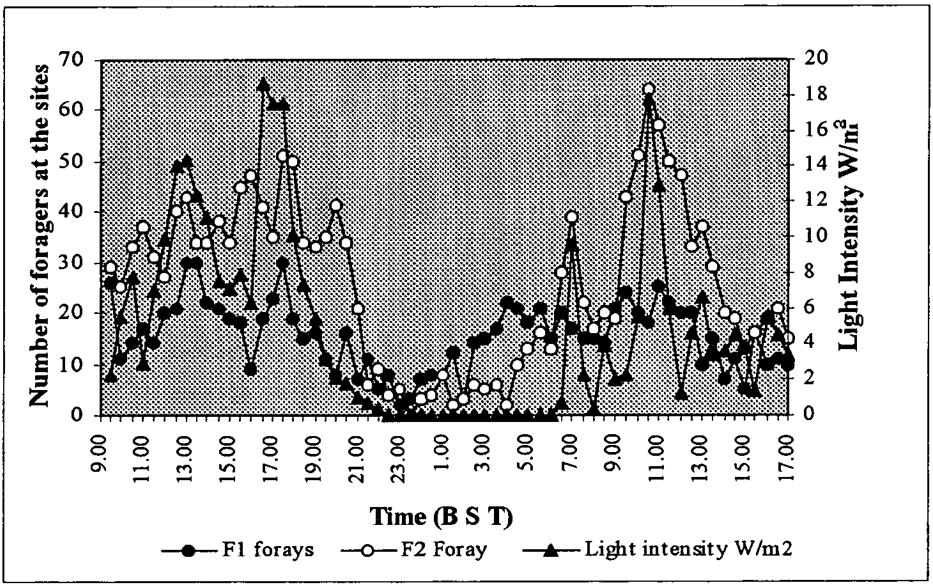


Figure 2.9 24 h daily foraging activity with light intensity variation: described by counts of the foragers at 5 minute intervals, here summed for half-hourly periods.

Table 2.1 Categorisation of foragers in the foraging population

Lower than 7 forays	Higher than 18 forays	In between 7-18 forays
Low raters	High raters	Transitional foragers

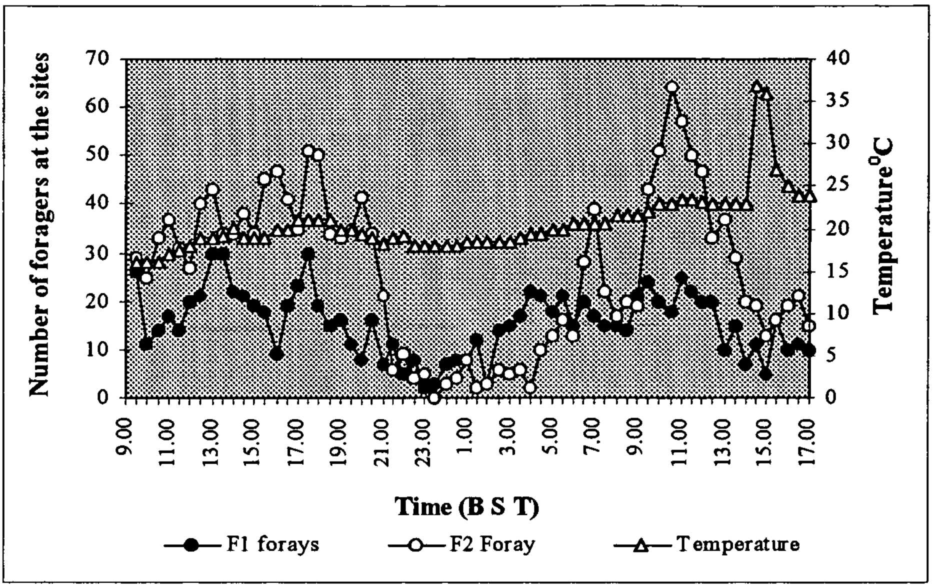


Figure 2.10 24 h daily foraging activity with temperature variation (temperature was not controlled): for comparison the same 24 h period as Fig. 2.9 is used. Note that foraging activity is more directly related to light intensity than temperature.

When considering the 24 h activity pattern, no unmarked foragers were observed foraging after darkness: as the marking of the individuals was carried out during 9.00-16.00 h, this implied that the same foragers work during both the day and night. Foraging activity was not affected by the minor temperature variations within the laboratory (nor by the anomalous increase at 15.00 h Fig. 2.10). However, the foraging activity was affected by light intensity (Fig. 2.9). North (1987) using actograph recordings of activity patterns of individual *F. rufa* foragers demonstrated that some individual workers were more active during the dark period than during the light period when exposed to longer photoperiods. Although these individuals did not avoid the light completely, their activity decreased after the onset of the light. The majority of the foraging population which was active during the day stopped foraging after 21.00 h: this caused a decline in activity during the night.

When Colony 1 was subjected to a 17.5:6.5 light:dark cycle, the number of forays was less in the dark period. However, the foraging activity declined gradually and not immediately after the light was switched off (Fig. 2.9; & Fig. 2.11 for Colony 7). The nature of this declining activity suggests an endogenous basis. When the

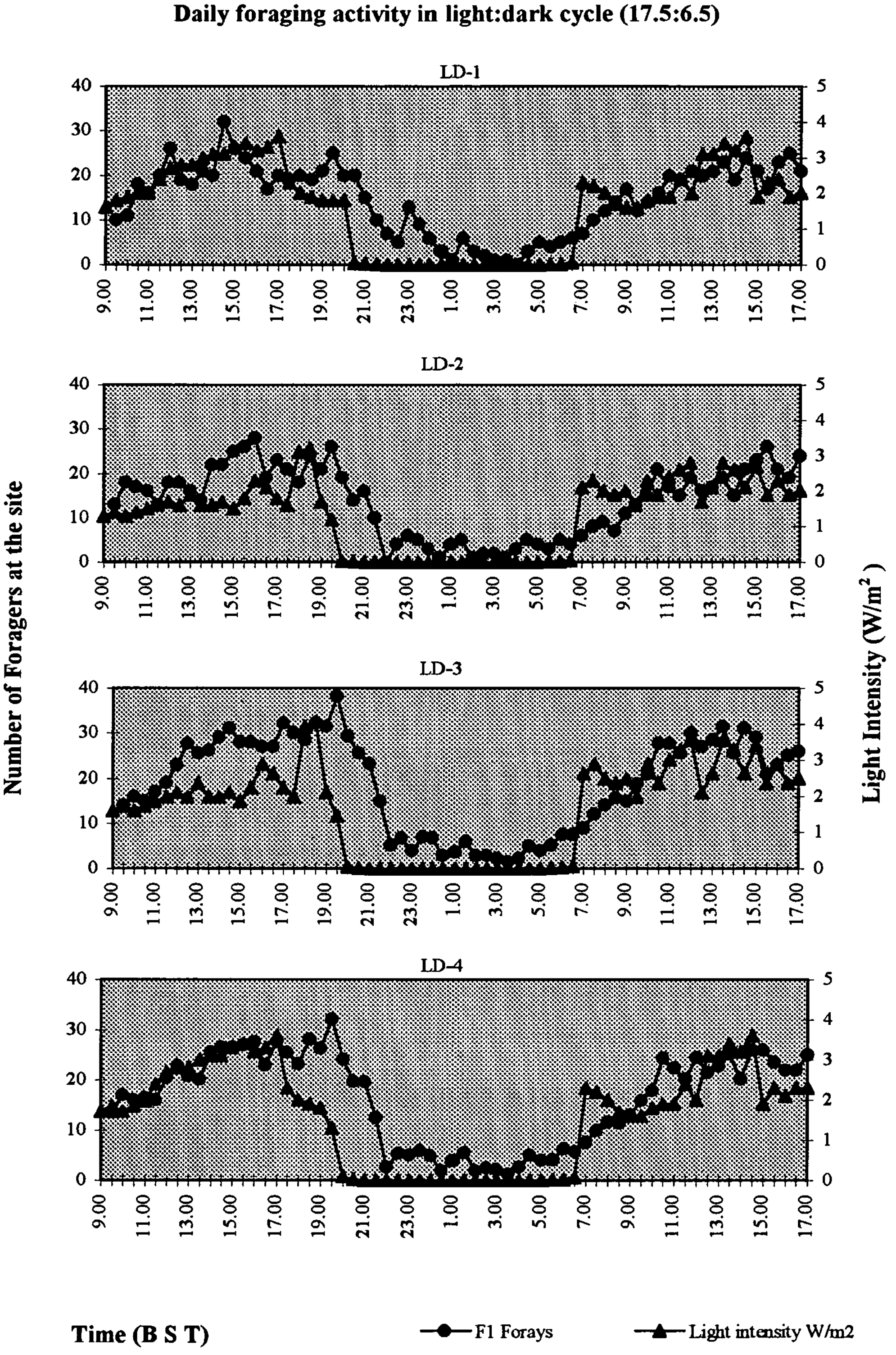


Figure 2.11 Daily foraging activity in light:dark cycle (17.5:6.5)
LD-1, LD-2, LD-3 and LD-4 were the days that colony was subjected to light:dark cycles of (17.5:6.5)

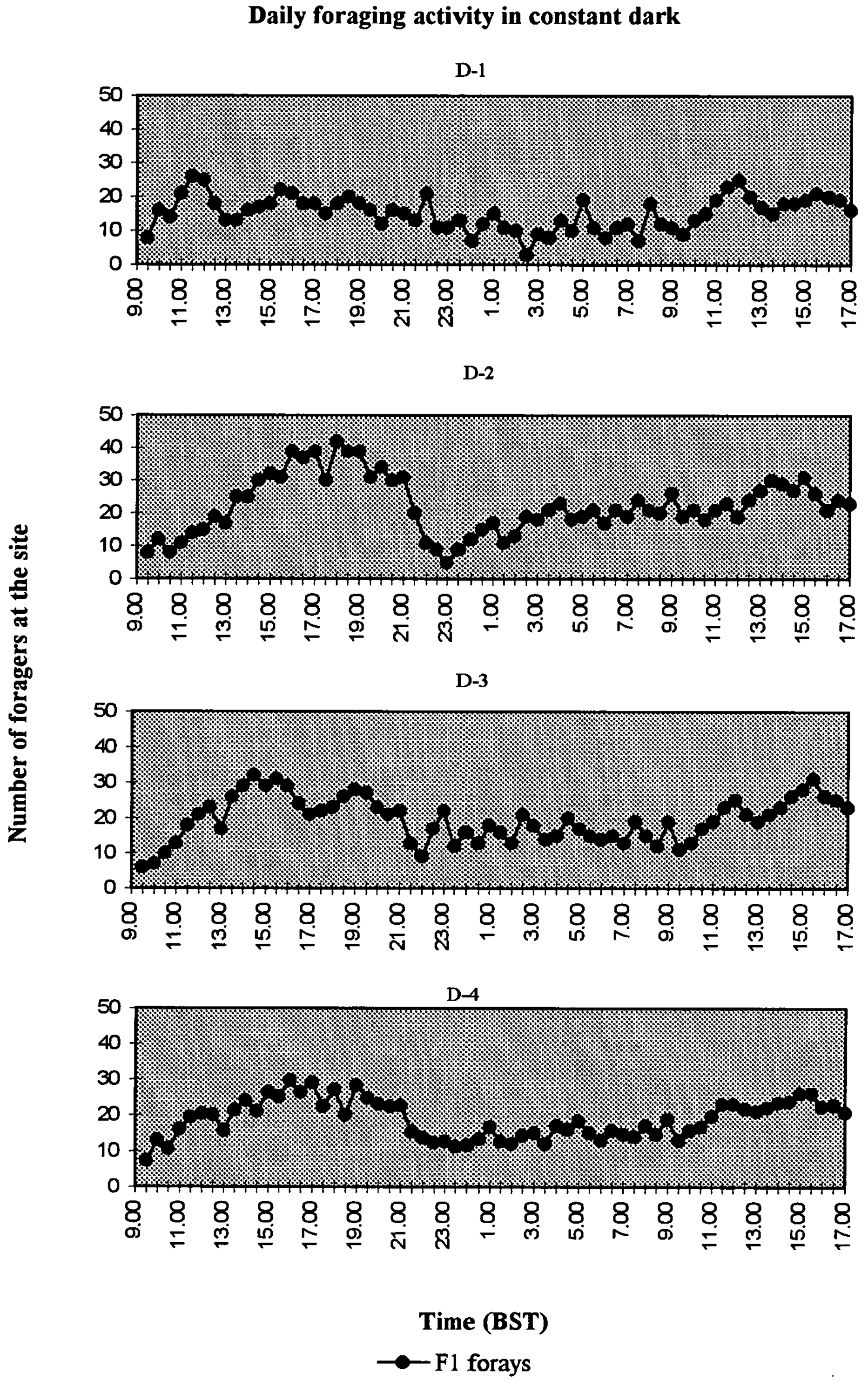


Figure 2.12 Daily foraging activity in constant dark

D-1, D-2, D-3, and D-4 were the days that colony was subjected to complete darkness

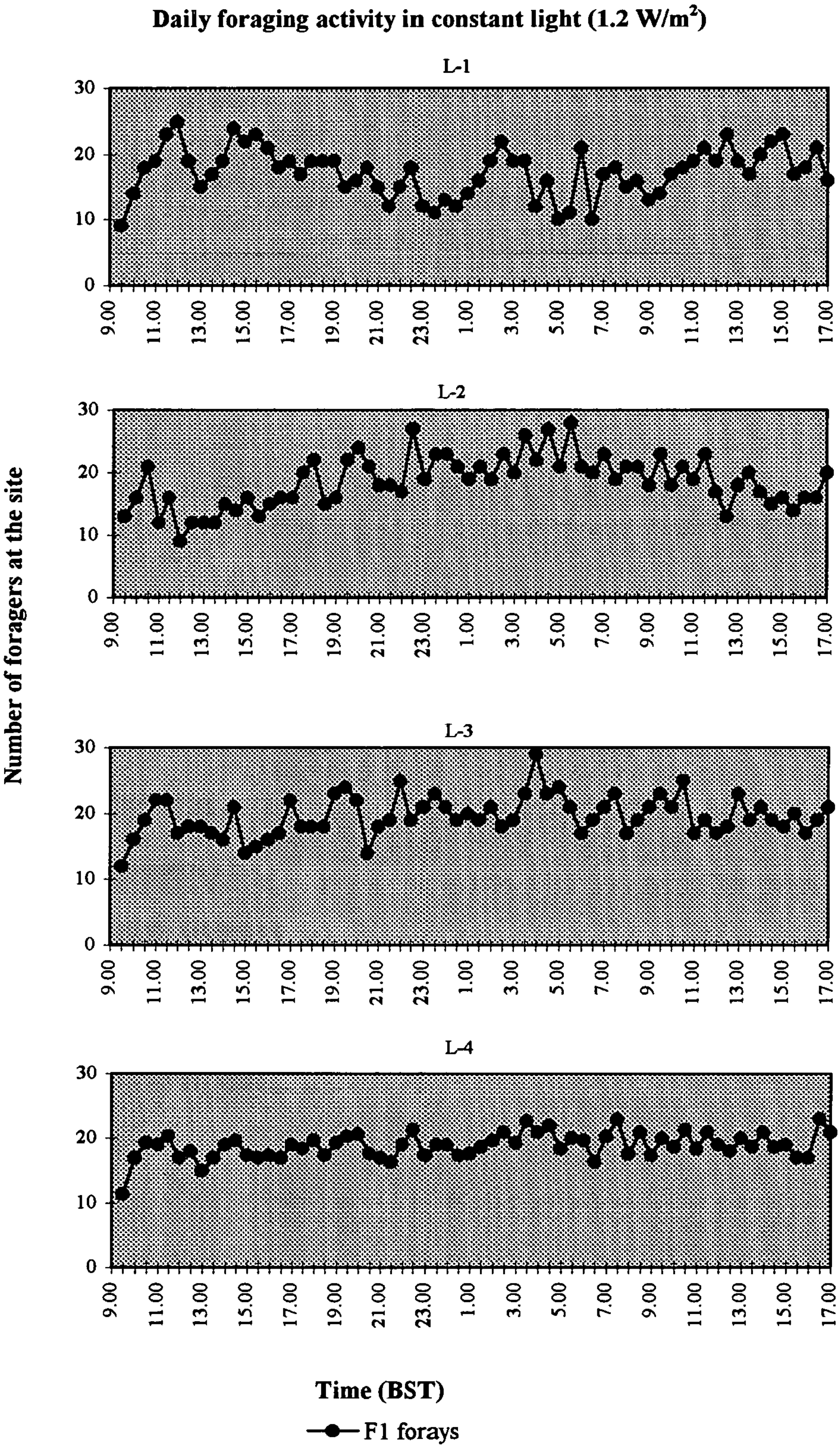


Figure 2.13 Daily foraging activity in constant light
L-1, L-2, L-3 and L-4 were the days that colony was subjected to constant light

colony was subjected to constant darkness the foraging activity was continued but showed poor rhythmicity (Fig. 2.12), although a residual rhythm is recognisable (x^2 = 33.7, df 1 $P<0.05$).

Table 2.2 Comparison of number of forays during light and dark hours of the day

	7.5:6.5 h Light:Dark	Constant dark	Constant light (1.2 W/m^2)
9.00-21.00 h	528	524	424
21.00-9.00 h	140	352	461

However, when the colony was subjected to constant light, rhythmicity was completely lost (Fig. 2.13) (x^2 =1.53, df 1 $P>0.05$). Amplitudes of the pattern in constant light and constant dark did not differ significantly from each other. This may have been due to extensive variation of activity between individuals obscuring any influence of continuous light or dark. Since the foraging activity's rhythmicity was poor in constant dark and completely rhythmless in constant light one could argue that the periodicity is not a true endogenous one.

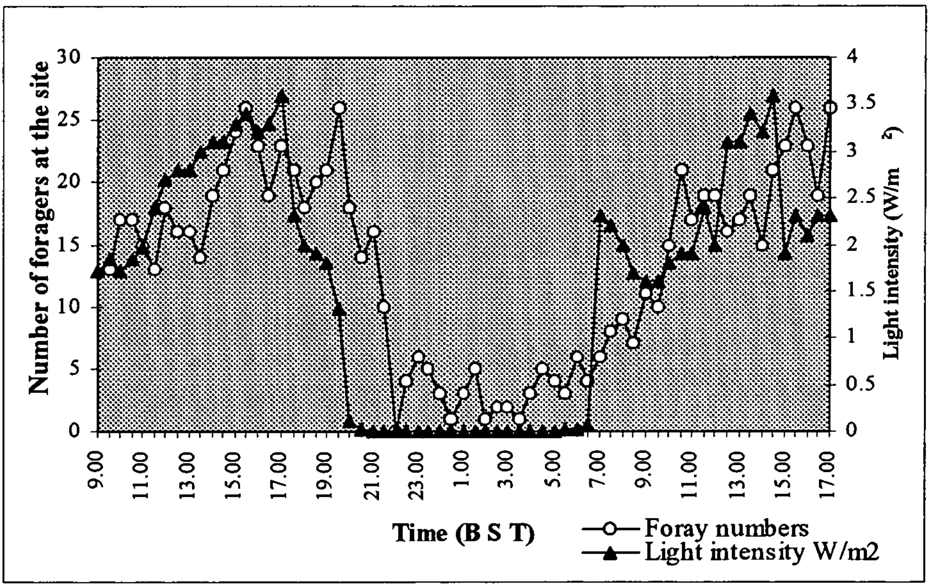


Figure 2.14 The reverted daily foraging activity (day 4) to a light:dark (17.5:6.5h) cycle after 7 days of constant darkness when the behaviour was much less rhythmic (Fig. 2.12).

The observation that the rhythmicity is remarkable in a light:dark cycle (17.5:6.5h); persists in constant dark and is absent in constant light, suggests that the foraging activity rhythm could be entrained by the light:dark cycles. North (1987) observed that under a 12:12h light:dark cycle most *F. rufa* individuals were arhythmic: although they showed a clear rhythmicity under 18:6h light:dark cycles. This observation implies that shorter photoperiods may not induce entrainment. It is also probable that other environmental constraints and many social inputs from other members of the colony may override the temporal patterns of activity, the extent depending on the social synchronisation within the population. For example, it has been observed that foraging activity was high in dark hours when pupal cases were discarded, when the colony was subjected to a 17.5:6.5h light:dark cycle. In fact many ant species seem capable of shifting the time of peak foraging back and forth as an adjustment to vagaries of the environment. *Atta cephalotes*, the dominant leaf cutter of the moist lowland forests in Central and South America, change from predominantly diurnal to nocturnal foraging over a period of a few days in Brazilian Amazonian forest (Hölldobler & Wilson, 1990). When considering the mean activity (Table 2.3) under three conditions, foraging activity (mean forays for 24 h) was similar at constant conditions (constant dark and constant light) (x^2 = 0.068, df 1 P>0.05), but was significantly different between constant conditions and a light:dark cycle (x^2 = 36.7, df 2 P<0.05). This difference was reflected in the amount of food gathered.

Table 2.3 Mean number of forays and amount of food collected in 24 h under different light-dark conditions.

	Forays			Food (mm^3)		
	LD	LL	DD	LD	LL	DD
Total	2675	3541	3503	18.6	23.2	22.7
$\bar{x}$	669	885	876	4.65	5.79	5.68
SD	91.1	57.2	146.9	0.20	0.27	0.66

Total: forays made and food gathered during four consecutive 24 h periods; $\bar{x}$: mean numbers for a 24 h period (N = 4), SD = Standard deviation.
LD = Light:Dark Cycle, DD = Constant Darkness, LL = Constant Light.

When considering foray loads and the number of forays throughout the day, there was a strong negative correlation ($r = -0.84$, $P<0.05$) between the number of forays and the mean factorial increase of gaster size. The mean factorial increase of gaster size in a replete forager was 1.67 (Chapter 1, Table 1.1; Cosens & Toussaint, 1985), and was attained when the number of foragers at a tree was between 60 and 70 per 20 min period (this particular experiment) (Fig. 2.15). The foragers which were active at the beginning of the foraging day (morning) worked hard and collected per foray a large amount of food (Table 2.4; see also Chapter 3, Table 3.14). As the day progressed (late morning) more individuals foraged and subsequently overcrowding may force them to gather less during the latter part of the foraging day.

Table 2.4: Anova table (two factor with replication) for the factorial increase of gaster size and number of forays

SUMMARY	Mean factorial increase in gaster size (R/NR)	Number of forays	Total
Morning			
Count	4	4	8
Sum	8.61	143	151.61
Average	2.1525	35.75	37.90
Variance	0.0078	95.58	95.59
Late morning			
Count	4	4	8
Sum	6.56	285	291.56
Average	1.64	71.25	72.89
Variance	0.0017	34.91	34.91
Total			
Count	8	8	
Sum	15.17	428	
Average	3.7925	107	
Variance	0.0096	130.5	

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Sample	1224.13	1	1224.12	37.52	5.13x10^{-05}	4.74
Columns	10651.79	1	10651.78	326.46	4.55x10^{-10}	4.74
Interaction	1296.90	1	1296.90	39.75	3.92x10^{-05}	4.74
Within	391.53	12	32.63			
Total	13564.34	15				

R = replete, NR = non replete

Note: Average number of forays made by individuals almost doubled in the late mornings compared to the mornings, although the factorial increase of gaster size did not show this type of increase (F= 39.75, df 1:12, $P<0.05$).

The interesting point with *F. aquilonia* was that the colony as a whole manipulated the effective number of foragers (60 - 70 foragers per 20 min period for this particular experiment) throughout the greater part of the day at a site to allow individuals to gather the maximum profitable amount: overcrowding was controlled (Fig. 2.15). The large crop loads gathered by individuals in the early part of the foraging day implied a demand for food at the colony due to the reduced activity of foragers at night: and in part due to the foragers own hunger.

The correlation between forager number and factorial increase of gaster size, and the maintenance of an effective number of foragers to maximise input throughout the greater part of the foraging day suggest that decisions about the foraging effort can also be made within the nest and may be communicated to the foraging population as a group rather than to individuals.

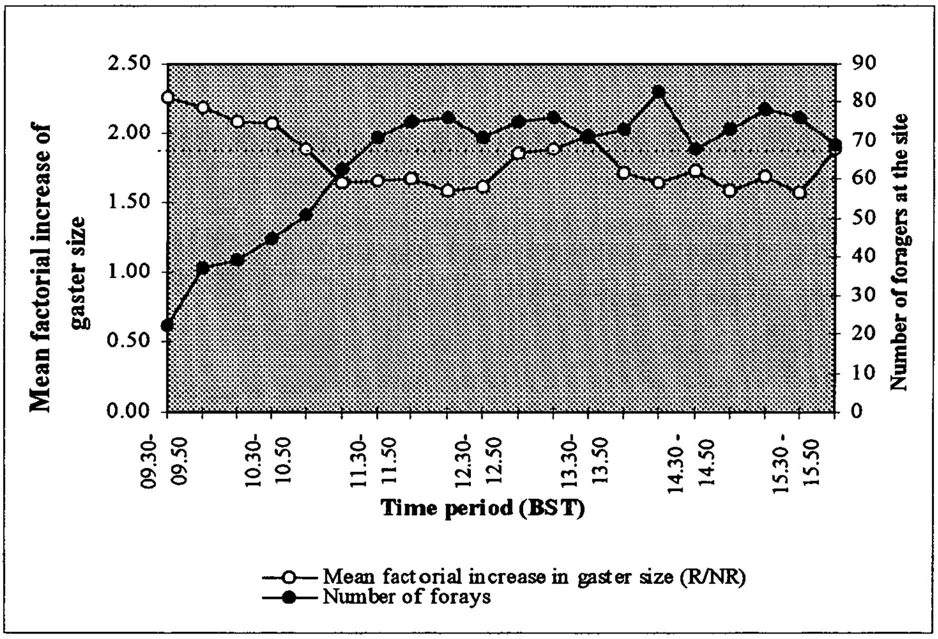


Figure 2.15 Comparison of factorial increase of gaster size and number of forays involved at different times of the experimental day. Dotted line represent the average factorial increase of gaster size 1.67; R replete, NR nonreplete. Note in the early morning when few ants forage they each carry large crop-loads; later when more ants forage crop-loads revert to the average value.

2.3.2 Allegiance to a particular food site: behaviour of colour-marked cohorts

To examine whether the foragers demonstrate allegiance to a particular food site, all the foragers were paint-marked between 9.00-17.00 h on days 2, 4, 9 and 10 of August 1993: at tree F1 white and at tree F2 yellow. Subsequently the foraging activities directed at the trees were assessed using instantaneous scan sampling. The behaviours of some uniquely marked foragers (focal sampling) were also recorded on these experimental days to examine the composition of daily foraging cohorts.

2.3.2a Results and Discussion

Some switching between the two trees (transient behaviour) was observed on experimental days (Table 2.5). Although the maintenance of a constant foraging rate (Fig. 2.5 and 2.6) by most individuals makes it unlikely that it was the predominant type of foraging behaviour. However, the foraging population at tree F1 (white) was more allegiant (mean 95.6%, Table 2.5) than yellow foragers to the tree F2 (mean 74.3%, Table 2.5). The interesting aspect here was despite the fact that the two trees, F1 and F2 were identical, the foraging population was not equally distributed between them as predicted in most optimal foraging theories. Rather, the main foraging activity was directed at the tree (food site) that was discovered first. This observation presents clear clues that the application of current optimal foraging models to the wood ants' social foraging is more complex than to the individual foraging by solitary animals.

Table 2.5 Use of trees F1 and F2 by the white and yellow cohorts of foragers

Date 1993	F1 (W) allegient	%A	F1 (Y) transient	%T	F2 (Y) allegient	%A	F2 (W) transient	%T	Total (W)	Total (Y)
3.8	1028	97.2	146	23.9	465	76.1	30	2.8	1058	611
5.8	865	87.8	47	10.2	411	89.8	106	12.2	971	458
11.8	800	99.8	120	42	162	58	2	0.2	802	282
12.8	762	97.4	105	26.7	287	73.3	20	2.6	782	392

W = white, Y = yellow. Dates in August 1993. Although counts of ants at the food sites, the numbers record forays rather than foragers since the latter make repeated visits throughout the day. The percentages show allegience, A, and non-allegiance, T, of each colour cohort.

Table 2.6 Estimation of number of individuals involved in foraging

Date	Total W forays	number of individuals	Total Y forays	number of individuals
3.8	1058	71 (5.7)	611	47 (5.6)
5.8	971	75 (6.1)	458	38 (4.5)
11.8	802	62 (5.0)	282	26 (3.1)
12.8	782	56 (4.5)	392	36 (4.3)

W = white Y = Yellow. Values within brackets represent the % of the total number of foragers marked with that colour: 1234 white and 834 yellow by 3.8.93.

The number of individuals are estimated using the mean number of forays made by focal individuals of the two colour-marked cohorts. For example, on 3.8.93, the mean number of forays made by the white marked foraging population was 15, thus the number of white-marked individuals involved in foraging on that day was 1058/15 ③ 71 and the % of white-marked individuals that foraged on that day was 71/1234 x 100 ③ 5.7%.

Although there are high and low raters in the foraging population it would be reasonable to obtain a mean number of foragers from a particular foraging cohort in this way because the high raters make a high proportional contribution to the total foraging effort.

Although 1234 foragers were marked white and 834 foragers marked yellow in the total foraging population, monitoring of focal individuals revealed that the daily foraging population was surprisingly comprised of a relatively small number of colour-marked foragers (Table 2.6) that each made many forays.

2.3.3 Turnover rate of the foraging population

Colour-marking of foraging cohorts: a particular colour was used to mark foragers until no unmarked forager was found at the trees (generally after 2-3 days). The activity of this cohort was subsequently monitored until only a small number of marked individuals (2-3 for the experimental day) was found in the daily foraging population. Then a different colour was used to mark the unmarked foragers at each tree. This procedure was repeated 4 times, the mean time period involved giving an estimate of the turnover rate of the foraging population.

2.3.3a Results and Discussion

When considering the contribution of the colour-marked cohorts to the foraging population on experimental days (Fig. 2.16), it was clear that a loss of the original marked cohorts occurred along with constant forager recruitment (unmarked individuals). This observation, of course, begs the question as to where the old cohorts are lost to? A study of the death-rate suffered by the colony did not provide evidence that death was the sole, or major, cause of these losses (Table 2.7); see also Abernethy (1990).

Table 2.7 Mortality in the colony during the experimental period August 3rd to October 17th 1993 (Fig. 2.6)

	Foragers' colour-mark			
	Unmarked	White	Pink	Blue
Total marked	*	483	299	148
Total mortality	256	35	73	21
% Dead	*	7.2	24	14

Nonetheless, foragers that otherwise 'disappeared' from the foraging population were not observed performing other extranidal duties. Although in an experiment using the observation nest (Section 2.3.5), it was observed that foragers which 'dropped out' from active foraging engage in intranidal duties such as attending larvae and the queens. The contributions of colour-marked cohorts showed that their turnover rate was 1-1.5 months in the laboratory colonies. De Bruin *et al.* (1977) observed the same turn-over rates in field colonies of *F. rufa*; which is encouraging because it verified the laboratory results and ligned them with field conditions.

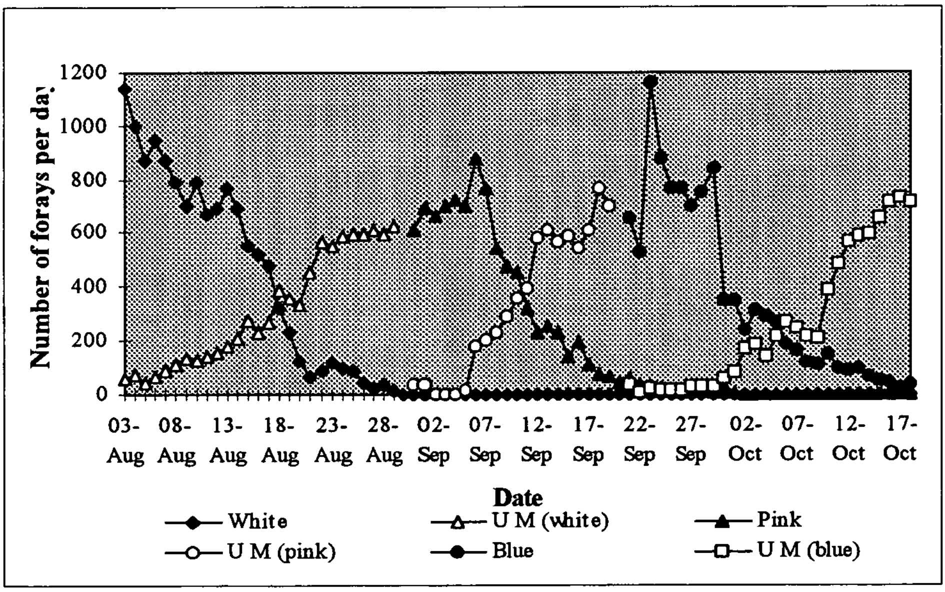


Figure 2.16 Turnover of the foraging population. Total number of foragers painted by white, pink and blue are 483, 299 and 148 respectively.

2.3.4 The foragers' response to a colony food-deficit

To examine the colony's response to a sudden accruing food-deficit, the colony was subjected to a period of food deprivation by removing food at 16.00 h and subsequently replacing the food at 9.00 h on the following day, the procedure being repeated for several days and, thus, subjecting the colony to an accruing food-deficit.

2.3.4a Results and Discussion

The colony's response to an accruing food deficit was to recruit (or deploy) a large number of unmarked foragers to the foraging population. However, this recruitment of unmarked foragers was not indefinite due to the limited number of potential foragers in the colony and overcrowding at food sites which may reduce the amount of food collected by an individual. It was observed in this experiment that foragers that had previously disappeared from the foraging population (section 2.3.3) were redeployed to the foraging effort (Table 2.8, white and yellow marked foragers).

When within the 24 h period access to food was restricted to between 9.00-16.00h, the amount of food collected by foragers fluctuated around the mean value 7.74 cm^3 (SD=0.18)/day (Fig. 2.17), irrespective of the increasing numbers of foragers recruited to the active foraging. This represented a 51.8% increase of the amount collected on standard days (food *ad.lib.*) between 9.00-16.00h, presumably representing the volume of food (2.64 cm^3) gathered overnight. The total number of forays and forays made by unmarked foragers followed a similar pattern but the unmarked foragers came to dominate the population (Table 2.8, Fig. 2.17).

When a food deficit (colony hunger) was caused by removing the food at 16.00h for a period of 41 h, that is until 9.00h two days later, on those subsequent days (days 9, 11, 13 & 15, Fig. 2.17) the foragers collected during the period 9.00-16.00h an amount that fluctuated about a mean volume of 8.21 cm^3 (SD=0.15)/day. Here the increase of 0.46 cm^3 must relate to the food deficit (colony hunger) accrued over the preceeding 41 h. Over the eight days the number of active foragers declined (Table 2.8) and unmarked foragers virtually replaced the marked cohort: at the beginning (day 7) unmarked individuals represented 77.4% of the active foragers, by day 15 they represented 93.8%. In comparison at the outset of the experimental sequence (day 3) unmarked individuals represented only 2.5% of the foragers.

Although the colony deployed an increasing number of uncommitted foragers to active foraging; the total profit to the colony by doing so was higher only until there was a certain number of foragers at the site. Beyond that number additional deployment was not profitable.

Table 2.8 Foragers' response to limited access to food and to food deficit

Date 10.93	Number of forays made by foragers												Period without food	Food acc. 7h
	P	**B**	**GN**	**GY**	**M**	**YB**	**GB**	**MX**	**UM**	**W**	**Y**	**total**	(h)	(cm^3)
3	40	68	78	40	35	8	3	89	11	0	0	447	0	5.1
4	43	89	93	51	47	14	5	102	209	0	0	653	17	7.7
5	32	67	86	53	67	0	18	148	840	0	0	1311	17	7.98
6	20	28	19	36	43	3	4	135	1230	0	0	1518	17	7.7
7	17	35	15	18	41	0	4	157	984	0	0	1271	17	7.56
9	25	47	6	15	45	1	5	139	1106	0	0	1389	41	8.41
11	23	19	4	9	36	0	0	43	1179	1	2	1311	41	8.21
13	22	11	7	0	5	0	2	53	889	0	0	989	41	8.1
15	13	0	11	0	7	0	0	16	716	0	0	763	41	8.1

P = pink, **B** = blue, **GN** = green, **GY** = gray, **M** = mustard, **YB** = yellow/blue, **GB** = green/blue, **MX** = mixture of colours; **UM** = unmarked; **W** = white, **Y** = yellow.

A similar situation was observed by Sakagami & Hayashida (1962) experimenting with *Formica* and *Polyergus*: that as the number of workers available for excavating sand increased, both the number of hard-working individuals and the average amount of work per individual decreased. This effect is just the opposite of social facilitation, which has long been assumed.

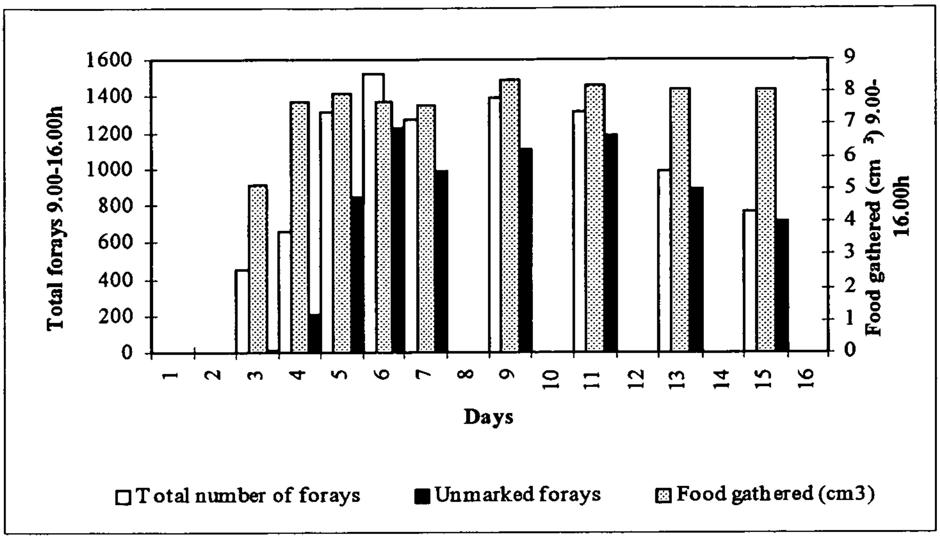


Figure 2.17 Response of the foragers to limited access and an accruing deficit of food

a) days 1-3 food provided ad lib. over 24h: note in day 3 virtually all foragers were marked, food was withdrawn at 16.00h.

b) days 4-7 food was available between 9.00-16.00h hence requirment for 24h period gathered in 7h ($\bar{x} = 7.7$ cm^3) in day 7 food removed at 16.00h.

c) days 9,11,13 and 15 food available between 9.00-16.00h subjecting 41h of food deficit:accruing colony hunger met by additional collection ($\bar{x} = 8.2$ cm^3)

d) note latterly (days 13 and 15) fewer foragers deployed which were unmarked and volume gathered was maintained therefore each carry more/crop load.

It is possible that *Pogonomyrmex* workers are idle for much of the time and that *Formica* workers work less in the presence of many companions because these behaviour patterns are adaptive in other ways. However, with respect to a territorial ant species like *F. aquilonia* it may well be that a large number of inefficient workers have their chief selective value, not in the greater productivity which they make under ordinary conditions, but in their importance in defence against enemies or for other unexpected changes in the physical environment.

2.3.5 Spatial organisation of workers

The aim of this experiment was to clarify how the cohorts of workers separated themselves spatially within the nest. This experiment was performed with a new colony (Colony 6) housed in an observation nest used by Swanson (1995) to study intercolony relationships (Fig. 2.18a). The observation nest was a wooden box 70 cm high, 50 cm wide and 3 cm thick in which one of the larger side walls was replaced by a 0.2 cm thick perspex sheet to allow observation of the inside of the nest.

The perspex wall of the nest was normally covered with black cardboard to provide a dark interior. Colony 6 was obtained from Aberfoyle and was self-established in the observation nest placed on the foraging table (Chapter 1), within two weeks.. However, methods attempted by Swanson (including video recording, still photography, and spot counts during the day) proved too invasive and resulted in frantic activity of the queen(s) and workers. So, the foraging population was marked yellow on the tree, as before, over three days (from the 2nd June, 1995). Then a 10 x 50 cm^2 strip was cut from the cardboard which covered the perspex side of the observation nest on Day 5 to allow observation under low light intensity and so restrict disturbance and reduce the frantic activity of the queen(s) and workers. By Day 7 the ants in the observation nest had settled and subsequently foraging activity and internal nest activity were monitored between 10.30-15.30 h. The behaviour of 10 uniquely marked foragers from 3 different spatial areas of observation nest (X, Y, Z) were followed for six consecutive days (Days 16 to 21) between 10.30-14.30 h. These particular individuals were initially identified within the observation nest using the shapes of their paint-marks and upon arrival at the top of the nest, or the sugar dish, they were re-marked with a different colour or colours. Unfortunately the period of observation was limited due to the subsequent movement of the ants to a shaded area of the nest.

Table 2.9 Number of colour-marked foragers

Day	Number of foragers marked
1 (2.6.95)	29
2	14
3	9

52 foragers were marked yellow

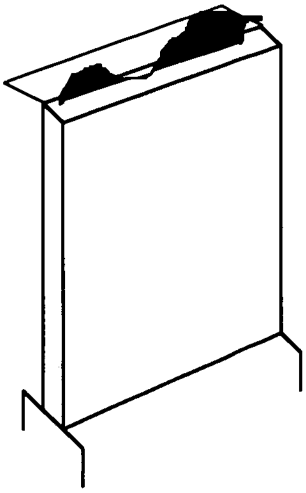


Figure 2.18a : Observation nest

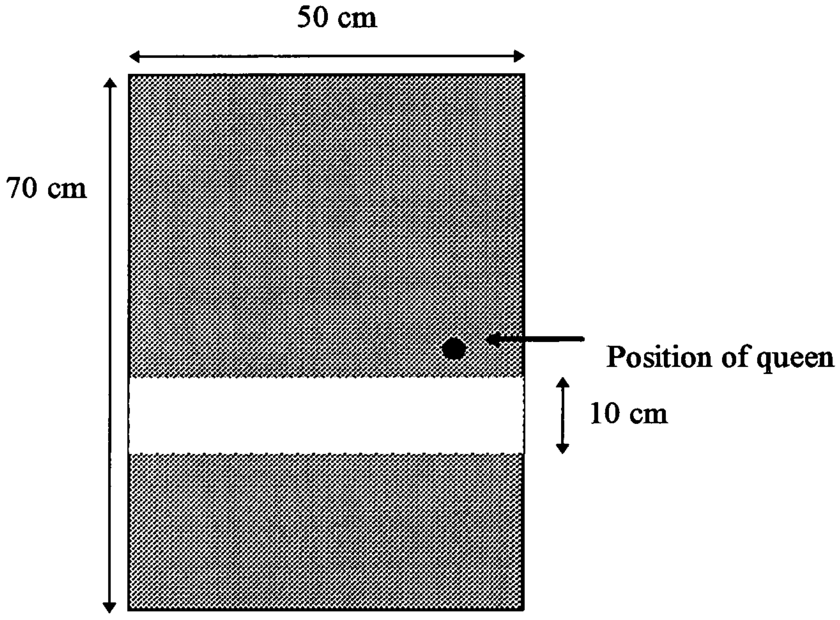


Figure 2.18b: The positions of the queen and the observable section of the nest after the foragers had settled in the observation nest

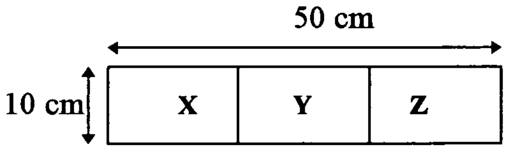


Figure 2.18c: 'Spatial' areas within the observation nest where particular foragers were initially selected

2.3.5a Results and Discussion

According to the results shown in Table 2.10 *F. aquilonia* foragers were allegiant to particular regions of the mound nest.

Table 2.10 Percentage unloading at different 'spatial' areas of 10 different foragers.

Ant	**17/6/95**			**18/6/95**			**19/6/95**			**20/6/95**			**21/6/95**			**22/6/95**			Σ (%)		
	X	Y	Z	X	Y	Z	X	Y	Z	X	Y	Z	X	Y	Z	X	Y	Z	X	Y	Z
XA	8	1	0	6	0	0	9	2	0	3	0	0	5	0	0	2	0	0	**92**	8	0
XB	2	0	0	5	0	0	6	0	1	8	0	0	3	2	0	4	0	0	**90**	7	3
XC	9	0	0	0	8	0	9	0	0	7	0	0	6	0	0	9	0	0	**%**	0	0
XD	11	2	0	**	**	**	**	**	**	3	0	0	5	1	0	**	**	**	**86**	14	0
YE	2	5	0	0	6	0	1	8	0	**	**	**	0	4	0	0	6	0	9	**91**	0
YF	1	9	0	**	**	**	0	10	0	2	8	0	0	8	0	1	7	0	9	**91**	0
YG	0	11	0	**	**	**	**	**	**	0	8	**	1	10	0	0	10	1	2	**95**	2.5
ZH	0	1	7	0	1	9	0	0	8	**	**	**	0	0	9	0	0	8	0	7	**93**
ZI	1	1	4	0	1	7	0	0	7	0	0	6	**	**	**	**	**	**	4	7	**89**
ZJ	0	0	12	0	2	13	0	0	12	0	0	11	0	0	8	0	0	10	0	3	**97**

The numbers in the daily columns refer to direct observations; in the final column to percentage zone use.

XA-ZJ are the uniquely marked individuals selected from three 'spatial' areas
X, Y and **Z** are the different 'spatial' areas within observation nest
** foragers did not foraged but were observed to be involved in intra-nest activities (carrying pupal cases, attending larvae)
Marked foragers were observed to attend brood
Marked replete foragers were observed to down-load directly to queens

Foragers selected from 'X' zone of the observation nest (Figs. 2.18b & 2.18c) were highly biased towards the 'X' region when down-loading: and likewise foragers selected from the 'Y' and 'Z' regions (Table 2.10). For example, the four individuals selected from the 'X' zone were observed 137 times over six days: now a null-hypothesis might claim these sighting would be at random across the three zones 'X', 'Y' and 'Z', $\bar{x}^2$ exp. 45.7 in each zone; but the observed distribution was 'X' 120, 'Y' 16 and 'Z' 1 giving a value of $\bar{x}^2$ of 183.95 with 2 df and indicating clearly that the foragers' choice of zone was not random. In this experiment replete foragers from the tree site (colour-marked) were observed to unload directly to the queen. They performed duties within their 'spatial fidelity zone' (section 2.3.1) depending on colony requirements without strict preference for the particular task. These observations are consistent with those reported by Gordon *et al.* (1992): after a period of a week foragers transferred from a different colony tend to develop route fidelity and site allegiance relative to their new position in the new colony.

2.4 Summarising points

Provision at two identical food sites of an unlimited supply of 10% w/v sugar solution resulted in predictable patterns of foraging activity but not in the distribution of foragers between sites as predicted by optimum foraging models. The foragers' site allegiance resulted in new food sites being sought only when necessary. On any one experimental day the foragers at a particular site represented a heterogeneous group comprising both high and low raters and others transitional between these categories. The foray rate of any one forager, particularly a high rater, was maintained throughout the foraging tenure. The foraging population was not subdivided between day and night time. Foraging activity was not affected by the minor temperature variations within the laboratory: but was shown to be clearly affected by light intensity. The rhythmicity of foraging activity was remarkable in a light:dark (17.5:6.5 h) cycle; persisted in constant darkness and was absent in constant light: suggesting that the foraging activity rhythm could be entrained by the light:dark cycles.

Foragers that were active at the beginning of the foraging day worked hard and collected large amounts of food. However, the maintenance of an effective number of foragers throughout the greater part of the foraging day suggests that decisions about the foraging effort can be made within the mound nest also, and may be communicated to the foraging population as a group. Turnover rate of a particular foraging population was between 1 and 1.5 months. The foragers active on any one day represented a small percentage of the potential foraging population within the mound nest. Foragers were allegiant to particular regions of the mound nest and performed duties within these 'spatial fidelity zones' depending on the colony's requirements without strict preference for the particular task.

CHAPTER 3

Behaviour of the foraging population with respect to food quality

3.1 Introduction

Numerous authors have argued that colonies of advanced social insects constitute cognitive, supraorganismal entities capable of evaluating situations and so producing adaptive solutions to problems (Hofstadler, 1979; Markl, 1985; Seeley & Levien, 1987; Wilson & Hölldobler, 1988; Franks, 1989). For example, a colony of honeypot ants assesses the strength of a neighbouring colony and decides accordingly whether or not to attack (Hölldobler, 1981; Lumsden & Hölldobler, 1983); and a colony of Army ants chooses the bearings of each day's swarm-raid so as to avoid the previous day's foraging zone (Franks & Fletcher, 1983; Deneubourg *et al.*, 1989). Implicit in these decisions is the fact that the colony may 'act' at different levels: the individual, group (cohort), and community - perhaps independently, but towards a common goal.

It has been widely accepted (optimal foraging theory) that animals will generally maximise their net rate of energy intake, and so optimise their harvesting over a range of nutrients, once they decide to forage. Selection in this way for the most efficient use of resources by individuals has consequences and these have been examined theoretically in two ways: firstly, how over the life-time of individuals it may channel resources between the alternative activities of growth, maintenance, and reproduction and so maximise some measure of fitness; and secondly, how it leads the individual to obtain food in a way that tends toward the maximisation of some measure of efficiency (Taylor, 1978).

The evolution of a worker caste has involved both morphological and behavioural specialisations which afford the efficient predominance of a specific group in particular activities. It is likely that each individual member of the group possesses the ability to undertake all activities such as nest building, nursing, defence and foraging, but the threshold of any one activity differs in different cases (Vowels, 1955). Thus, while ant foraging is a collective process encompassing the activities of individuals as well as behaviourally integrated groups, the task of studying the foraging behaviour is simplified because foragers may do little more than forage during their tenure as food harvesters. As a result they are often viewed as the products of selection for traits that maximise energy return to the colony (Traniello, 1989). The seed harvester ants *Pogonomyrmex rugosus* and *Pogonomyrmex barbatus* modify their seed choice with increasing distance of seed patches from the nest (Davidson, 1978). The basic premise of Davidson's study is that the net energy value of seeds of all sizes decreases with increasing distance from the nest owing to the added cost of travel and transport: hence energy maximisation is achieved at the more distant patches by selecting large seeds. So ant colonies operate as a tightly integrated unit of behavioural action. One manifestation of this in the context of the wood ant, is a colony's ability to adjust its selectivity among carbohydrate sources in relation to their quality (Holt, 1955; Skinner, 1980a & b; Rosengren & Sundström, 1987). Yet the harvester ant, *Pogonomyrmex occidentalis* displays a directional fidelity that constrains individual decisions: when offered seeds of different quality in two directions, foragers did not switch directions to obtain the energetically more rewarding seeds. However, colony-level recruitment was increased for the more profitable seeds (Fewell, 1990). So the foraging strategy at colony-level is not necessarily the same as that of the individuals (Oster & Wilson, 1978; Pasteels *et al.*, 1987).

The behaviour of social insects has often been documented as one of the supreme examples of instinctive activity (Vowels, 1955). Vowels claimed there is no substantial evidence that hungry, experienced workers stimulate other workers to forage; indeed soliciting for food is uncommon except in regard to returning replete foragers that must empty their crops in order to continue foraging. However, foraging may be elicited by callows (Schneirla, 1938) and by excited, successful foragers upon returning to the nest (Lubbock, 1894; Eidmann, 1927; Goetsch, 1937). The foraging elicited in this way does not differ from foraging elicited by larvae or from 'spontaneous' (response to own hunger) foraging (Vowels, 1955). The stimuli by which the larvae excite the workers to forage are largely tactile and the stimuli by which callows and successful foragers excite other workers are of a similar tactile nature (Schneirla, 1938): the callow or successful forager runs excitedly about the nest and gives sharp blows to other workers with its head, forelegs, and antennae (Wasmann, 1899; Eidmann, 1927; Forel, 1928; Goetseh, 1934; Barnes, 1941), this excites some workers which then may leave the nest in search of food. When collecting honeydew from aphids or nectar from nectaries, it is not known whether odour or colour is of use to the ant but it seems quite possible that an individual forager might learn to associate such stimuli with food (Vowels, 1955). Foraging behaviour has been conceived of as a complex and interacting sequence of responses to a variety of stimuli culminating in ingestion to repletion. The discrimination of quality, which sets the pattern of feeding and determines the success or failure of ingestion, is accomplished by the whole procedure, but each successive step in sequence constitutes a check on quality (Dethier, 1966).

Two examples illustrate the generality of sequential responses leading to ingestion and will expose the variation in details. The blow fly *Phormia regina* is guided by odour to its food and steps in it on arrival. Stimulation of chemo receptors on the tarsi triggers proboscis extension; extension places the chemo sensory aboral hairs of the labellum in contact with the food; stimulation of these hairs results in spreading of labellar lobes which places oral taste papillae in contact with the food; stimulation of the papillae triggers and drives ingestion (Dethier *et al.,* 1956). At each one of these steps quality is monitored. The locust *Schistocerca gregaria* approaches its food, lowers the tips of the antennae and palpi, then bites, and continues feeding accompanied only by palpal testing (Goodhue, 1963). The significance as well as the mode of action of the stimuli operating at each level of feeding behaviour has engendered controversy. Part of the reason derives from the fact that most of the research on factors regulating quality discrimination (diet selection, choice and preference) has been conducted with phytophagous insects.

The following experiments were designed to investigate how the colonies of the wood ant *F. aquilonia* respond to changing concentrations (quality) of carbohydrate food.

3.2 Objectives of the experiment

1) To determine the site allegiance and route fidelity displayed by wood ant foragers act as constraints to the foraging system. Site allegiance (and the consequential route fidelity) would constrain if it prevents foragers from switching to exploit new foraging sites when doing so could result in an individual obtaining a more profitable load and the colony a greater energetic gain.

2) To Identify which sub set of foragers is sensitive to changing circumstances by following randomly selected focal individuals and to determine whether the foragers individually differed in behaviour with respect to the changes of quality at food sites (behavioural plasticity of individual foragers).

3.3 Materials and Methods

These objectives were achieved initially by testing colony 1 with two concentrations of sugar solutions (5% w/v and 10% w/v sugar solutions). Since the switching of foraging effort was observed from 5% w/v sugar solution to 10% w/v sugar solution a second experiment was performed providing the colony with three concentrations of (5% w/v, 10% w/v and 15% w/v) sugar solutions in order to identify how this switching was initiated within the foraging system

Two series of experiments were performed. Series 1 was performed with Colony 1 and Series 2 was performed with Colony 2.

3.3.1 Feeding system for Colony 1

Four model trees, made from pine wood trunks 10 cm in diameter and of varying height, were placed on the foraging table and four calibrated feeders (described in Chapter 1) were fitted to them. Two of the trees each provided a food site and were designated F1 and F2. The other two trees were designated as controls, their isolated feeders were used to correct for evaporation. The trees F1 and F2 bearing the food sites were positioned equidistant from the stanchion of the wooden bridge joining the nest to the foraging area. 10% (w/v) raw cane sugar solution (typical value of energy per 100g=375 kcal) was available in a dish connected by a polythene tube to a narrow-bore, 10 cm^3 pipette which acted as a siphon gauge allowing the amount of sugar solution taken by foragers over time to be monitored. On standard days this carbohydrate diet was supplemented with protein in the form of blow fly larvae (*Calliphora* sp.) at irregular intervals as described in Chapter 1.

3.3.2 Feeding system for Colony 2

Two model trees were used, made from bark-stripped Spruce tree trunks (6 cm in diameter, 60 and 70 cm in height) drilled to take doweling branches (1 cm diameter). One branch on each tree ended with a 3x3 cm^2 hardboard platform, onto which a Petri dish (5 cm diameter) containing sugar solution (10% w/v) could be placed. These two trees, designated as F1 and F2, were placed on the foraging table equidistant from the bridge stanchion.

3.3.3 Methods

In the experimental Series 1 (Colony 1) the 10% w/v raw cane sugar solution was provided *ad libitum* and observations were made from 9.00 h to 16.00 h. Preliminary trials in which the alternative sites (patches) on F1 and F2 had sugar solution of equal concentration showed that the foragers distributed unequally at the sites and that this difference in foraging activity persisted over time (days). Hence when altering the concentration of food at sites, the richer site was always made poorer and *vice versa.* Randomising the switch in the quality of the food ensured that any corresponding change in the distribution of foragers was unlikely to be independent of food quality. To assess the stability of the new distribution of foragers between trees F1 and F2, each altered food concentration was maintained for 8 days. Series 1 was performed during the period April-June of 1994. The foragers which foraged to the sites on trees F1 and F2 were marked with green and blue paint respectively. The food sources on trees F1 and F2 were manipulated. For example, initially the food sites on F1 and F2 were each provided with a 10% w/v solution of raw cane sugar, and then at the site where the majority of ants foraged, food was altered to a 5% w/v sugar solution. Subsequently the response of the colony's food harvesters to the particular change was assessed by comparing the mean number of forays made to, and the volume collected from each site after the foraging population had stabilised at both sites. Comparison of the mean number of forays was performed with the Chi squared test, and of the volume collected from each site with the Student t-test assuming equal variances.

3.3.4 Modifications adopted in Series 2, with respect to Series 1:

a) The feeding regimen was altered by withdrawing the food at 16.00 h, so foragers were forced to gather the colony's food requirements within 6.5 h (9.30 -16.00 h).

b) Three concentrations of food (5%, 10% and 15% w/v sugar solutions) were used.

c) Before altering the food concentrations each site was provisioned with the standard concentration (10% w/v sugar solution) for 6 days, afterwards the poorer site wasmade richer and *vice versa.*

d) The duration of each experiment was 6 days instead of 8 days as in Series 1.

e) Gaster measurements of uniquely marked individuals were obtained on some experimental days using closed-circuit TV and a video-tape recorder.

f) The ants that foraged to the site on tree F1 were marked with white paint, and those to the site on tree F2 with green paint.

g) The daily intake was monitored by measuring the amount taken from each dish (F1 and F2), whilst controlling for evaporation.

h) The experimental Series 2 was performed during the period January-March 1995.

During both series of experiments behavioural patterns of several uniquely marked and therefore recognisable individuals were obtained. Sampling of the foraging activity was carried out at each site as described in Chapter 1. To determine the proportioning of the colony's foraging effort with respect to the food quality, comparisons were made of the distributions of forays and amount of food gathered over the last five days of each trial in Series 1, and the last four days of each trial in Series 2 using x^2 test and 't' test assuming equal variances respectively. The earlier days of each trial in each series were considered as transitional days and were omitted from the analysis.

3.3.5 Estimation of the real number of forays made to the sites

By marking foragers so that they may be recognised as individuals and monitoring their specific foray frequencies together with spot sampling of the overall foraging population, revealed that 5 min sampling of daily foraging activity records only 55% of the actual forays made. Hence 1.8 was used as a correction factor for obtaining the real foray numbers (Table 3.1).

Table 3.1 Estimation of real foray numbers

Total number of forays observed	467
Real number of forays	467 x 1.8 = 841

3.3.6 Load per foray data

Since the amount of food gathered was measured directly at the end of each experimental day, the load per foray after the stabilising of the foraging population was calculated by dividing the mean volume gathered by the mean number of forays (Table 3.2).

Table 3.2 Estimation of load per foray

Amount of food gathered from particular site	3952.3 mm^3	
Real number of forays made to that site	571 mm^3	
Load per foray	6.9 mm^3	(3952.3/571)

The load per foray was also measured during the experimental Series 2 from the video recordings of randomly selected individuals that foraged to a particular site during the study period (9.30-16.00 h) of the experimental day, after stabilisation of the foraging population at the two sites. Measurements of the change in gaster size were made directly from the monitor screen as described by Cosens and Toussaint (1985), taking into account the magnification of the video image. The scale of magnification was obtained from the head-widths of a sample of 31 ants from the experimental colony measured using a microscope with a micrometer eye-piece. Head-width was chosen because it is subjected to little variation among individuals. The mean head-width derived from the micrometer measured heads was compared with the mean head-width of 31 individuals measured directly from the monitor screen. This procedure was repeated each time when the position of the video camera was changed. The measurements of gaster widths and lengths were adjusted accordingly before entering them into the equation (Chapter 1).

Table 3.3 Number of forays made and amount of food gathered over 34 days

Day	F1 Rec.	F1 All.	F1 Tra.	F1 Forays	F1 Food (mm^3)	Load/ Foray F1 (mm^3)	F2 Rec.	F2 All.	F2 Tra.	F2 Forays	F2 Food (mm3)	Load/ Foray F2 (mm^3)
F1 (10%) : F2 (10%)												
3	2	524	14	540	4000	7.41	5	904	41	950	5100	5.37
4	2	711	2	715	3384	4.74	1	1303	41	1345	4984	3.71
5	0	562	16	578	4210	7.29	0	954	45	999	4210	4.21
6	2	648	38	688	4900	7.13	2	1238	74	1314	7200	5.48
7	2	463	25	490	4000	8.17	0	841	54	895	4200	4.69
8	0	378	40	418	3220	7.71	0	873	88	961	4520	4.70
mean	**1.33**	**548**	**23**	**571**	**3952**	**7.07**	**1.33**	**1019**	**57**	**1077**	**5036**	**4.69**
SD	**1.03**	**121**	**15**	**114**	**605**	**1.20**	**1.96**	**200**	**19**	**198**	**1126**	**0.67**
F1 (10%) : F2 (5%)												
12	3	495	632	1130	7826	6.92	2	239	0	241	1626	6.74
13	18	441	724	1183	9000	7.61	0	538	0	538	3600	6.69
14	16	347	497	860	7500	8.72	4	144	0	148	750	5.08
15	76	491	437	1004	6000	5.97	3	353	2	358	2200	6.14
16	48	574	301	923	7100	7.69	2	101	5	108	750	6.94
17	14	760	324	1098	7500	6.83	2	99	5	106	2090	8.67
mean	**29.16**	**518**	**486**	**1033**	**7488**	7.29	**2.1**	**238**	**2**	**272**	**1836**	**6.71**
SD	**27.42**	**128**	**186**	**159**	**898**	0.94	**1.32**	**182**	**3**	**157**	**1069**	**1.17**
F1 (5%) : F2 (10%)												
21	2	130	16	148	1000	6.78	39	1208	279	1526	7200	4.72
22	0	167	20	187	1663	8.88	11	1089	140	1240	5829	4.70
23	0	79	18	97	840	8.64	32	929	99	1060	9000	8.49
24	4	23	32	59	375	6.31	115	1343	119	1577	7800	4.95
25	0	13	38	51	260	5.16	23	799	101	923	5340	5.78
26	0	184	27	211	1260	5.98	10	958	47	1015	5100	5.02
mean	**0.33**	**99**	**25**	**125**	**900**	**6.96**	**38.3**	**1054**	**131**	**1224**	**6712**	**5.61**
SD	**0.8**	**73**	**9**	**67**	**531**	**1.50**	**39.2**	**199**	**79**	**275**	**1544**	**1.46**
F1 (10%) : F2 (5%)												
29	70	340	560	970	7250	7.47	0	112	0	113	510	4.50
30	26	365	682	1073	8100	7.55	0	74	2	76	320	4.23
31	29	401	722	1152	8500	7.38	0	41	0	41	155	3.74
32	24	466	736	1226	9200	7.51	0	146	0	146	720	4.94
33	38	484	751	1273	8750	6.88	0	126	0	126	830	6.59
34	57	488	765	1310	9900	7.55	0	50	0	50	350	6.94
mean	**40.6**	**424**	**703**	**1167**	**8617**	7.39	**0**	**92**	**0**	**92**	**481**	**5.16**
SD	**18.7**	**64**	**76**	**129**	**911**	0.26	**0**	**43**	**1**	**43**	**257**	**1.31**

F1Rec. F1 Recruits; F1All. F1 Alliegiant foragers; F1Tra. F1 Transient foragers; Load/forayF1 F1 Food/F1 total forays. F2Rec. F2 Recruits; F2All. F2 Alliegiant foragers; F2Tra. F2 Transient foragers; Load/forayF2 F2 Food/F2 total forays

3.4 Results of experimental Series 1

3.4.1 Daily foraging activity

Although more forays were made to tree F2, the pattern of the foraging activity at each site was similar with respect to the timing of maximum and minimal levels (Fig. 2.2 Chapter 2): there was an increase up to a maximum and then this level of activity was sustained throughout the monitored period. After the first control period (days 3-8), the quality of the food at the site on F2 where the maximum activity was observed, was decreased to 5% w/v sugar solution. This procedure was continued, changing the quality at alternative sites throughout the experimental series. Data collected are summarised in Table 3.3.

3.4.2 Control period

On control days (day 3-8) the mean total forays to sites F1 and F2 were quite different: (571 and 1077 respectively) activity was highest at site F2 ($x^2 = 155.4$, df 1, $P<0.05$). However, the amounts of food collected from the two sites were surprisingly similar ($t=-0.38$, df 10, $P>0.05$; Tables 3.3, 3.4 & 3. 5) contrary to expectation and the overall mean total volumes collected from two sites (3952 mm^3 and 5036 mm^3).

Table 3.4 Comparison of the amount of food gathered in each experimental period

(Days) Trees	Conc. F1 %	Conc. F2 %	df	t Stat	P(<=t) two-tail	Result
(3-8) F1 & F2	10	10	10	-0.38	0.712	NS
(11-17) F1 & F2	10	5	12	15.21	3.3×10^{-9}	S
(3-8) F1 & (11-17) F1	10,10		11	4.77	5.8×10^{-4}	S
(3-8) F2 & (11-17) F2		10,5	11	5.26	2.7×10^{-4}	S
(20-26) F1 & F2	5	10	12	-5.85	7.8×10^{-5}	S
(11-17) F1 & (20-26) F1	10,5		12	2.91	1.32×10^{-2}	S
(11-17) F2 & (20-26) F2		5,10	12	- 6.36	3.6×10^{-5}	S
(29-34) F1 & F2	10	5	10	28.29	7.1×10^{-11}	S
(20-26) F1 & (29-34) F1	5,10		11	-12.74	6.27×10^{-8}	S
(20-26) F2 & (29-34) F2		10,5	11	9.06	1.97×10^{-6}	S

S = Significant and NS = Not Significant (at P=0.05 significant level)
df = Degrees of freedom

Day 3-8	Control period
Day 11-17	First experimental period
Day 20-26	Second experimental period
Day 29-34	Third experimental period

3.4.3 First experimental period

During the first experimental period (days 11-17) site F2 was decreased in quality (5% w/v sugar solution) whilst site F1 remained unaltered (10% w/v sugar solution). The colony's response to this alteration was an increase of the forays to site F1 and decrease to site F2 (1033 and 272 forays respectively (x^2 =445.3, df 1, P<0.05). The mean amount of food collected was also significantly increased at F1 relative to F2 7488 mm^3 and 1836 mm^3 (t=15.2, df 12, P<0.05).

Table 3.5 Comparison of total, transient and allegiant forays in each experimental period

Day	Conc. F1 %	Conc. F2 %	Total forays x^2	Transient forays x^2	Allegiant forays x^2
(3-8) F1 & F2	10	10	155.38(S)	15.1(S)	141.81(S)
(11-17) F1 & F2	10	5	445.28(S)	519.96(S)	86.45(S)
(3-8) F1 & 11-17 (F1)	10,10		149.86(S)	461.54(S)	0.712(NS)
(3-8) F2 & (11-17) F2		10,5	454.01(S)	52.12(S)	449.98(S)
(20-26) F1 & F2	5	10	867.5(S)	95.91(S)	742.07(S)
(11-17) F1 & (20-26) F1	10,5		766.53(S)	462.58(S)	304.53(S)
(11-17) F2 & (20-26) F2		5,10	532.22(S)	145.23(S)	417.7(S)
(29-34) F1 & F2	10	5	845.44(S)	671.92(S)	179.72(S)
(20-26) F1 & (29-34) F1	5,10		805.92(S)	609.9(S)	192.61(S)
(20-26) F2 & (29-34) F2		10,5	907.63(S)	149.40(S)	723.45(S)

S = Significant and NS = Not Significant (at P=0.05 significant level)
All x^2 values are at degrees of freedom 1
Day 3-8 Control period Day 11-17 First experimental period
Day 20-26 Second experimental period Day 29-34 Third experimental period

It was clear that foragers were able to recognise the altered circumstance: some shifted their activity towards the better quality site (for them), while those that continued to use F2 increased their foray loads (6.71 mm^3) compared to that of (4.69 mm^3) during control period (Table 3.3). The foragers using F1 worked as during the previous control period.

3.4.4 Control period and First experimental period

A comparison of the activity at site F1 during the standard period (days 3-8) and during the first experimental period (days 11-17) indicates that: although the mean number of forays 571 and 1033 (x^2=149.9, df 1, P<0.05) and the mean amounts of food collected 3952 mm^3 and 7488 mm^3 during the two periods (t=4.7, df 11,

$P<0.05$) were different, the mean number of allegiant forays to the site (548 and 518) were not ($x^2=0.71$, df 1, $P>0.05$; Tables 3.4 & 3.5). The increase of transient forays to site F1 by foragers marked blue at site F2 were responsible for the increase in the mean total number of forays to the 10% w/v sugar solution bearing site.

When considering site F2 during the same periods, the mean total forays 1077 and 272 ($x^2=454.01$, df 1, $P<0.05$), mean transient forays 57 and 2 ($x^2=52.1$, df 1, $P<0.05$), mean allegiant forays 1019 and 238 ($x^2=449.9$, df 1, $P<0.05$) to the site and the mean amount of food collected from the site 5036 mm^3 and 1836 mm^3 ($t=5.26$, df 11, $P<0.05$) were significantly reduced during the first experimental period (Tables 3.4 & 3.5).

3.4.5 Second experimental period

The activity at sites F1 (5% w/v sugar solution) and F2 (10% w/v sugar solution) were compared during the second experimental period (days 20-26). The mean total forays 125 and 1224 ($x^2=867.5$, df 1, $P<0.05$), mean transient forays 25 and 131 ($x^2=95.9$, df 1, $P<0.05$), mean allegiant forays 99 and 1054 ($x^2=742.07$, df 1, $P<0.05$) to the sites, and the mean amount of food collected from two sites 900 mm^3 and 6712 mm^3 ($t=-5.85$, df 12, $P<0.05$) showed significant differences (the highest activity was directed towards F2, 10% w/v sugar solution). Again foragers at site F1 have clearly recognised the alteration at the site to which they were allegiant and altered their behaviour accordingly.

3.4.6 First and Second experimental periods

The activity at site F1 (10% w/v sugar solution) during the first experimental period (day 11-17) and the activity at same site (5% w/v sugar solution) during the second experimental period (day 20-26) were compared. The mean total forays 1033 and 125 ($x^2=766.5$, df 1, $P<0.05$), mean transient forays 486 and 25 ($x^2=462.6$, df 1, $P<0.05$), mean allegiant forays 518 and 99 ($x^2=304.53$, df 1, $P<0.05$) to the site, and amount of food collected 7488 mm^3 and 900 mm^3 ($t=2.91$, df 12, $P<0.05$) from the site during the two periods were significantly different and decreased during the second experimental period (Tables 3.4 & 3.5). Similarly, when considering the activity at F2: the mean total forays 272 and 1224 (x^2 =532.2, df 1, P<0.05), mean transient forays 2 and 131 (x^2 =145.2, df 1, P<0.05), mean allegiant forays 238 and 1054 (x^2 =417.7, df 1, P<0.05), and mean amount of food collected 1836 mm^3 6712 mm^3 (t=-6.36 df 12, P<0.05) were significantly increased during the second experimental period.

3.4.7 Third experimental period

The altered activity at the sites was apparent also during a third experimental period (days 29-34). The activity at sites F1 (5% w/v sugar solution) and F2 (10% w/v sugar solution) were compared during this period (Tables 3.3; Tables 3.4 & 3.5). when considering the activity at F1: the mean total forays 1167 and 92 (x^2 =845.4, df 1, P<0.05), mean transient forays 703 and 0 (x^2 =671.9, df 1, P<0.05), mean allegiant forays 424 and 92 (x^2 =179.7, df 1, P<0.05), and mean amount of food collected 8617 mm^3 and 481 mm^3 (t=28.3 df 10, P<0.05) were significantly increased during the third experimental period.

3.4.8 Proportionate use of sites during experimental Series 1

During the control period (days 1-8) the proportionate use of sites F1 and F2 was quite stable(Fig. 3.1, Figs. 3.1.1 and 3.1.1a) and although a few transient forays were observed at each site (see the x^2 value for transient forays compared to the x^2 values for total and allegiant forays; Table 3.4), by and large the marked foragers displayed a clear site allegiance. Since site F2 was dominant during the control period, the food there was decreased in quality during the first experimental period (day 9-17). Subsequently the proportionate use of site F2 was significantly reduced as a consequence of this alteration: decreases in the proportion of allegiant (blue) forays, of transient (green) forays and of food collected from the site were observed (Fig 3.1.2a). Corresponding increases in the proportion of transient (blue) forays and of food collected from F1, and an increase of allegiant (green) forays at F1 (caused by the reduction of transient forays (green) to F2) were observed (Fig. 3.1.2a). During subsequent experimental periods a similar result was obtained (Figs. 3.1.3, 3.1.3a, 3.1.4 and 3.1.4a). It has been clearly shown that foragers are able to distinguish the 10% w/v sugar solution from the 5% w/v sugar solution (poorer quality) food and adapt their foraging effort accordingly.

Figure 3.1 Proportionate use of sites Series 1

Fig 3.1.1

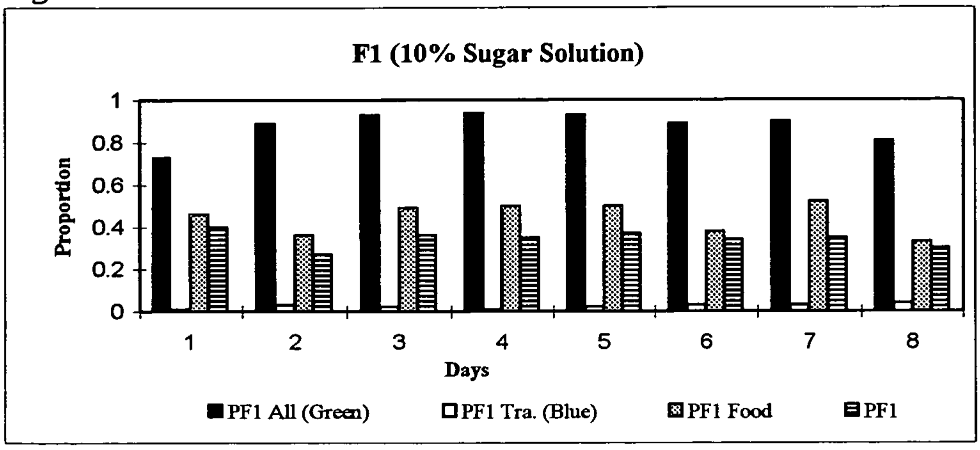


Fig. 3.1.2

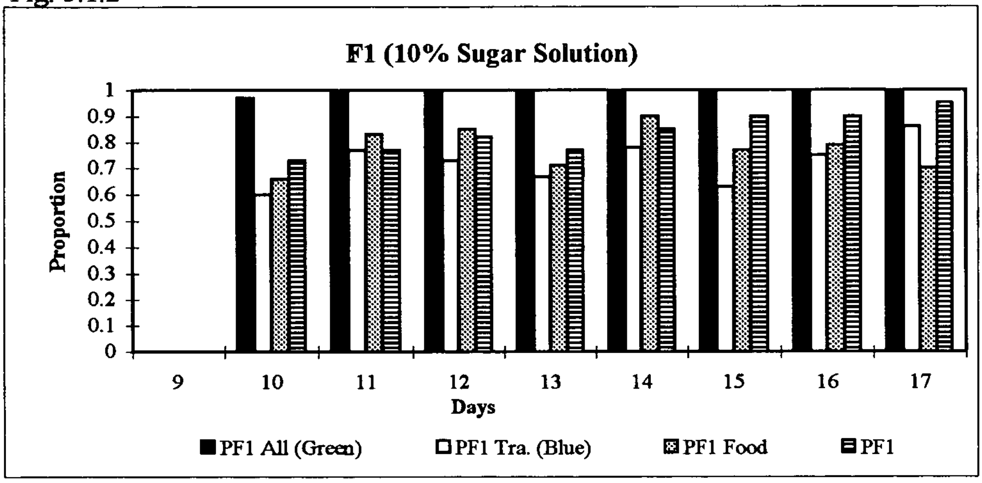


Fig. 3.1.3

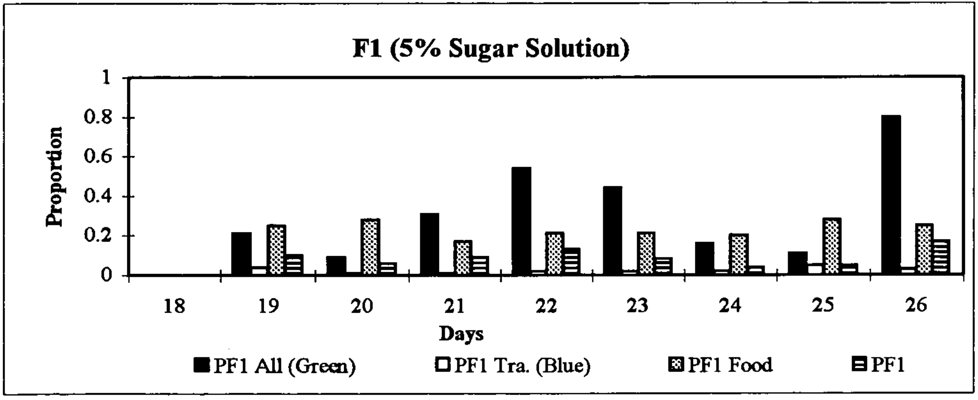


Fig. 3.1.4

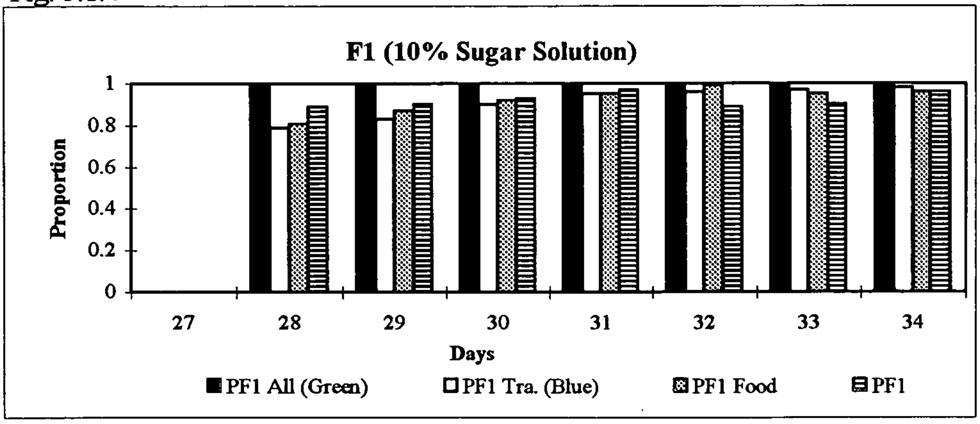


Fig. 3.1.1a

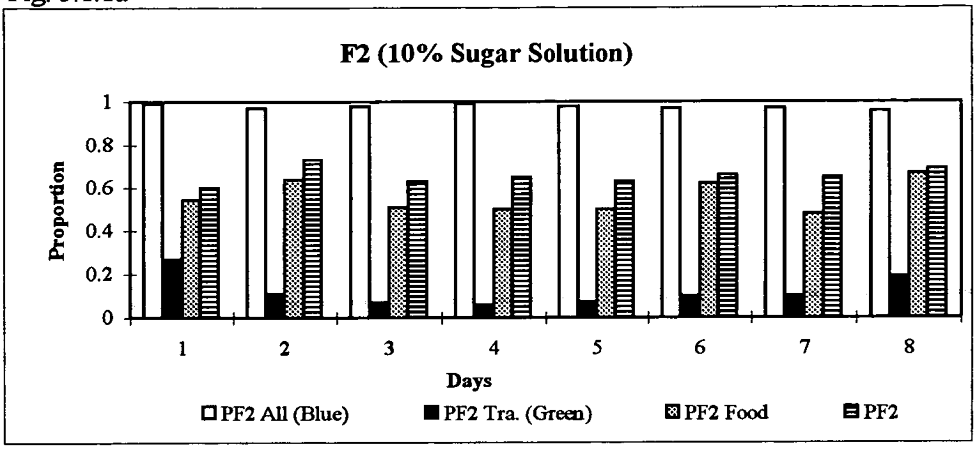


Fig. 3.1.2a

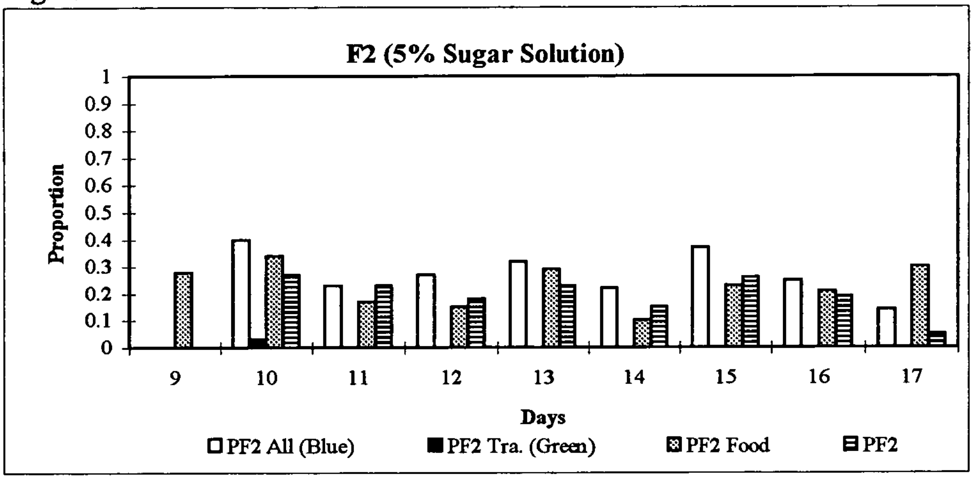


Fig. 3.1.3a

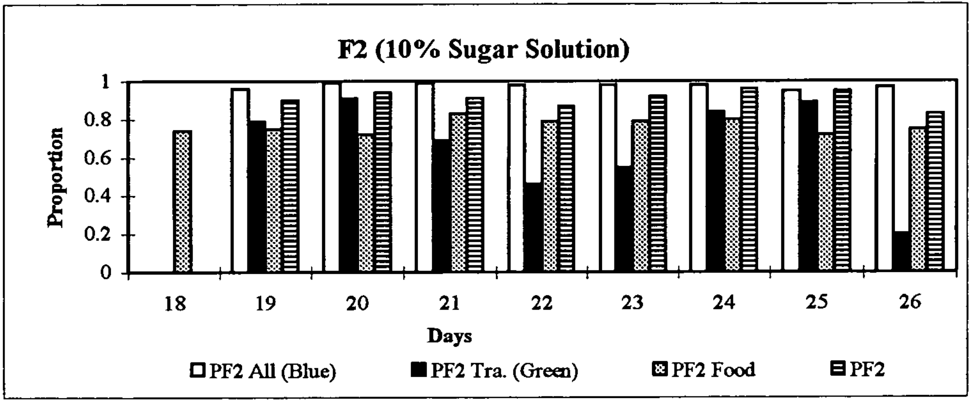
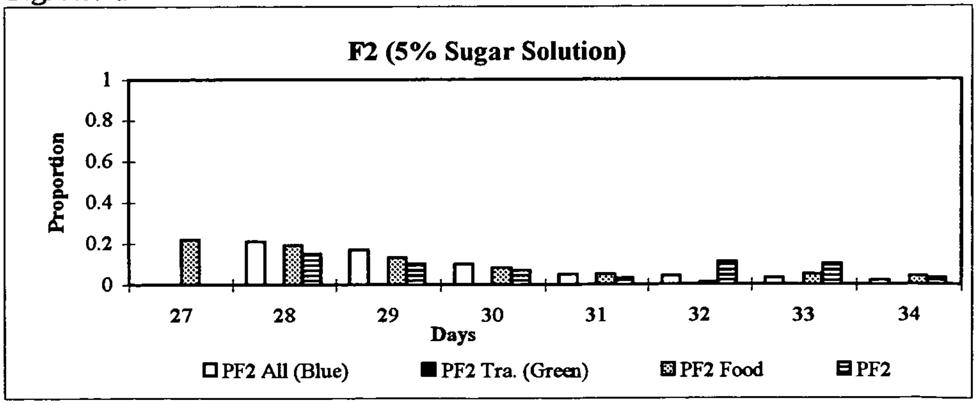


Fig. 3.1.4a



3.4.9 Comparison of the amount of food collected and number of forays involved

At each site, the number of forays involved and the amount of food collected were comparable (troughs and peaks coincide: Figs. 3.2a & 3.2b). When the number of foragers increased so that the daily foray number to a site exceeded 1300, the amount of food collected from the site was not increased in proportion (Fig. 3.2b). This observation could be explained by considering the experimental results obtained by Sakagami and Hayashida (1962) with other *Formica* and *Polyergus* species. They found that, as the number of workers available for a particular task is increased, the amount of work per individual decreased (opposite of social facilitation). However, the lowest number above which social facilitation diminishes could be depended on several factors: such as size of the colony, space available for the individual to collect food (perimeter of the dish), quality of food, nutritional status of the colony, and composition of the foraging population (proportions of naive and veteran foragers). Nonetheless, the colony's overall effort seems to be quite efficient and, despite the foragers' individual and variable efforts at sites F1 and F2, they do indeed transport a sufficient volume to maintain a relatively constant daily intake (Fig. 3.2c).

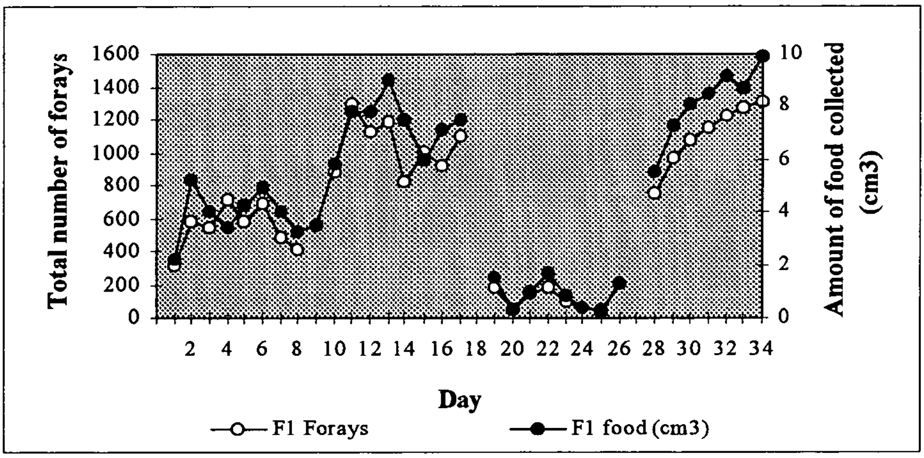


Figure. 3.2a Amount of food collected and number of forays involved at tree F1

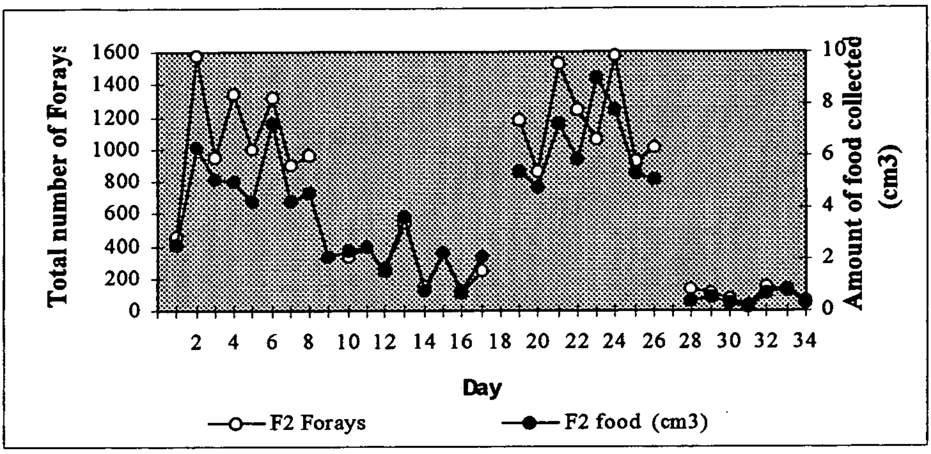


Figure 3.2b Amount of food collected and number of forays involved at tree F2

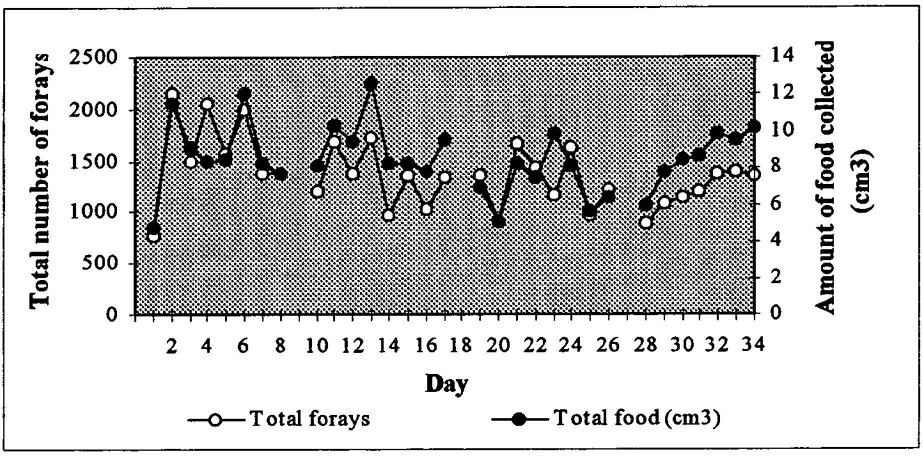


Figure 3.2c Comparison of amount of food collected and total number of forays involved

3.5 Results of experimental Series 2

3.5.1 Daily foraging activity

Daily provisioning of 10 cm^3 of 10% sugar solution at both F1 and F2 at 9.30 h and removal of the residues at 16.00 h provided a 'busy day' for the colony's foragers in that they must gather a sufficient amount of food to statiate the colony within that limited period of 6.5 h. On each of the standard days the pattern of daily foraging activity was similar and readily superimposable. There was an initial increase in the number of forays to the sites over a period of 1.5-2.5 h to a maximum level (which may be to repair a food deficit accrued during the previous night), activity then 'levelled off' and subsequently declined towards the end of the imposed foraging period (9.30-16.00 h, Fig. 3.3a.).

Since an amount of sugar solution was left at the end of each period, this decline of foraging activity was not due to exhaustion of the food supply, but rather to internal nest circumstances. To continue foraging replete foragers must locate nestbound workers prepared to accept their loads of sugar solution; the number of such workers must be finite as was, therefore, the volume of sugar solution that may be stored within their 'corporate crop' for a given time. Hence replete foragers spend increasingly more time within the nest unable to forage, however, since the colony continually uses the food gathered, after a time the foragers will be able to pass on their loads and to forage again.

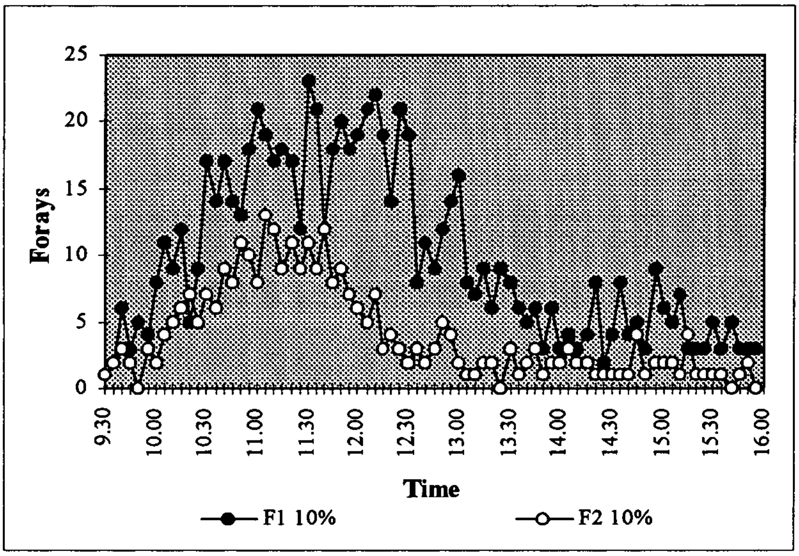


Figure 3.3a Daily foraging activity in a control day
Axis 'x' indicates the number of forays to the sites based on 5 min sampling.
Sites F1 and F2 contained 10% w/v sugar solution

Such a constraint would not operate when only few replete foragers return from a feeding site. On experimental days (days 9-12, 21-24, 35-38 and days 71-74) variations in food quality altered the recorded pattern of activity and caused changes in the maximum and minimum levels observed at the sites on the trees (Fig. 3.3b).

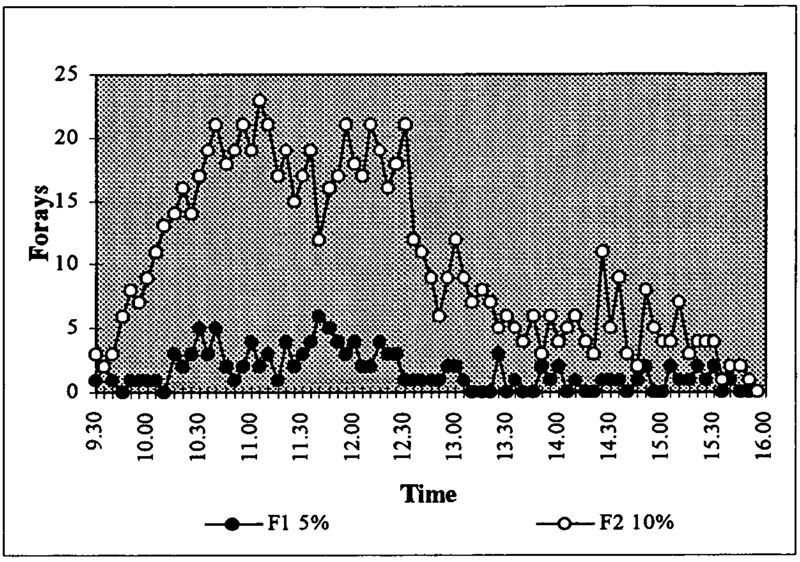


Figure 3.3b Daily foraging activity in a experimental day
Axis 'x' indicates the number of forays to the sites based on 5 min sampling.
Sites F1 and F2 contained 5% and 10% w/v sugar solution respectively.

3.5.2 Behaviour of the foraging population during the initial 38 days

The first 38 days of the second series of experiments encompassed three control periods (days 3-6, 15-18 and 27-32) during which conditions on F2 remained unaltered (10% w/v sugar solution) for most of the time, and three experimental periods (days 9-12, F1 5% w/v sugar solution; 21-24, F2 5% w/v sugar solution and 35-38, F1 5% w/v sugar solution). The first two days of each period, being transitional days, were omitted from the statistical analysis (Tables 3.6, 3.7, 3.8 & 3.9). Foragers distinguished the 5% w/v sugar solution and 10% w/v sugar solution and distributed their foraging effort to maximise the gathering of the higher quality sugar solution, as observed in experimental Series 1 with the first colony (Tables 3.10, 3.11). This outcome is clearly shown by the ratio of tree usage (F1/F2) and the relatively constant daily food intake. For instance, during the first control period the tree usage ratio was 1.83 (F1 dominant) all the food was 10% w/v sugar solution, then during the following experimental period when F1 was reduced to 5% w/v sugar solution the usage ratio became 0.21 activity switched to F2 so that 80% of the food gathered was 10% w/v sugar solution.

During the second control period the ratio of tree usage remained low at 0.44 (site allegiance remained unaltered), yet during the following experimental period when F2 was reduced to 5% w/v sugar solution the ratio became 1.54 and 65% of the food intake was 10% w/v sugar solution. This pattern of deployment and level of 10% w/v sugar solution intake was sustained (Table 3.12).

3.5.3 Behaviour of foraging population during the latter 36 days (Days 39-74)

The latter 36 days also encompassed three control periods (days 41-44, 53-56 and 65-68) and three experimental periods (days 47-50, 59-62 and 71-74). During the first two experimental periods (days 47-50 and 59-62) site F1 was provided with 15% w/v sugar solution. There was no recognisable change in the behaviour of the foraging population in response to the food quality at the sites (Table 3.11): the foragers deployed in the same manner during both the experimental and control periods and effectively maintained the intake of 10% w/v sugar solution. For instance, during the initial control period (days 41-44) the ratio of tree usage was 0.36 and during the following experimental period when F1 was improved to 15% w/v sugar solution it remained low at 0.44 and the intake of 10% w/v sugar solution was 60%. Throughout the subsequent periods the ratio of tree usage was 0.44, 0.33 and 0.29 respectively and the 10% w/v sugar solution intake during the experimental period (days 59-62) was 63% (Table 3.12). Tree F2 remained the dominant site throughout the sequence. However, when subsequently site F2 was decreased in quality to 5% w/v sugar solution (days 71-74) an immediate switch by the foraging population to site F1 (10% w/v sugar solution) was observed; the ratio of tree usage became 7.03 (site F2 was virtually abandoned) and the 10% w/v sugar solution intake increased to 87% reflecting earlier observations. Statistical comparisons of experimental periods and control periods are included in Tables 3.8 & 3.9.

In this series of experiments, it had been clearly shown that the forager's response to a decrease in food quality was more pronounced than to an increase in the quality of the same resource.

Table 3.6 Behaviour of the foraging population during the initial 38 days

Day	F1 recruit	F1 All.	F1 Tra.	F1 forays	F1 Food (mm^3)	F1 Load/ Foray	F2 recruits	F2 All.	F2 Tra.	F2 forays	F2 Food (mm^3)	F2 Load/ Foray
F1 (10%) : F2 (10%)												
3	9	500	108	617	1500	2.43	4	286	0	290	3000	10.35
4	5	486	128	619	2300	3.71	5	392	11	409	1300	3.18
5	13	391	131	535	2200	4.12	5	297	45	347	1300	3.74
6	20	437	139	596	3000	5.04	7	221	20	248	1000	4.03
mean	**12**	**454**	**126**	**592**	**2250**	3.82	**5**	**299**	**19**	**324**	**1650**	**5.33**
SD	**6**	**50**	**13**	**40**	**614**	1.08	**1**	**71**	**19**	**70**	**911**	**3.37**
F1 (5%) : F2 (10%)												
9	0	155	2	157	800	5.11	9	509	148	666	2000	3.00
10	0	128	2	130	400	3.09	16	581	200	797	3100	3.89
11	0	140	0	140	300	2.14	18	436	151	605	1900	3.14
12	0	139	0	139	700	5.05	16	353	203	572	2000	3.49
mean	**0**	**140**	**1**	**141**	**550**	3.85	**15**	**470**	**176**	**660**	**2250**	**3.38**
SD	**0**	**11**	**1**	**11**	**238**	1.48	**4**	**98**	**30**	**99**	**569**	**0.40**
F1 (10%) : F2 (10%)												
15	0	230	33	263	1200	4.57	7	371	72	450	2500	5.56
16												
17	0	94	1	95	500	5.24	11	223	27	261	1000	3.83
18	4	191	5	200	750	3.75	11	477	61	549	2000	3.64
mean	**1**	**172**	**13**	**186**	**817**	4.52	**10**	**357**	**53**	**420**	**1792**	**4.26**
SD	**2**	**70**	**17**	**85**	**355**	0.74	**2**	**127**	**23**	**146.32**	**763.76**	**5.22**
F1 (10%) : F2 (5%)												
21	5	380	245	635	1500	2.38	11	533	67	612	500	0.82
22	23	518	265	806	1500	1.86	0	405	52	457	1500	3.28
23												
24	2	196	85	283	1000	3.54	0	52	2	54	200	3.70
mean	**10**	**365**	**198**	**575**	**1333**	2.59	**4**	**330**	**40**	**374**	**733**	**1.96**
SD	**12**	**162**	**99**	**267**	**289**	0.86	**6**	**249**	**34**	**288**	**681**	**1.56**
F1 (10%) : F2 (10%)												
27	2	648	142	792	1900	2.40	5	430	95	531	1500	2.82
28	18	502	103	623	2100	3.37	5	340	74	419	1100	2.62
29	0	493	101	594	1200	2.02	2	259	79	340	900	2.65
30	0	724	167	891	2750	3.09	11	619	122	752	2250	2.99
31	0	293	38	331	500	1.51	11	227	43	281	500	1.78
32	22	466	131	619	3000	4.84	4	270	18	292	2000	6.86
mean	**5**	**494**	**109**	**609**	**1863**	2.87	**7**	**344**	**66**	**436**	**1375**	**3.15**
SD	**11**	**177**	**55**	**229**	**1208**	1.47	**5**	**185**	**45**	**180.85**	**669.14**	**3.70**
F1 (5%) : F2 (10%)												
35	4	214	27	245	2600	10.62	9	585	234	828	3200	3.86
36	0	175	23	198	1800	9.09	7	335	250	592	2000	3.38
37	2	153	32	187	1200	6.41	49	715	254	1017	4100	4.03
38	4	162	52	218	900	4.13	9	779	286	1075	3000	2.79
mean	**2**	**176**	**34**	**212**	**1625**	7.56	**18**	**603**	**256**	**878**	**3075**	**3.50**
SD	**2**	**27**	**13**	**25**	**750**	2.87	**20**	**196**	**22**	**217.68**	**861.68**	**3.96**

F1Rec. F1 Recruits; F1All. F1 Alliegiant foragers; F1Tra. F1 Transient foragers; Load/forayF1 F1 Food/F1 total forays. F2Rec. F2 Recruits; F2All. F2 Alliegiant foragers; F2Tra. F2 Transient foragers; Load/forayF2 F2 Food/F2 total forays

Table 3.7 Behaviour of the foraging population during the latter 36 days

Day	F1 recruit	F1 All.	F1 Tra.	F1 forays	F1 food (mm^3)	F1 Load/ Foray	F2 recruit	F2 All.	F2 Tra.	F2 forays	F2 food (mm^3)	F2 Load/ Foray
F1 (10%) : F2 (10%)												
41	4	259	90	353	1500	4.25	7	221	59	288	1400	4.86
42	0	124	23	148	1000	6.78	2	319	56	376	1700	4.52
43	2	151	83	236	1300	5.51	49	680	101	830	2700	3.25
44	2	95	32	130	1000	7.72	32	797	76	905	3000	3.31
mean	**2**	**158**	**57**	**216**	**1200**	**6.06**	**23**	**504**	**73**	**600**	**2200**	**3.99**
SD	**1**	**72**	**34**	**102**	**245**	**1.51**	**22**	**278**	**20**	**313**	**770**	**0.82**
F1 (15%) : F2 (10%)												
47	34	223	83	340	1600	4.70	22	598	146	765	2100	2.75
48	2	194	121	317	1600	5.05	36	432	144	612	1900	3.10
49	20	191	103	313	1200	3.83	16	517	135	668	2100	3.14
50	0	77	112	189	1100	5.82	16	493	108	617	2200	3.56
mean	**14**	**171**	**104**	**290**	**1375**	**4.85**	**23**	**510**	**133**	**666**	**2075**	**3.14**
SD	**16**	**64**	**16**	**68**	**263**	**0.82**	**9**	**69**	**17**	**71**	**126**	**0.33**
F1 (10%) : F2 (10%)												
53	13	286	166	465	2000	4.31	52	781	189	1022	3900	3.81
54	0	250	99	349	1500	4.30	5	821	167	994	2200	2.21
55	4	209	153	365	1800	4.93	18	691	131	841	3000	3.57
56	11	322	110	443	1400	3.16	5	659	160	824	2400	2.91
mean	**7**	**267**	**132**	**406**	**1675**	**4.17**	**20**	**738**	**162**	**920**	**2875**	**3.13**
SD	**6**	**49**	**32**	**57**	**275**	**0.74**	**22**	**76**	**24**	**102**	**763**	**0.72**
F1 (15%) : F2 (10%)												
59	0	128	160	288	1200	4.17	4	603	90	697	1200	1.72
60	9	112	137	257	1400	5.44	23	704	115	842	2600	3.09
61	0	182	74	256	1500	5.87	16	527	76	619	2200	3.55
62	18	135	85	238	1200	5.05	43	778	122	943	3200	3.34
mean	**7**	**139**	**114**	**260**	**1325**	**5.13**	**22**	**653**	**101**	**776**	**2300**	**2.92**
SD	**9**	**30**	**41**	**21**	**150**	**0.72**	**17**	**110**	**22**	**145**	**841**	**0.82**
F1 (10%) : F2 (10%)												
65	9	54	235	298	1200	6.06	14	535	135	684	2100	3.26
66	0	61	178	239	1000	7.22	65	1003	77	1145	4000	3.36
67	0	7	261	268	900	7.35	61	878	115	1054	3400	3.57
68	0	14	209	223	150	6.41	18	689	9	716	3000	4.07
mean	**2**	**34**	**221**	**257**	**813**	**6.76**	**40**	**776**	**84**	**900**	**3125**	**3.56**
SD	**5**	**27**	**36**	**33**	**459**	**0.62**	**27**	**206**	**56**	**234**	**797**	**0.36**
F1 (10%) : F2 (5%)												
71	0	527	767	1294	4900	3.79	13	238	68	319	1500	4.90
72	0	130	270	400	1200	3.00	0	29	5	34	100	2.92
73	0	574	558	1132	3200	2.83	0	131	13	144	200	1.39
74	0	702	464	1166	3500	3.00	0	47	27	74	200	2.71
mean	**0**	**483**	**515**	**998**	**3200**	**3.15**	**3**	**111**	**28**	**142**	**500**	**2.98**
SD	**0**	**247**	**206**	**405**	**1525**	**0.43**	**6**	**95**	**28**	**126**	**668**	**1.45**

F1Rec. F1 Recruits; F1All. F1 Alliegiant foragers; F1Tra. F1 Transient foragers; Load/forayF1 F1 Food/F1 total forays. F2Rec. F2 Recruits; F2All. F2 Alliegiant foragers; F2Tra. F2 Transient foragers; Load/forayF2 F2 Food/F2 total forays

Table 3.8 Comparison of amount of food gathered from the sites during different periods using 't' test assuming equal variance (Data from Tables 3.6 and 3.7).

Day and site	Conc. F1 (%)	Conc. F2 (%)	df	t stat	p(<=t) two-tail	Result
* (3-6) F1 & F2 (1st control)	10	10	6	1.09	0.316560965	NS
(9-12) F1 & F2 (1st experimental)	5	10	6	-5.52	0.001493120	S
*(3-6) F1 & (9-12) F1	10,5		6	5.16	0.002084605	S
*(3-6) F2 & (9-12) F2		10,10	6	-1.12	0.306563812	NS
*(15-18) F1 & F2 (2nd control)	10	10	4	-2.09	0.104706031	NS
*(15-18) F1 & *(3-6) F1	10,10		4	-2.96	0.041730621	S
*(15-18) F2 & *(3-6) F2		10,10	4	0.09	0.934576198	NS
*(15-18) F1 & (9-12) F1	10,5		4	-2.96	0.041730621	S
*(15-18) F2 & (9-12) F2		10,10	4	-0.32	0.764483771	NS
(21-24) F1 & F2 (2nd experimental)	10	5	4	1.41	0.232565824	NS
*(15-18) F1 & (21-24) F1	10,10		4	-1.96	0.122015172	NS
*(15-18) F2 & (21-24) F2		10,5	4	1.40	0.233187983	NS
*(27-32) F1 & F2 (3rd control)	10	10	10	1.13	0.284102255	NS
*(27-32) F1 & (21-24) F1	10,10		7	1.00	0.348657996	NS
*(27-32) F2 & (21-24) F2		10,5	7	1.35	0.219204259	NS
(35-38) F1 & F2 (3rd experimental)	5	10	6	-2.54	0.044164761	S
*(27-32) F1 & (35-38) F1	10,5		8	0.50	0.629004349	NS
*(27-32) F1 & (35-38) F2	10	10	8	-1.98	0.082735599	NS
*(27-32) F2 & (35-38) F2		10,10	8	-1.98	0.082735599	NS
*(41-44) F1 & F2 (4th control)	10	10	6	-2.47	0.048172243	NS
*(41-44) F1 & (35-38) F1	10,5		6	-1.08	0.322729365	NS
*(41-44) F2 & (35-38) F2		10,10	6	-2.54	0.044164761	S
(47-50) F1 & F2 (4th experimental)	15	10	6	-4.80	0.002994737	S
*(41-44) F1 & (47-50) F1	15,10		6	0.97	0.367740209	NS
*(41-44) F2 & (47-50) F2		10,10	6	1.18	0.281386498	NS
*(53-56) F1 & F2 (5th control)	10	10	6	-2.96	0.025350781	S
*(53-56) F1 & (47-50) F1	10,15		6	1.58	0.166170141	NS
*(53-56) F2 & (47-50) F2		10,10	6	2.07	0.084065703	NS
(59-62) F1 & F2 (5th experimental)	15	10	6	-2.28	0.062489754	NS
*(53-56) F1 & (59-62) F1	10,15		6	2.23	0.067055745	NS
*(53-56) F2 & (59-62) F2		10,10	6	-0.53	0.615526461	NS
*(65-68) F1 & F2 (6th control)	10	10	6	-5.03	0.002387408	S
*(65-68) F1 & (59-62) F1	10,15		6	-2.12	0.077970439	NS
*(65-68) F1 & (59-62) F2	10	10	6	-3.11	0.020949375	S
(71-74) F1 & F2 (6th experimental)	10	5	6	3.24	0.017629363	S
*(65-68) F1 & (71-74) F1	10,10		6	-3.00	0.024079572	S
*(65-68) F2 & (71-74) F2		10,5	6	5.05	0.002342937	S

S = Significant and NS = Not Significant (at P=0.05 level)

* Represent the control periods

Table 3.9 Comparison of total, transient and allegiant forays to the sites using x^2 test

Day and site	Conc. F1 (%)	Conc. F2 (%)	Total forays (x^2 value)	Transient forays (x^2 value)	Allegiant forays (x^2 value)
* (3-6) F1 & F2 (1st control)	10	10	78.59(S)	44.21(S)	17.58(S)
(9-12) F1 & F2 (1st experimental)	5	10	335.9(S)	96.01(S)	98.78(S)
*(3-6) F1& (9-12) F1	10,5		276.8(S)	68.76(S)	91.75(S)
*(3-6) F2 & (9-12) F2		10,10	115.18(S)	70.08(S)	21.01(S)
*(15-18) F1 & F2 (2nd control)	10	10	133.93(S)	13.48(S)	36.13(S)
*(15-18) F1 & *(3-6) F1	10,10		270.63(S)	51.03(S)	70.66(S)
*(15-18) F2 & *(3-6) F2		10,10	12.60(S)	9.15(S)	2.82(NS)
*(15-18) F1 & (9-12) F1	10,5		0.0522(NS)	6.125(S)	1.73(NS)
*(15-18) F2 & (9-12) F2		10,10	53.19(S)	36.18(S)	8.55(S))
(21-24) F1 & F2 (2nd experimental)	10	5	3.809(NS)	58.08(S)	0.96(NS)
*(15-18) F1 & (21-24) F1	10,10		140.87(S)	89.84(S)	38.66(S)
*(15-18) F2 & (21-24) F2		10,5	2.66(NS)	1.03(NS)	0.651(NS)
*(27-32) F1 & F2 (3rd control)	10	10	39.3(S)	6.0(S)	14.97(S)
*(27-32) F1 & (21-24) F1	10,10		41.93(S)	14.21(S)	10.81(S)
*(27-32) F2 & (21-24) F2		10,5	4.67(S)	3.41(NS)	0.157(NS)
(35-38) F1 & F2 (3rd experimental)	5	10	406.97(S)	94.73(S)	130.27(S)
*(27-32) F1 & (35-38) F1	10,5		216.35(S)	22.19(S)	83.92(S)
*(27-32) F1 & (35-38) F2	10	10	36.72(S)		
*(27-32) F2 & (35-38) F2		10,10	148.73(S)	62.56(S)	39.54(S)
*(41-44) F1 & F2 (4th control)	10	10	180.07(S)	1.51(NS)	101.025(S)
*(41-44) F1 & (35-38) F1	10,5		0.0472(NS)	3.34(NS)	0.567(NS)
*(41-44) F2 & (35-38) F2		10,10	52.33(S)	56.65(S)	4.91(S)
(47-50) F1 & F2 (4th experimental)	15	10	147.78(S)	1.93(NS)	93.38(S)
*(41-44) F1 & (47-50) F1	15,10		10.63(S)	7.68(S)	0.020(NS)
*(41-44) F2 & (47-50) F2		10,10	3.41(NS)	9.8(S)	0.0159(NS)
*(53-56) F1 & F2 (5th control)	10	10	199.91(S)	1.71(NS)	122.73(S)
*(53-56) F1 & (47-50) F1	10,15		19.24(S)	11.53(S)	1.77(NS)
*(53-56) F2 & (47-50) F2		10,10	40.91(S)	23.174(S)	1.56(NS)
(59-62) F1 & F2 (5th experimental)	15	10	259.98(S)	0.44(NS)	185.25(S)
*(53-56) F1 & (59-62) F1	10,15		31.96(S)	0.73(NS)	22.35(S)
*(53-56) F2 & (59-62) F2		10,10	11.67(S)	7.91(S)	2.889(NS)
*(65-68) F1 & F2 (6th control)	10	10	226.66(S)	0.376(NS)	377.45(S)
*(65-68) F1 & (59-62) F1	10,15		15.25(S)	2.48(NS)	35.25(S)
*(65-68) F1 & (59-62) F2	10	10	24.15(S)	2.32(NS)	5.91(S)
(71-74) F1 & F2 (6th experimental)	10	5	248.16(S)	144.6(S)	129.43(S)
*(65-68) F1 & (71-74) F1	10,10		193.59(S)	172.02(S)	216.52(S)
*(65-68) F2 & (71-74) F2		10,5	284.25(S)	11.23(S)	276.93(S)

S = Significant and NS = Not Significant (at P=0.05 level)

* Represent the control periods

Table 3.10 Foray ratio of Series 1 Data from Table 3.3

Days	F1 forays/ F2 forays	F1 All.	F1 Tra.	F1 forays	F1 food (mm^3)	F2 All.	F2 Tra.	F2 forays	F2 food (mm^3)	Total forays	Total food (mm^3)
F1 (10%) : F2 (10%)											
3 to 8	**0.53**	548	23	571	3952	1019	57	1077	5036	1648	8988
F1 (10%) : F2 (5%)											
11 to 17	**3.80**	518	486	1033	7488	238	2	272	1836	1305	9324
F1 (5%) : F2 (10%)											
20 to 26	**0.10**	99	25	125	900	1054	131	1224	6712	1349	7612
F1 (10%) : F2 (5%)											
29 to 34	**12.68**	424	703	1167	8617	92	0	92	481	1259	9098

Table 3.11 Foray ratio of Series 2 Data from Table 3.3

Days	F1 forays/ F2 forays	F1 All.	F1 Tra.	F1 forays	F1 food (mm^3)	F2 All.	F2 Tra.	F2 forays	F2 food (mm^3)	Total forays	Total food (mm^3)
F1 (10%) : F2 (10%)											
3 to 6	**1.83**	454	126	592	2250	299	19	324	1650	915	3900
F1 (5%) : F2 (10%)											
9 to 12	**0.21**	140	1	141	550	470	176	660	2250	801	2800
F1 (10%) : F2 (10%)											
15 to 18	**0.44**	172	13	186	817	357	53	420	1792	606	2609
F1 (10%) : F2 (5%)											
21 to 24	**1.54**	365	198	575	1333	330	40	374	733	949	2067
F1 (10%) : F2 (10%)											
27 to 32	**1.40**	494	109	609	1863	344	66	436	1375	1045	3238
F1 (5%) : F2 (10%)											
35 to 38	**0.24**	176	34	212	1625	603	256	878	3075	1090	4700
F1 (10%) : F2 (10%)											
41 to 44	**0.36**	158	57	216	1200	504	73	600	2200	816	3400
F1 (15%) : F2 (10%)											
47 to 50	**0.44**	171	104	290	1375	510	133	666	2075	955	3450
F1 (10%) : F2 (10%)											
53 to 56	**0.44**	267	132	406	1675	738	162	920	2875	1326	4550
F1 (15%) : F2 (10%)											
59 to 62	**0.33**	139	114	260	1325	653	104	776	2300	1036	3625
F1 (10%) : F2 (10%)											
65 to 68	**0.29**	34	84	257	813	776	84	900	3125	1157	3938
F1 (10%) : F2 (5%)											
71 to 74	**7.03**	483	515	998	3200	111	28	142	500	1140	3700

These results could be explained in two ways:-

1) Foragers can not distinguish 10% w/v sugar solution and 15% w/v sugar solutions.
2) Foragers avoid the 15% w/v solution because of dehydration problems.

Table 3.12 10% w/v sugar solution intake over experimental days (Series 2)

	Period	% concentration F1	% concentration F2	foray ratio (F1/F2)	10% w/v sugar solution intake (%)
Control	3-6	10	10	1.83	
Experimental	9-12	5	10	0.21	80
Control	15-18	10	10	0.44	
Experimental	21-24	10	5	1.54	65
Control	27-32	10	10	1.40	
Experimental	35-38	5	10	0.24	65
Control	41-44	10	10	0.36	
Experimental	47-50	15	10	0.44	60
Control	53-56	10	10	0.44	
Experimental	59-62	15	10	0.33	63
Control	65-68	10	10	0.29	
Experimental	71-74	10	5	7.03	87

If the foragers actively avoid the 15% w/v sugar solution, then a reduction of forays to that site, as in the 5% w/v sugar solution case, would be expected: yet no such reduction was evident in these experiments (Table 3.11). Therefore it can be concluded that foragers were not able to recognise the difference between 10% w/v sugar solution and 15% w/v sugar solution.

3.6 Individual behavioural traits

The foraging population is made up of individuals which may stay in the system for some time and then drop out to perform other duties. It was observed in the laboratory that some foragers (previously marked on a tree) engaged in nest building and sometimes carrying dead nest mates to the 'middens'. These individuals, when foraging, may work at different rates: for example, they not only differ in the total number of forays which they make, but also in the timing of these forays throughout the day. When an individual joins the foraging population, it makes fewer forays than veteran foragers: this was clearly observed by marking the foragers over 6 consecutive days and following their individual behaviours. For example, after the total foraging population had been marked: there after unmarked foragers recruited to

Table 3.13 Observations of individual behaviours

		Starting		Dissappearing					
Ant no:	Name	Day	Site	Day	Site	Number of forays on recruiting day	Duties other than foraging	Transient behaviour due to change	Transient behaviour without change
1	GO	6	F2,10%	17	F2,10%		yes	no	no
2	GYL	1	F2,10%	24	F2,5%		yes	no	no
3	GDOT	8	F2,10%	16	F2,5%		no	no	no
4	Gmet*	5	F2,10%	27	F2,10%	4	yes	yes	yes
5	Gyel*	15	F2,10%	35	F1,5%	2	no	yes	no
6	Gora*	25	F2,10%	45	F2,10%	4	yes	no	yes
7	GR2DOT*	15	F2,10%	34	F1,5%	3	yes	yes	no
8	Gblu*	17	F2,10%	34	F1,5%	2	yes	yes	no
9	GMETBL	13	F2,10%	22	F2,5%		no	no	no
10	GS	6	F2,10%	20	F2,5%		yes	no	yes
11	Gmbtot*	13	F2,10%	20	F1,10%	5	yes	yes	yes
12	Gpink band*	14	F2,10%	44	F1,10%	4	yes	yes	yes
13	Gbig red	14	F2,10%	20	F2,5%		no	no	yes
14	G one eye*	15	F2,10%	29	F1,10%	4	yes	yes	no
15	GRgg*	14	F2,10%	27	F2,10%	1	yes	no	no
16	Gcrusty*	14	F2,10%	30	F1,10%	4	yes	yes	no
17	GRed2 dot	18	F2,10%	33	F2,10%		no	no	no
18	GLime*	33	F2,10%	41	F2,10%	1	yes	no	yes
19	Gtail*	27	F2,10%	42 (dead)	F2,10%	5	no	no	yes
20	Gbird*	39	F2,10%	46	F2,10%	3	yes	no	yes
21	G big blu	18	F2,10%	39	F2,10%		no	no	no
22	Gnom*	17	F2,10%	34	F1,5%	5	no	yes	no
23	Gblack*	10	F2,10%	21	F2,5%	4	yes	no	yes
24	GBLDOT	14	F2,10%	32	F2,10%		yes	yes	yes
25	Gprimary	44	F2,10%	59	F2,10%		no	no	yes
26	Gsnow*	44	F2,10%	53	F2,10%	5	yes	no	yes
27	WO	6	F1,10%	16	F1,10%		no	no	no
28	WY	6	F1,10%	10	F1,5%		no	no	no
29	WZ*	6	F1,10%	14	F2,10%	5	no	yes	yes
30	Wall*	3	F1,10%	20	F1,10%	5	yes	yes	no
31	Web*	6	F1,10%	16	F2,10%	3	no	yes	no
32	Wik*	3	F1,10%	21	F1,10%	6	no	yes	yes
33	WAQUA*	5	F1,10%	21	F2,10%	6	yes	yes	yes
34	WYR	14	F1,10%	18	F1,5%		no	no	no
35	WHface	14	F1,10%	34	F1,10%		no	yes	yes
36	Wwhite	14	F1,10%	36	F1,5%		no	no	yes
37	Wpink	9	F1,10%	20	F1,5%		no	no	no
38	Wblue	32	F1,10%	48	F2,10%	3	yes	yes	no
39	Wblush*	32	F1,10%	46	F2,10%	4	yes	yes	no
40	Wrose	40	F1,10%	53	F2,10%		Yes	no	yes
41	Waqua 1 dot*	39	F1,10%	45	F1,15%	5	Yes	no	yes
42	Waqua ora	21	F1,10%	41	F1,10%		yes	yes	no
43	Wbaby*	21	F1,10%	39	F2,10%	1	yes	yes	no
44	Wsea*	46	F1,10%	58	F1,15%	7	no	no	no
45	Wbag	53	F1,10%	59	F1,15%		no	no	no
46	Wfrog eyes*	59	F1,10%	63	F2,10%	4	yes	yes	no
47	Wdash	52	F1,10%	59	F1,15%	3	yes	yes	no
48	Wcitrus	43	F1,10%	57	F1,10%	4	no	no	yes
49	Wpakman	14	F1,10%	25	F1,10%		no	no	no

* Individuals which were followed since recruiting to the foraging population
Values within ( ) represent the standard deviations

		Mean Foray Frequency		
Whether transfered allegiance	Number of successful forays on the day of alteration	Control days (both trees are 10%)	Allegiant tree 5% or 15%	Alternative tree 5% or 15%
no	-	9.75(4.1)		16 (4)
no	16	16.08(4.9)	6.8 (3.7)	16.2 (5.5) 5%
no	21	14(7.5)		23.6 (2.9) 5%
no	18	14.32(2.3)	11.6 (6.17)	
yes	9	17.2(4.1)	5.9 (3.8)	13.42(2.8)5%
no	18	15.35(3.4)		16.32(4.2)5%
yes	10	16.23(5.1)	15.45 (3.23)	
yes	9	12.53(2.81)	10.56 (3.1)	
no	17	16.1(3.2)	6.8 (4.2)	
no	19	17.42	10.4 (5.6)	16.8 (2.9) 5%
yes	7	13.45(2.8)		16.8 (4.2) 5%
yes	6	11.33(0.21), 13.7(3.8), 12.33(4.5)	7.1 (3.3)	
no	16	12.75(3.2)		
yes	8	11.7(2.08), 12.5(4.3)	11.4 (1.9)	
no	12	13.75(4.04), 18.5(2.1)	8.5 (7.7)	
yes	10	17.3(4.9)	9 (6.7)	
no	16	8, 19.6(4.2)	11 (3.9)	
no		1.5(0.98)		12.7 (2.08) 5%
no		12.6(4.9)		12 (6.9) 5%
no	14	12(3.08		16 (1.4) 15%
no	14	28, 15.575(3.5)	17.4 (6.4)	16.3 (3.98) 5%
yes	6	9(3.6)		7.41 (3.8) 5%
no	16	13.75(2.03)	8.75 (3.82)	10.3 (3.8) 5%
yes	11	12.25(3.5)	7.5 (3.2)	
no	18	12.32(2.7)	13.23 (3.7)	
no		8.23(0.707)		9.42 (3.6) F1 15%
no	19	12, 10.67(4.1)		
no	23	21	11.25 (4.06)	
yes	11	16.53(3.02)	18.67 (10.48)	
no	21	15.75(6.2), 20.25,(2.06)	10.27 (4.7)	
yes	6	19(4.24)	10.14 (8.7)	
no	18	13.25(5.25), 19.4(4.4)	11.6 (6.17)	
yes	5	6.9(4.96), 9.45(6.3)	9.32 (5.45)	
no		14.8(1.8), 14.2(1.8)	14.4 (6.7)	
no	15	11.8(9.4), 16.3(8.4)		15.8 (5.2) F2 5%
no	32	23(4.9), 19(7.3)	12.3 (0.57)	20.2 (4.4) 5%
no	16	14.35(3.1)	5.92 (3.1)	
yes	10	15.35(3.8)	15.7 (3.12)	
yes	8	11.32(3.72)	13.23 (3.7)	12.48 (2.73)
no	16	11.6(6)	14.2 (2.1) F1 15%	
no	15	9.6(3.2)	2.1 (1.78)	
no	21	24.25(6.1), 21.3(10.7)	16.8 (3.2) F1 5%	18 (8.75) F2 5%
yes	18	13.7(6.31)		15.3 (5.5) F2 5%
no	23	24.3(4.9)	14 (4.6) F1 15%	
no	39	30(5.2)	35 (8.4) F1 10%	
no	23	12.7(6.3)	5.8 (3.2)	
no	18	14.35(3.8)		7.8 (3.6)
no	17	12.78(2.9), 12.5(3.8)	7.28 (4.35) F1 15%	
no		8(3.2)		10.5 (4.3)

the foraging population made fewer forays (average 4 forays per foraging day) on recruiting day compared to an already marked average veteran forager (average 17 forays per foraging day) in the same population.(Table 3.13). It was observed also that these unmarked foragers may attempt to take part in trophallaxis, and run backwards and forwards along the branch bearing food before actual feeding.

3.6.1 Foray loads over different times of the foraging period

Gaster volume measurements obtained from gaster profiles clearly demonstrated that different individuals carried different amounts, and also that each individual carried different amounts at different times of the day. Typically they carried more during the initial 1.5-2.5 h of the foraging period and the foray loads transported on successive control days may be superimposed (Fig 3.4a, b & c). A significant difference in the foray loads throughout the period was revealed by using the one-way unrelated Anova test to analyse gaster volume data obtained from video recordings over 3 consecutive control days, split into morning (10.00-12.00 h), afternoon (12.00-14.00 h) and late afternoon (14.00-16.00 h) periods (F=7.55, df 2 & 181, P<0.001). Furthermore Tukey's multiple comparison procedure was used to separate the means of three periods (Table 3.14).

Table 3.14 Results of Tukey's multiple comparison test

Time of the day (h)	Mean
Morning (10.00-12.00)	1.48^a
Afternoon (12.00-14.00)	1.50^a
Late afternoon (14.00-16.00)	1.09^b

Means with same superscript do not differ significantly : P>0.05
SD = 0.658 Standard deviation of any one of the three means is approximately equal to this value. P = 0.001 Level of significance

These results imply that foray loads were not significantly different between morning and early afternoon, but were between morning or early afternoon and late afternoon. This may be explained by considering that the foray load was not solely controlled by the individual itself, but also by the colony as a whole (see Cosens & Toussaint, 1986). As the colony was subjected to a food deficit during the previous night, individuals may work hard during the early part of the day to repair the deficit,

Figure 3.4 Load per foray over different times on three days for individual marked ants

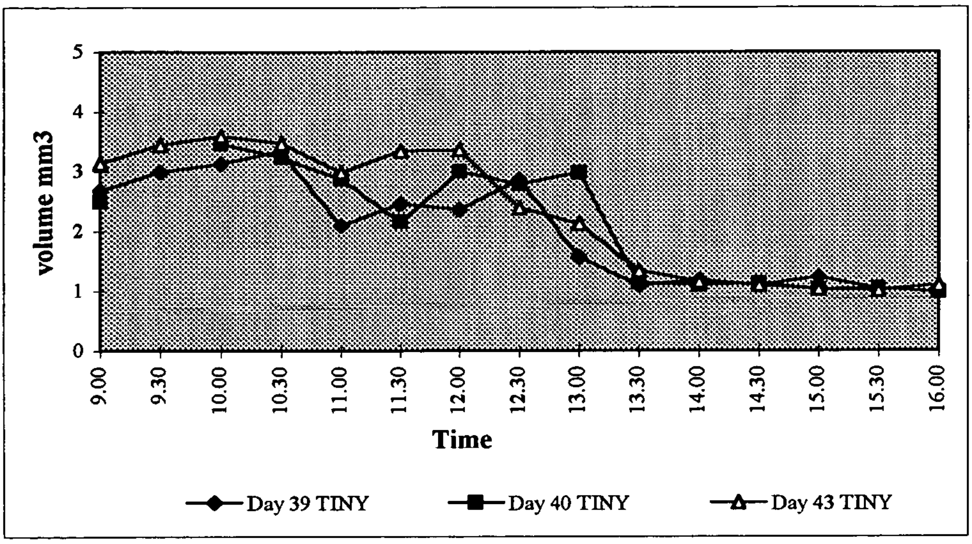


Fig. 3.4a TINY White ant (F1), foraged to the white tree (F1) 10% on days 39,40,43

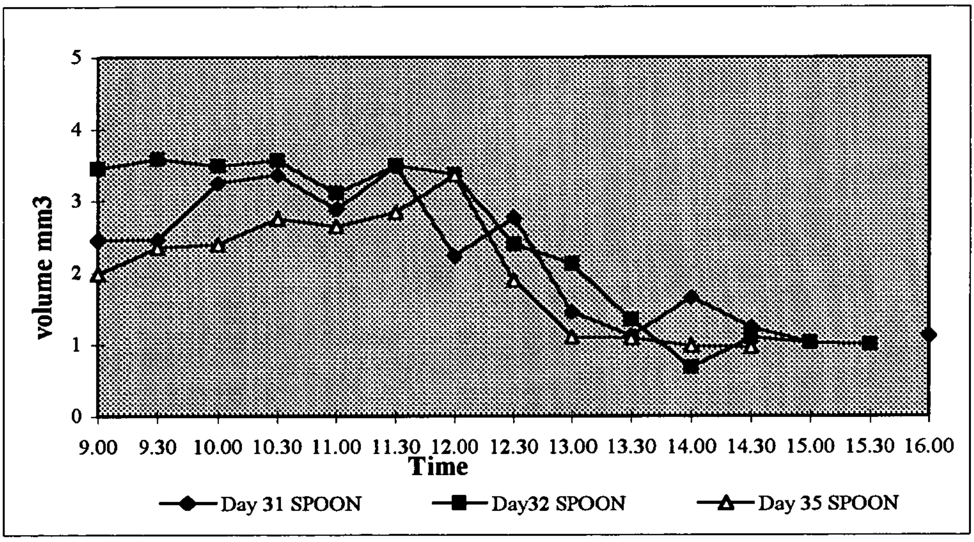


Fig. 3.4b SPOON Green ant (F2), foraged to the green tree (F2) 10% on days 31,32,35

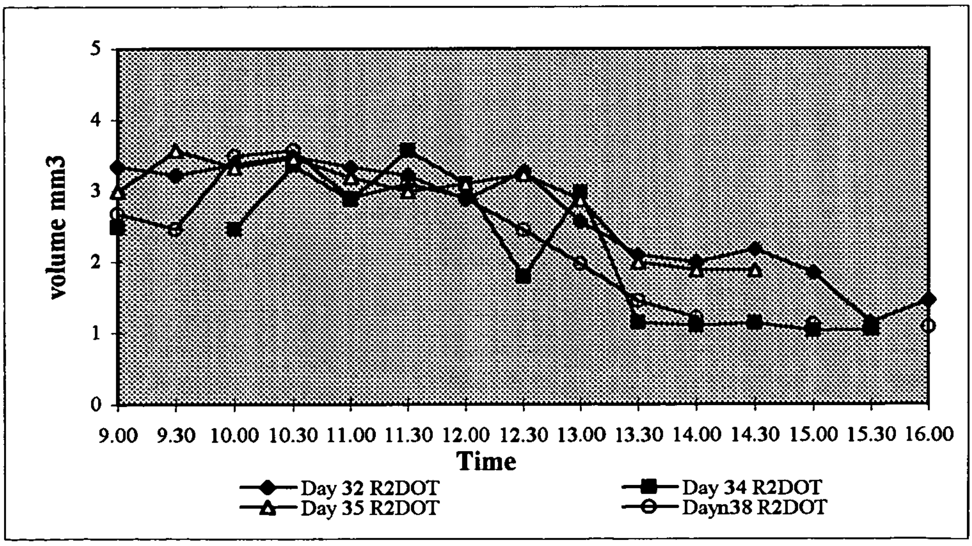


Fig. 3.4c R2DOT Green ant (F2), foraged to the green tree (F2) 10% on days 32,34,35,38

and they might by satisfying their own hunger respond to the colony's hunger by collecting more during the early hours of the foraging period. Also, foray load data obtained from the amount of food collected/mean forays over different experimental and control days, have clearly shown that individuals carried more per load when fewer individuals forage than when a large number do so (Tables 3.6 & 3.7).

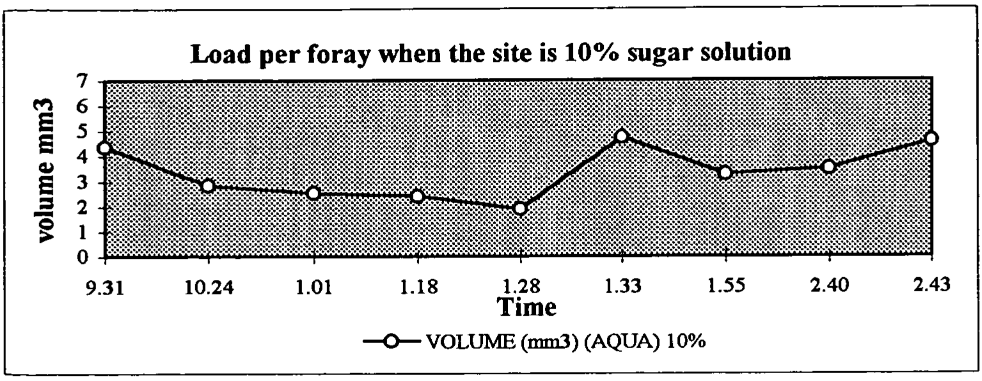
When the food quality at one site was altered by decreasing it to 5% w/v sugar solution, some individuals were observed to spend more time at site 'analysing' the food: touching the antennae and mouth parts of other foragers, and even though they fed at the site their gasters did not become replete. Later it became clear that the individuals that behaved in this manner were the transient foragers which, in effect, had transferred allegiance to the other site bearing 10% w/v sugar solution. Some proportion (0.69) of the individuals ignored the alteration at the site and continued to feed as before: they were the allegiant individuals which stayed at the particular site irrespective of the food quality.

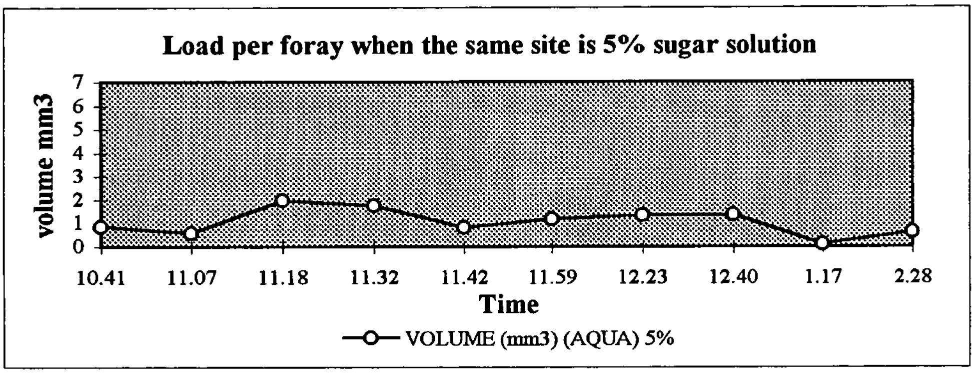
To formalise these observations for analysis the behaviour of several individuals selected at random from the 'analysing' group, and from the normally feeding group, was monitored. At the outset 10 individuals per group were selected: the 'analysing' group are referred to as 'switchers' and the feeding group as 'stayers'. However, because some individual switchers were lost from the foraging population (they presumably assumed other tasks) and it proved difficult to obtain from the video recordings a complete series of gaster profiles for the same period (to avoid error due to individual foragers carrying different amounts at different times of the day), the number of individuals that were followed successfully was 5 from each group (Table 3.15).

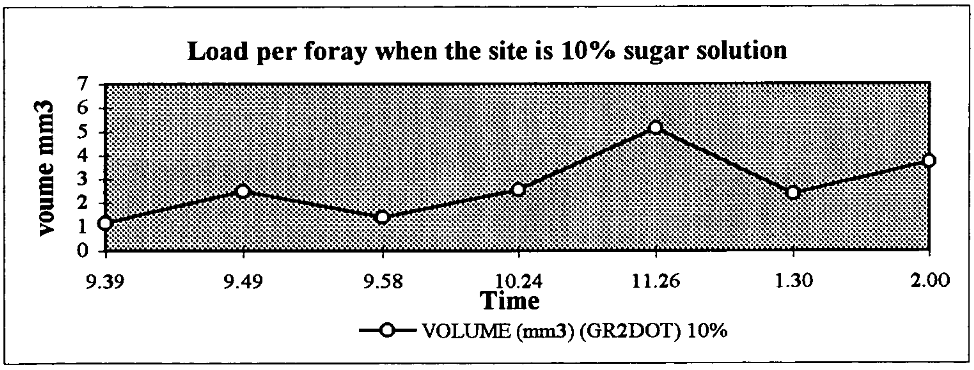
3.6.2 Load per foray

The colony as a whole collected less food from the 5% w/v sugar solution bearing sites by the end of the 4 days, but individually foragers tended to transport larger crop loads/foray from the sites (Fig. 3.5). The decreased amount of food gathered from the 5% w/v sugar solution bearing sites was due to the small number of foragers involved and the fewer forays made (Tables 3.6 & 3.7).

Figure 3.5 Load per forays of individuals that later transferred their alliegiance to better quality site (response of switchers)







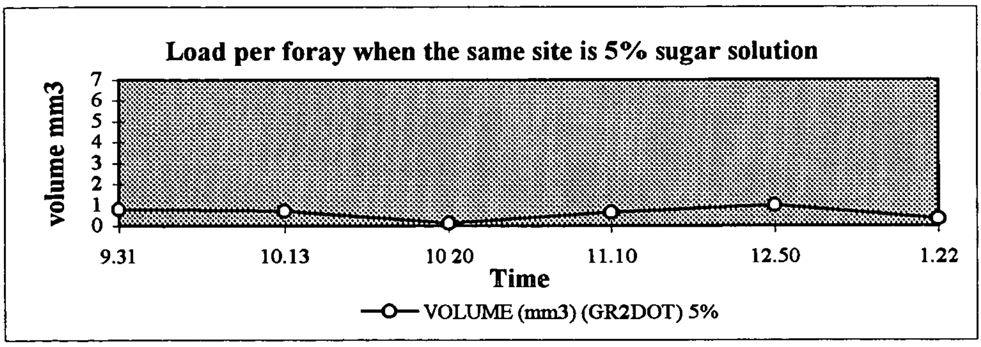
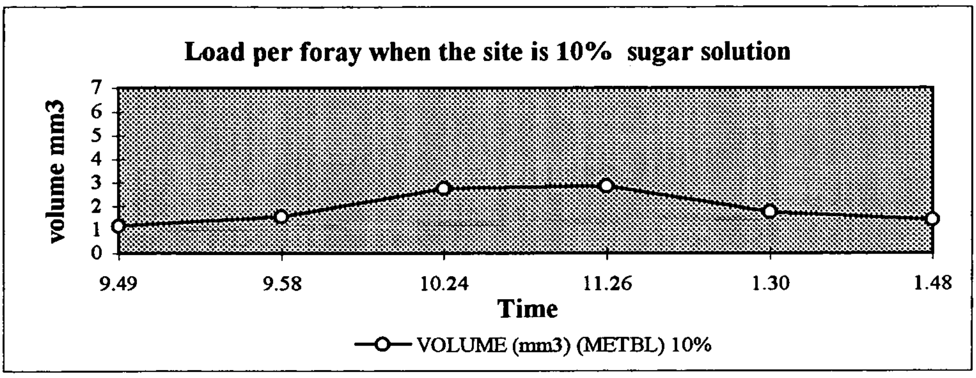
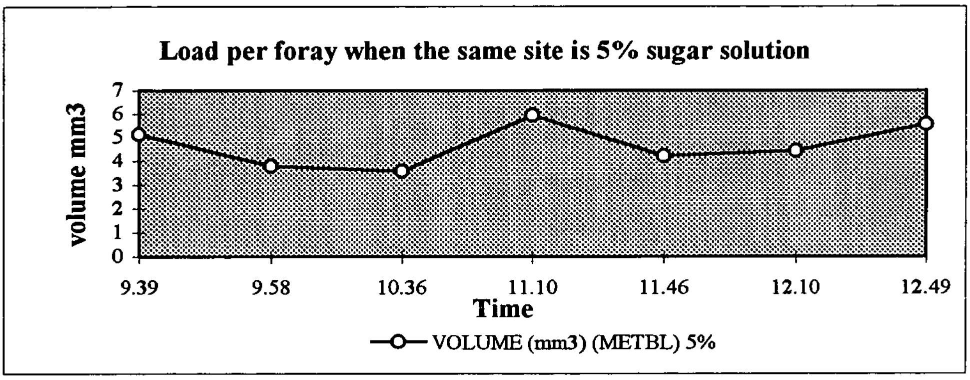
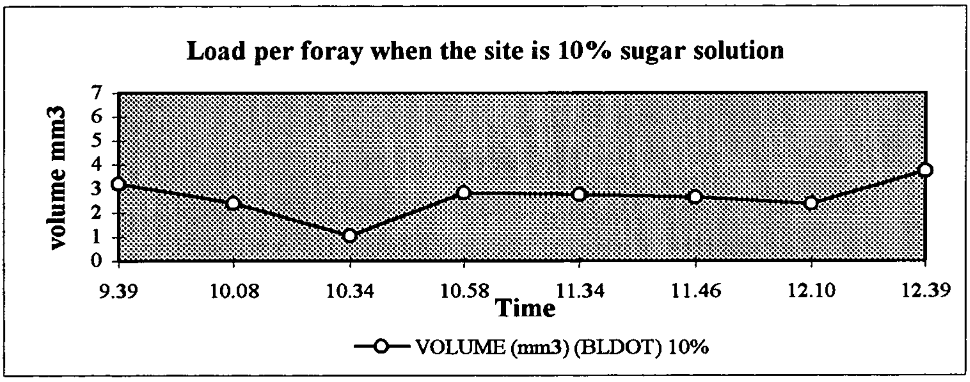


Figure 3.5a Load per forays of indivduals that stayed in the site irrespectve of the quality (Response of stayers)


Load per foray when the site is 10% sugar solution


Load per foray when the same site is 5% sugar solution


Load per foray when the site is 10% sugar solution

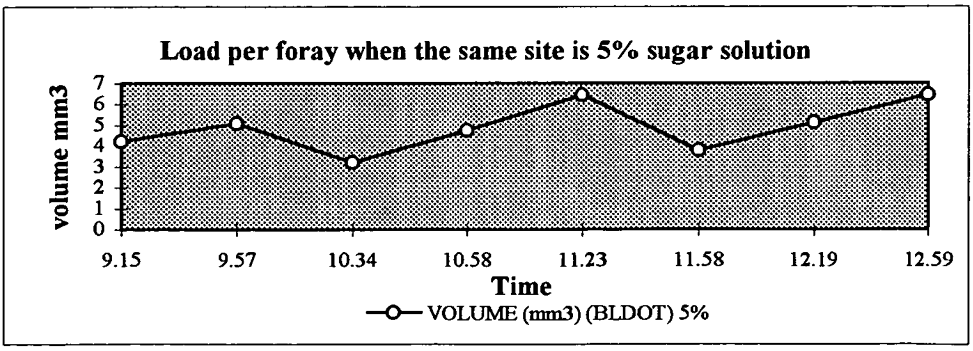
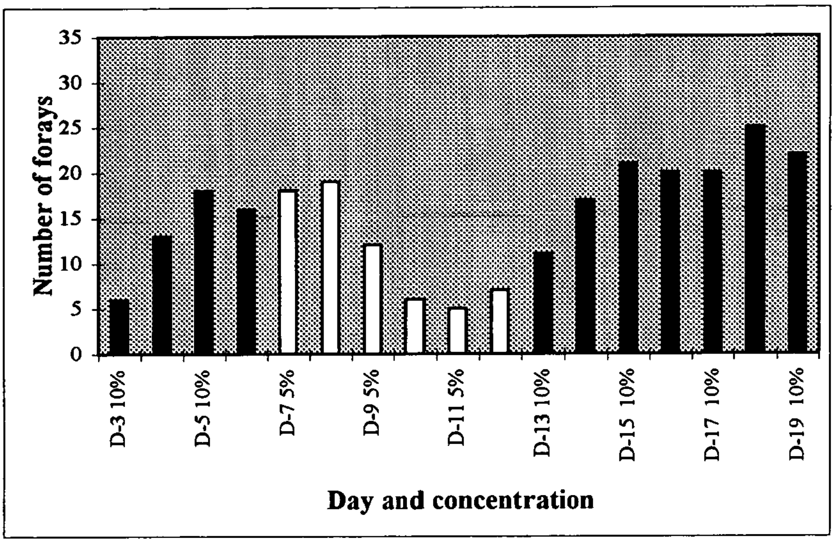
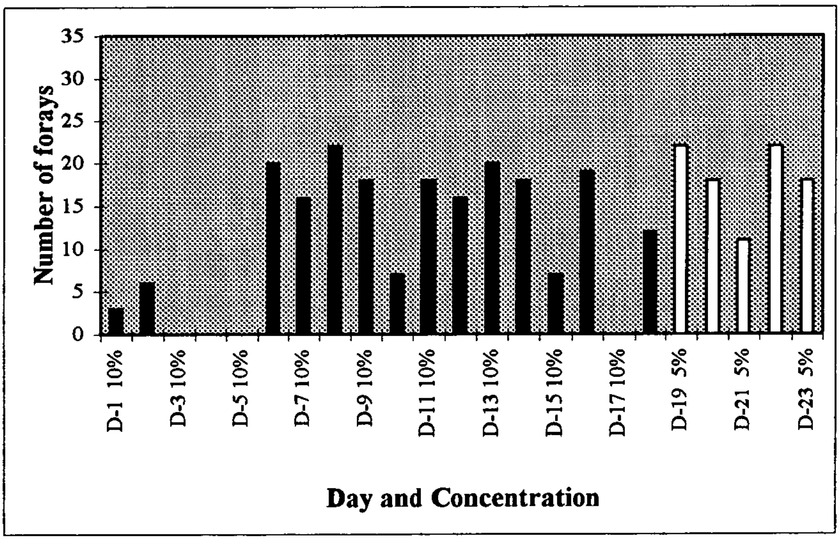

Load per foray when the same site is 5% sugar solution

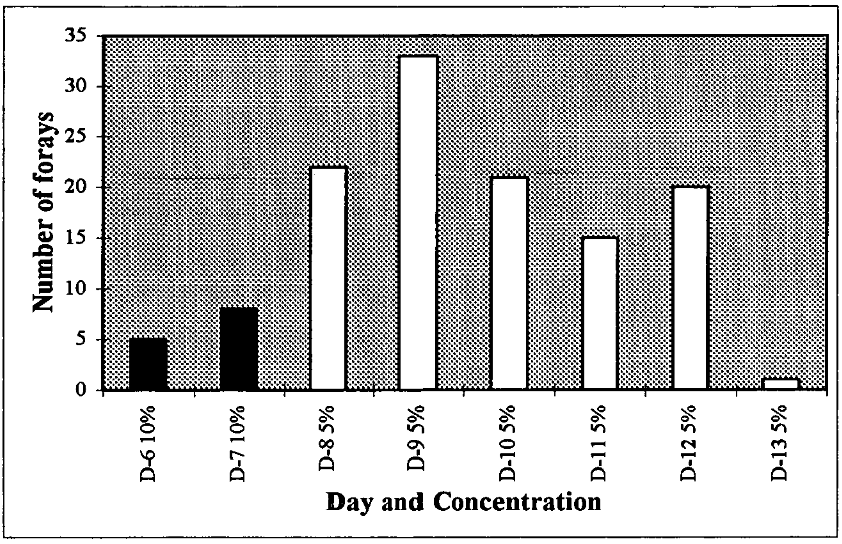
Fig. 3.6 Number of forays made by different individuals on their tenure of foraging



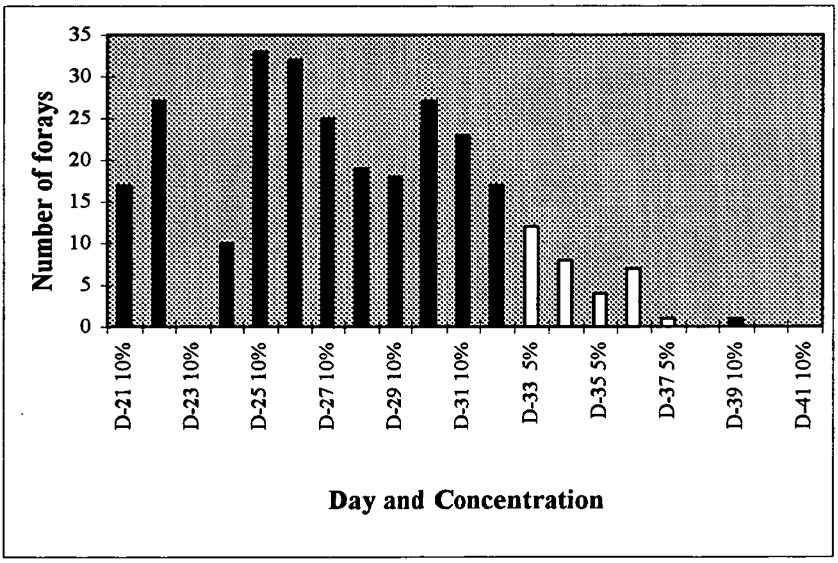
(a) 'WIK' at tree F1.
She dissappeared from the foraging population after the day 19
On day 24 'WIK' was observed carrying dead nest mate.



(b) 'GYL' at tree F2. she did foragrd on days 3, 4, 5 and 17
'GYL' was observed engaged in nest building on day 24 and afterwards was not observed



(c) 'WZ' at tree F1, was followed since recruiting to the foraging population
She was not observed foraging after the day 13 but was observed
on the foraging table



'Aqua' at tree F1
She did not forage on day 23, and started transient behaviour on day 33.
'AQUA' transfered her allegiance to tree F2 and continue to forage there until dissappearing from the foraging population on day 42

Foragers which had transferred their allegiance initially made forays to both (5% w/v sugar solution and 10% w/v sugar solution) bearing sites before transferring their allegiance to the high quality site (Fig. 3.6). Furthermore, even after transferring allegiance some of these foragers made forays to the new site via their previously allegiant (5% w/v sugar solution) site (switchers). To find whether there is a significant difference in foray loads due to the alterations at one site, an Anova two-factor with replication test was performed using foray loads obtained from 5 individuals from each group ('switchers' and 'stayers') during the same part of the foraging period (Table 3.16). Since the difference was significant (F=118.06, df 1 & 16, $P<0.05$) that is switchers and stayers carried different amounts when their allegient site was provisioned with 5% w/v sugar solution (Figs. 3.5 and 3.5a), the Anova one factor with replication test was performed to find whether there was a significant difference in foray loads between 'switchers' and 'stayers' with respect to 10% w/v sugar solution and 5% w/v sugar solution.

Table 3.15 Volume of food (mm^3) carried by the switchers and stayers from allegient site, bearing 10% w/v sugar solution and the same site bearing 5% w/v sugar solution between 9.30 - 11.30

Conc.	Switchers					Stayers				
	Waqua	Gr2dot	Gblu	Web	Wblush	Bl2dot	Metblue	Wo	Wbag	Gs
10%	4.37	1.16	2.50	1.63	1.73	3.15	1.16	1.02	1.83	1.15
	2.83	2.48	2.47	2.06	2.15	3.03	1.57	0.87	2.87	1.57
	2.54	1.39	2.29	2.47	2.12	1.63	2.75	1.03	2.07	2.74
	2.40	2.56	3.68	3.15	2.47	2.52	2.87	2.06	2.86	2.87
	1.89	5.14	4.66	3.58	2.86	4.07	1.76	1.35	3.14	1.76
	4.74	2.38	5.99	4.13	2.87	4.86	1.44	2.33	3.15	1.44
5%	0.85	0.81	0.82	0.85	1.09	4.23	5.14	4.45	4.36	5.14
	0.56	0.72	0.60	0.56	0.78	5.08	3.80	4.14	5.09	3.80
	1.98	0.12	0.98	0.12	0.85	5.11	3.59	5.45	6.02	3.58
	1.75	0.63	1.14	0.63	0.56	6.46	5.95	5.30	5.98	5.95
	0.81	0.98	1.44	0.21	0.82	6.45	4.23	6.40	6.07	4.23
	1.16	0.34	1.30	0.54	0.60	3.78	4.44	6.05	5.98	4.44

Table 3.16 Anova two factor with replication for switchers and stayers (fed from 5% w/v sugar solution and 10% w/v sugar solution). Data from Table 3.15

SUMMARY	Switchers	Stayers	Total
10%			
Count	5	5	10
Sum	14.42	11.28	25.70
Average	2.88	2.26	5.14
Variance	0.25	0.47	0.72
5%			
Count	5	5	10
Sum	4.12	26.63	30.75
Average	0.82	5.33	6.15
Variance	0.09	0.31	0.39
Total			
Count	10	10	
Sum	18.54	37.91	
Average	3.71	7.58	
Variance	0.34	0.78	

ANOVA

Source of Variation	SS	df	MS	F	P-value	F crit
Sample	1.28	1	1.28	4.58	0.05	4.49
Columns	18.77	1	18.77	67.37	3.97x 10^{-07}	4.49
Interaction	32.89	1	32.89	118.06	8.55x 10^{-09}	4.49
Within	4.46	16	0.28			
Total	57.39	19				

With respect to the 10% sugar solution both ‘switchers’ and ‘stayers’ behaved similarly (F=2.72, df 1 & 8, P>0.05 Table 3.17). However, they did show a significant difference in behaviour to the 5% w/v sugar solution (F=258.66, df 1 & 8, P<0.05 Table 3.18): switchers left the site non-replete, while stayers left very replete (Table 3.15).

Table 3.17 Anova single factor for switchers and stayers fed from 10% w/v sugar solution

SUMMARY

Groups	Count	Sum	Average	Variance
Switchers 10%	5	14.42	2.88	0.25
Stayers 10%	5	11.28	2.26	0.47

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.98	1	0.98	2.72	0.14	5.32
Within Groups	2.89	8	0.36			
Total	3.87	9				

Table 3.18 Anova single factor switchers and stayers fed from 5% w/v sugar solution

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
Switchers 5%	5	4.12	0.82	0.09
Stayers 5%	5	26.63	5.33	0.31

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	50.67	1	50.67	258.66	2.24×10^{-07}	5.32
Within Groups	1.57	8	0.20			
Total	52.24	9				

3.6.3 Number of 'trophallactic communications' per foray

Since the 'analysing' behaviour, which involved more frequent trophallaxis, was displayed when the food quality at a particular site was initially changed, the number of trophallactic communications per foray was calculated for the first two days of the alteration (increase or decrease the quality at a particular site) and the last two days of that particular experimental period to find whether or not there was a significant difference in frequency of trophallaxis during these two periods. An Anova Two Factor with replication test was performed using the data shown in Table 3.19: there was a significant difference in number of trophallactic communications per foray between these two periods (F=22.9, df 1 &16, P<0.05 Table 3.20). So an Anova Single Factor test was performed separately for the first two days (F=33.28, df 1 & 10, P<0.05 Table 3.21) and the last two days (F=0.91, df 1 & 8, P>0.05 Table 3.22). These results confirm that there was a significant increase of 'trophallactic communications' per foray when circumstances have initially changed, compared to when the circumstances have resumed stability.

Table 3.19 Number of 'trophallactic communications' per foray

	10% w/v sugar solution bearing Site	5% w/v sugar solution bearing Site
First two days of the experimental alteration	0.073810	0.607692
	0.148649	0.229773
	0.113281	0.413953
	0.082803	0.329609
	0.086466	0.401198
Last two days of the experimental alteration	0.086310	0.051282
	0.072327	0.025974
	0.070064	0.066667
	0.069027	0.105769
	0.082077	0.066116

Table 3.20 Anova two factor with replication for number of trophallactic communications per foray (First and last two days) of the experimental alteration at sites. Data from Table 3.19

SUMMARY	10% w/v sugar solution bearing site	5% w/v sugar solution bearing site	Total
First two days of experimental alteration			
Count	5	5	10
Sum	0.52	2.04	2.56
Average	0.10	0.41	0.51
Variance	0.0008	0.02	0.02
Last two days of experimental alteration			
Count	5	5	10
Sum	0.38	0.32	0.70
Average	0.08	0.06	0.14
Variance	0.00006	0.0008	0.0009
Total			
Count	10	10	
Sum	0.90	2.35	
Average	0.18	0.47	
Variance	0.0009	0.021	

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Sample	0.17	1	0.17	31.85	0.00004	4.49
Columns	0.11	1	0.11	19.34	0.00045	4.49
Interaction	0.13	1	0.13	22.90	0.0002	4.49
Within	0.09	16	0.0055			
Total	0.49	19				

Table 3.21 Anova single factor for number of trophallactic communications per foray (First two days of experimental alteration). Data from Table 3.19

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
10% w/v sugar solution bearing site	6	0.61	0.10	0.0007
5% w/v sugar solution bearing site	6	2.44	0.41	0.02

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.28	1	0.28	33.28	0.0002	4.96
Within Groups	0.08	10	0.01			
Total	0.36	11				

Table 3.22 Anova single factor for number of trophallactic communications per foray (Last two days of experimental alteration). Data from Table 3.19

SUMMARY

Groups	*Count*	*Sum*	*Average*	*Variance*
10% w/v sugar solution bearing site	5	0.38	0.08	6.01421×10^{-05}
5% w/v sugar solution bearing site	5	0.32	0.06	0.0008

ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Between Groups	0.00041	1	0.00041	0.91	0.37	5.32
Within Groups	0.0036	8	0.00045			
Total	0.004	9				

3.6.4 The time spent within the mound nest

Since the lowest foray numbers were observed at the 5% w/v sugar solution bearing sites, the time spent within the nest was observed for individuals that had fed from the 5% w/v sugar solution bearing site and those from the 10% w/v sugar solution bearing site during the particular experimental period. t-test: two sample, assuming equal variances was performed with the data obtained (Table 3.23). There was no significant difference in the times spent within the nest by individuals whether fed from 5% w/v sugar solution bearing site or the 10% w/v sugar solution bearing site (t=-0.91, df 44, P>0.05 Table 3.24).

Table 3.23 Time spent within the nest by individuals fed from 5% w/v sugar solution bearing Site and 10% w/v sugar solution bearing Site.

5% w/v sugar solution bearing Site (sec)	10% w/v sugar solution bearing Site (sec)
172	154
180	180
137	199
162	161
156	96
169	113
208	169
240	209
168	156
133	173
111	162
163	156
196	209
219	214
161	239
89	119
159	167
123	161
199	213
180	180
149	161
159	137
229	156

Table 3.24 t-test: two-sample assuming equal variances for the time spent within the mound nest by individuals fed from 5% w/v sugar solution bearing site and 10% w/v sugar solution bearing site (First 3 days of alteration). Data from Table 3.23

	Variable 1(5% w/v sugar solution bearing site)	*Variable 2*(10% w/v sugar solution bearing site)
Mean	167.91	168.87
Variance	1346.99	1190.21
Observations	23	23
Pooled Variance	1268.60	
Hypothesised Mean Difference	0	
df	44	
t Stat	-0.092	
P(T<=t) one-tail	0.47	
t Critical one-tail	1.68	
P(T<=t) two-tail	0.93	
t Critical two-tail	2.02	

3.6.5 Individual performances within the foraging cohort

In these experiments 'naive' foragers were selected on the basis that once the total foraging cohort had been marked (after 3-4 days no unmarked foragers were found at the sites), unmarked foragers seen at the sites on the days following were individuals that were foraging for the first time: these particular individuals were colour marked differently for subsequent identification (Tables 3.13 & 3.25). Indeed they were probably on the foraging table for the first time since virtually all the ants on the foraging table during control days were involved in foraging, rather than in exploratory, behaviours.

Table 3.25 Some observations based on newly recruited (naive) foragers to the foraging cohort (data obtained from Table 3.13)

Ant no:	Name	Number of forays on recruiting day	Transient behaviour due to change at the site	Transient behaviour without change at the site	Whether transferred allegiance
4	Gmet	4	yes	yes	no
5	Gyel	2	yes	no	yes
6	Gora	4	no	yes	no
7	Gr2dot	3	yes	no	yes
8	Gblu	2	yes	no	yes
11	Gmbtot	5	yes	yes	Yes
12	Gpink band	4	yes	yes	Yes
14	Gone eye	4	yes	no	yes
15	Grgg	1	no	no	no
16	Gcrusty	4	yes	no	Yes
18	GLime	1	no	yes	no
19	Gtail	5	no	yes	no
20	Gbird	3	no	yes	no
22	Gnom	5	yes	no	yes
23	Gblack	4	no	yes	no
26	Gsnow	5	no	yes	no
29	WZ	5	yes	yes	yes
30	Wall	5	yes	no	no
31	Web	3	yes	no	yes
32	Wik	6	yes	yes	no
33	Waqua	6	yes	yes	yes
39	Wblush	4	yes	no	yes
41	Waqua 1 dot	5	no	yes	no
43	Wbaby	1	yes	no	yes
44	Wsea	7	no	no	no
46	Wfrog eyes	4	yes	no	no
47	Wdash	3	yes	no	no
48	Wcitrus	4	no	yes	no

Total number of foragers (N) followed for the experimental series 2 was 49. From these 49, individuals total number of naive foragers (n_1) was 28; total number of veterans was (n_2) 21.

- The proportion of 'naive' foragers which showed transient behaviour at least once in their foraging activity was ($26/n_1 = 26/28$) 0.93.
- The proportion of 'veterans' which showed transient behaviour at least once in their foraging activity was ($10/n_2 = 10/21$) 0.48.
- The proportion of foragers which transferred allegiance to the better quality site was($15/N = 15/49$) 0.31.
- The proportion of 'naive' foragers which transferred allegiance to the better quality site was ($15/n_1 = 15/28$) 0.54.
- The proportion of 'veterans' which transferred allegiance to the better quality site was (0/N) 0.

When looking at individual performances on control days, upon joining the foraging cohort the naive forager usually makes fewer forays ($\bar{x}=4$, SD=1.5, N=28) compared to the veteran members ($\bar{x}=17$, SD=3.2, N=28) of the same foraging cohort (Table 3.13 & 3.25) per experimental day. Moreover, 93% of naive foragers, were observed to make transient forays at least once, for the veterans this was 48%. When the foraging system was perturbed by altering one of the paired 10% w/v sugar solution bearing sites to a 5% w/v sugar solution bearing site, a certain number of the allegiant foragers ('stayers') respond by increasing their foray frequencies as well as their foray loads from the altered site, while the others ('switchers') decrease their foray frequencies and loads from the altered site, and shift their allegiance to the unaltered 10% w/v sugar solution bearing site (Fig. 3.5). Amongst all the individuals that have been followed during the experimental Series 2, 54% of those that transferred their allegiance to the better quality site were the 'naive' foragers eventually ($15/n_1 = 15/28$: 0.54) 31% of the total foraging cohort followed ($15/N = 15/49$: 0.31) Table 3.25.

3.7 Discussion

The main aim of this study was to understand how a wood ant colony regulates the distribution of its foragers among available food sources. In this series of experiments, it has been clearly shown that when foragers were offered paired sites of equal food quality and then one site was reduced in quality, foragers were able to recognise the change and shifted their foraging effort towards the unchanged (high quality) site, so diminishing the flow of food from the lower quality site into the colony. According to the model developed by Ollason (1987) an 'ideal animal' moves to the patch where it has the best chance of success: consistent with any rule of movement which maximises the animal's intake of energy from its environment. However, a particular *F. aquilonia* forager is often aware only of the circumstances prevailing a) at a particular site to which she has become allegiant, and b) within the nest where she passes on her crop-load. At the site she is affected by the behaviour and numbers of other foragers and of the aphids. In the nest she may be affected by colony hunger and by the rate of food intake because it influences the availability of receivers within the nest: a forager can only forage again if her crop is empty. In forest or woodland canopies the foragers gather honeydew from aphid aggregations which are distributed randomly among the branches of the trees, hence all the feeding sites cannot be known to all foragers. Thus, explicit co-operation would be necessary for a colony's full exploitation of the available resources within their territory. Independent foraging by wood ants is likely to be reinforced by their capacity for learning and remembering topographic detail, by which they orient to known foraging sites: individual foragers become allegiant to a familiar site (Rosengren, 1971; 1977a; Cosens & Toussaint, 1985; Rosengren & Fortelius, 1986; Rosengren & Sundström, 1987). Given that this is the case with wood ants, application of Ollason's (1987) ideal distribution model is questionable: because not every individual moves to every site assessing the food quality. In *F. aquilonia*'s case, maximisation of the net energetic yield of the colony as a whole may conflict with optimal foraging as measured at the individual level of behaviour. However, a successful foraging system should match the distribution of resources, including resources yet to be discovered. A forager searching for new food sources will, as an individual, appear uneconomical compared with a forager visiting a 'known' source of food (Deneubourg, *et al.*, 1987), at least in a stable habitat containing self-renewing food sources which the aphid aggregations represent. Another factor is that ant species which monopolise their habitats (to counter competition) have to allocate workers to defend both profitable and less profitable sectors of the territory and hence cannot optimise short term resource exploitation. In the experimental Series 1 and 2 it had been demonstrated that some foragers ('stayers') did not behave according to the predictions of 'ideal free distribution' theory (Lamb & Ollason, 1993). Lamb and Ollason (1994a) later found that site allegiance is a constant property of certain individuals of the colony's foraging population and subsequently revised their original idea by saying there should be a minimum number of individuals which show transient (mobile) behaviours below which 'ideal free distribution' could not be achieved. Even with allegiant members in the foraging population, *F. aquilonia* foragers manage, within a short period, to distribute their foraging effort economically to exploit the 10% w/v sugar solution bearing site when provided with an alternative 5% w/v sugar solution bearing site. However, when they were provided with a choice of 10% w/v sugar solution and 15% w/v sugar solution bearing sites no such economic distribution of foraging effort was observed. This observation was contradictory to what would be expected from predictions of 'ideal free distribution' and the optimal foraging behaviour said to be achieved by the social insects when collecting food in a regenerating environment. A high concentration of a desired food must contain a higher amount of energy than a low concentration of the same food resource (Taylor, 1978). If foragers were able, by comparison, to recognise that a 10% w/v sugar solution is energetically richer than a 5% w/v sugar solution and, as observed, distribute appropriately at the sites; it is curious that they did not behave likewise when the choice was between 10% w/v sugar solution and 15% w/v sugar solution.

Communication must play a major role in eusocial foraging strategies, hence it was also expected that knowledge of changes in the food quality at a site would be made available to foragers at other sites. So these individuals would also modify (compensate) their behaviours accordingly. Seeley (1985 & 1989) proposed that in honeybee colonies the finding of rich food sources was mainly based on the mass effort of the thousands of individual foragers in a colony following three shared rules:-

1) If working a rich patch of flowers, perform recruitment dances for the patch.
2) If on a poor patch of flowers, abandon the patch.
3) To find a new patch of flowers, nearly always follow recruitment dances and only occasionally search independently.

The net result is a steady migration of foragers away from poor patches, back to the nest where they follow recruitment dances, and ultimately out onto rich patches. The key to the honeybee social foraging system is the dance language, a communication behaviour which enables colony members to share information about locations of rich food sources (Seeley, 1986). In the wood ants' foraging system, no such dancing language has been observed, instead intense trophallaxes and antennal interactions have been observed frequently near the food sites; at a point along a trail where the routes to rich and poor quality food sources diverge; and near the mound nests on transitional days after the alterations. Ants use their antennae in a variety of behavioural rituals (Lenoir & Jaisson, 1982; HÖlldobler, 1984) and if ants transmit information when they touch antennae, keeping the frequency of contact relatively constant may stabilise decision-making behaviour at the colony level (Gordon *et al.*,1993). In addition they suggested the possibility of the use of contact rates, as short-term adjustments in worker allocation. An ant colony generally engages in a variety of tasks and the numbers active in each task depend on the numbers engaged in another, although all of these are subject to the current requirements of the colony (Gordon, 1987 & 1989). Regulating the rate of contact in undisturbed conditions may facilitate an individual's ability to recognise when a shift in worker allocation is needed. This may be perceived as a change in the interval between contacts (Gordon *et al.*, 1993). Ants might perceive contact rates as a frequency, that is number of contacts per unit time, or they might perceive time interval between contacts: which would be a consequence of contact rate. Unlike the honeybees, when one of the paired sites was lowered in quality compared to the other the wood ants did not completely abandon the poor quality source. This could have been due to the wood ants' strong allegiance to the food site implying a limited knowledge of the tropic zone. It could also have been due to their territorial nature: they have to defend profitable and non profitable sites in particular sectors of the territory. A key component of the wood ants' foraging system is the mechanism whereby a colony keeps a large proportion of its forager force distributed on the most profitable food sites whilst its members show strong site allegiance. A major challenge in the analysis of the wood ants' foraging system is unravelling how individual foragers are programmed to follow economic decisions, enabling the colony to gain maximum profitability. To identify the communication within the mound nest between replete foragers returning from 10% w/v sugar solution and 5% w/v sugar solution bearing sites, an artificial nest which allows observation of internal events is required.

It is also possible that factors besides the properties of the site such as weather conditions, time of day, and the colony's need for food also influence a forager's behaviour at a particular site in response to an altered situation. In the present study, carried out in the laboratory, all such factors could be assumed constant for both sites. How does a forager assess the profitability of its food source? The factors underlying the selection of 'food' are predominantly chemical. It has been shown experimentally that the senses of taste and smell were the means whereby insects detect the chemicals in question (Dethier, 1937). Detheir (1941, 1947 & 1953) pointed out the importance in food selection of special compounds not necessarily related to the insects' nutritional requirements: these were conceived of as 'sign' or 'token' stimuli. Fraenkel (1953) described that the food specificity in insects was based solely on the presence or absence of 'tokens'. Kennedy and Booth (1951) had already demonstrated with aphids, that nutritional factors actually do play an important role, and suggested that 'flavours' equivalent to 'token' stimuli were important in the discrimination of different food sources. Of compounds that are clearly of nutritional importance to insects, sucrose is one of the most widespread; it is an effective stimulus for the majority of insects even those in which it forms no necessary part of feeding activity (Beck, 1956). Mittler and Dadd (1963 & 1964) have shown that the initial stimuli used to determine acceptability or non-acceptability of a diet are gustatory. In the aphid, *Myzus persicae*, acceptability of sucrose increases up to 40% in concentration beyond which there is a decrease. Logically, food discrimination is based on olfactory or gustatory stimuli or on both. At the neural level there are differences either in the way the sense organs or the integrated centres of the central nervous system (via the sense organs), or both, interact with the chemicals present in the food that is rejected. To understand these interactions completely it is necessary to know not only what compounds are presented to an insect by a food, but what their effect on the sense organs may be. The ultimate realisation would be an understanding of food discrimination in terms of neural action (Dethier, 1966). It was suggested that caterpillars discriminate their food-plant firstly on the basis of olfactory stimuli received through the antennae and maxillae and then, after biting, by stimuli perceived by organs of taste (Dethier, 1937). The first direct indication of sensory function of the maxillae come from the electrophysiological studies of Isikawa (1963), who proved that the two sensilla styloconica on the maxillary lobe of *Bombyx mori* are contact chemoreceptors. One contains receptors for salt and for sucrose, glucose and inositol; the other contains a receptor for water, two for salt, and one for repellent substances. The hypothesis was advanced that preferred food stimulates principally the sugar and inositol receptors while rejected food stimulates repellent receptor. Feeding preferences of individuals may also be modified by previous experience. Larvae of *Pieris brassicae* can distinguish among their preferred plants and tend to choose the species upon which they have previously fed, thus demonstrating an acquired taste (Johanssson, 1951; Horanitz & Chang, 1962). Young larvae of the swallow tail *Papilio aegeus* exhibit a certain polyphagy and tend to become conditioned to the plant upon which they have fed whether it is a natural food or not (Stride & Straatman, 1962). This type of hypothesis regarding 'acquired taste' to the standard 10% w/v sugar solution could be attributed to the wood ants' discrimination of 5%, 10% and 15% w/v sugar solutions. Wood ant foragers' gustatory mechanisms are adapted to identify concentration thresholds only up to 10% w/v sugar solution since the concentration of honeydew available at the field is 10% (Sudd & Sudd, 1985) and also they were conditioned to the 10% w/v sugar solution with in the laboratory system before any experimental trials. However, *Solenopsis geminata* a Myrmecine ant, was recruited at higher rates to a sugar solution resource when the concentration increased (Taylor, 1978), although the ants were not tested with concentrations above that to which ants had been conditioned in control trials. It seems that *F. aquilonia* foragers did not always behave as predicted by energy maximisation models since certain members of the foraging population ('stayers') show strong site allegiance, which must cause a degree of inertia and impede any alteration in behaviour.

Wood ants discriminate food quality without making the comparisons among sources suggested by Lamb and Ollason (1993). Initially when both sites were of equal quality the number of transient forays observed at each site was very low: this implies that most foragers were allegiant and perhaps had knowledge only of that site and the route to it. But after the alteration (10% w/v sugar solution to 5% w/v sugar solution) at one site, the resultant massive influx of transient foragers to the unaltered 10% w/v sugar solution bearing site implies that the unaltered circumstance had been communicated to them and that the route to the alternative site was known, or was also communicated by other colony members. It had been observed that when the quality at a particular site was decreased, the foray frequencies of some foragers ('switchers') to that site was also reduced (see individual data Fig. 3.6, Table 3.13) causing eventual reduction of total food flow rate to the colony. In these experiments, (Figs. 3.2a, b & c) the total food intake was not drastically reduced, and this stability was maintained by having two behaviourally distinct groups of foragers: the 'switchers' and 'stayers' that respond to alterations differently. The 'stayers' increased their foray loads and frequencies, compensating for the food deficit (amount) caused by the 'switchers' who reduced their forays to their allegiance site. The deficit, in large proportion, was countered by the foraging effort of the 'switchers' (now transient foragers) and the allegiant foragers at the alternative high quality site. Thus there was a diminishing amount of low quality food flow to the colony. Somehow the 'transient' foragers must be drawn to the richer site: his could be achieved by the purposeful activity of the allegiant foragers towards the high quality 10% w/v sugar solution bearing site and the high incidence of trophallaxis along the route to it with transient and naive foragers. The fact that individual foragers change their behaviour in response to the rate of food collection by the colony as a whole raises the question how the foragers sense this colony-level attribute. One might argue, as several authors have suggested (Lindauer, 1948; Vowles, 1955; Cosens & Toussaint, 1985), that this information was encoded in the reception a forager receives upon returning to the nest. The possible elements of communication which could be perceived by the replete forager are:-

a) time lag between entering the nest and finding a receiver to unload the forage.
b) time needed to unload where this requires more than one receiver.
c) the number of receivers simultaneously available for unloading the forage.
d) number of aborted food transfers (lack of receivers), when the flow rate is high but not when the flow rate is low.
e) intensity of antennal interaction during food transfer.

The only quantification relating to these elements which I was able to perform readily was the time spent within the mound nest. Seeley (1986) found no evidence of hesitation by receiver bees when unloading foragers returning with dilute sugar solutions, or a decrease of maximum number of receivers simultaneously attending a forager, or an increase of aborted food transfers, or a decrease in the intensity of antennal palpations between foragers which repleted from richer and poor quality patches. Instead he found the number of aborted transfers decreased, and the percentage of intense antennal interactions increased significantly with a decreasing concentration at the patch. These observations are exactly opposite to what would be expected if bees with dilute nectar experience difficulty getting unloaded. However, he did observe major differences between the two groups of foragers in their recruitment activity: indicating that the sweetness difference between their solutions was significant to the bees. In this study over the first three days (covering the more important transitional stages), I found that the times spent in the nest by foragers repleted from 5% and 10% w/v sugar solution bearing sites were not significantly different, indicating that 'receivers' who unload the replete foragers within the nest did not initially discriminate the sugar solutions; even though they are in a position to compare the quality of food from the various sites. Thus wood ant foragers may not get information of food quality directly from the receivers within the nest. If the receivers were to discriminate after a delay, the 'stayers' replete with 5% w/v sugar solution would be forced to stop foraging - which was indeed observed after several days. It was also observed that the number of trophallactic contacts per foray near the food sources is significantly higher on the first two days of alteration than on the last two days Tables 3.21 & 3.22). This implies that foragers simply taste the food's sweetness and then together with information gained through the trophallactic contacts with other foragers from the other feeding sites, grade their behaviour according to some fixed internal scale of response. Nonacs and Dill (1990) found that ants can also respond to both risk and food quality simultaneously and may choose a low quality, safe food over a high risk, quality food.

Using an observation nest previously used by Swanson (1995), I found that some uniquely marked foragers almost always unloaded in a specific area within the nest explaining the little variability in individual foragers' foray frequencies and foray intervals. It also explains why the 'stayers' increase their foray loads when the food quality decreases at their allegiant site: the 'switchers' perturbed the foraging system creating a local food deficit within an area of the nest to which they were spatially allegiant. A random group of 'naive' individuals and marked foragers ('veterans') were uniquely marked and their behaviours were subsequently followed during the experiment. These observations (Tables 3.13 & 3.25) revealed that individuals once recruited to the foraging population did not exclusively forage, they were involved also in nest building, carrying dead nestmates or in unseen, intranidal duties in between forays. Newly recruited foragers often showed more transient behaviour in their foraging repertory than veteran, allegiant foragers: one reason for the very low incidence of transient forays at the beginning of experiments when the foraging population comprises largely the latter foragers. Daily recruitment of a small number of novel foragers had been observed in previous laboratory experiments (Chapter 2) and in these particular experiments. The unique markings identified these novel foragers as the behaviourally flexible 'switchers' in the foraging population, and veteran foragers as the behaviourally tight 'stayers'. Rosengren and Fortelius (1986) and Rosengren and Sundström (1987) found that inexperienced wood ants were less firm in their choice of feeding site, while experienced veterans were constant to one site. The distribution of foragers among feeding sites may be a balance between these two types of behaviour. 'Switchers' could be the individuals which bear more sensitive nervous (probably the gustatory sense) mechanisms enabling the colony to swiftly distribute its forager force among sites according to the quality judged by taste or smell (whatever the factor associated with food) which leads 'stayers' to collect more until the system becomes stabilised and then 'stayers' dropped out to perform other duties enabling the colony to deploy more behaviourally flexible 'switchers' by rotation. In this way they were able to overcome the dominance of site allegiance and the possible inertia inherent in this strategy.

CHAPTER 4

How do the workers of *Formica aquilonia* orientate to food sources?

4.1 Introduction

Wood ants of the *F. rufa* group have distinct, collectively used foraging routes radiating out in different directions from a mound nest (Rosengren & Fortelius, 1986). In some cases systems of ramifying routes, sometimes covering an area of more than 1 ha (Gösswald, 1951), have been observed to remain virtually unchanged for several years in succession (Stäger, 1931; Chauvin, 1962; Rosengren, 1971). Field studies in Knapdale forest, Argyllshire, Scotland over a 10 year period have also shown that an established community of *Formica aquilonia* may spread 100 m along the edge of the forest and remain virtually unchanged over the years (Ashmole & Cosens, personal communication).

Directional recruitment is an obvious adaptive strategy and is often easy to confirm in opportunistic ant species utilising ephemeral sources of clumped food where it is based upon the use of pheromones. The wood ant *F. aquilonia* does not belong to this ecological category. Instead they show permanent defence of a habitat that provides spatially stable point sources of honeydew in the form of aphid aggregations in the forest canopy, and they also collect insect prey scattered throughout the territory (Rosengren & Fortelius, 1987). This resource structure is likely to favour foraging tactics based upon the foragers individually searching and partitioning the foraging territory, and consistent with this veteran foragers maintain a persistent site allegiance based on a hierarchy of individually remembered topographic cues (Rosengren & Fortelius, 1986a). However, debate over the importance of pheromone trails and other external cues as opposed to visual and internal perceptive cues is extended back as far as 1898 when Bethe dismissed claims of spatial memory in ants as anthropomorphic delusions, while Brun (1914) held the opposite view. Today with the invention of neuronal 'networks' capable of undertaking relatively complex tasks, it is apparent that much processing can be done with a small number of interconnected neurones (Vowles, 1967; Barlow, 1972). A great capacity for processing and a dominant use of visual information are indicated by several recent studies of ants, sphecid wasps and honey bees (Wehner, 1981; Menzel, 1985). Yet some sensory physiologists still doubt that the visual systems of insects, famous for millisecond reactions to velocity parameters, can be used for storage of 'objective' spatial relations (Marr, 1982). Hence the notion that ant colonies are 'memory free' super organisms still persists (Lumsden, 1982).

Several types of orienting cues have been documented in studies of red wood ants: thermal gradients (Kneitz, 1964), gravity (Markl, 1964), celestial cues (Jander, 1957), land mark and canopy pattern (Rosengren, 1971; Kaul, 1985), chemical cues (Horstmann, 1982), idiothetic (kinaesthetic) orientation (Schöne, 1984) and a remembered 'spatial concept' (Cosens & Toussaint, 1985). Any explanation of the route fidelity and site allegiance displayed by wood ant foragers must account for the stable nature of the phenomena, hence it dismisses wind direction and thermal gradients. Site allegiance implies an ability to remember directions and to repeatedly locate a specific spot in the habitat to which the ants become 'attached'. Orienting cues such as celestial or terrestrial 'guide posts' do not give an complete explanation of the latter point (Wehner, 1981). Zakharov (1973) argued that a wood ant colony may be divided into cohesive subgroups, each inhabiting a given sector of the nest and exploiting the habitat using a group-specific trunk-route: his intra-nest sampling showed a weak but statistically significant site allegiance. Rosengren and Fortelius (1986b) found that turning an artificial 'forest' arena through 180^0 resulted in the reversal of the site allegiance pattern relative to cardinal points. They also found no difference between experiments made in clear and overcast weather, provided that land marks were present: this argues against celestial cues having a major role in the route fidelity consequent on site allegiance. However, the weakening of site allegiance resulting from a disruption of route fidelity caused by removal of all land marks was more pronounced under an overcast, rather than a clear, sky indicating some use of celestial cues. Based on the disruption caused by winter felling (Rosengren & Pamilo, 1977), Kaul (1985) proposed that wood ants rely on the pattern formed by the canopy overhead, assuming they can use this canopy pattern at night, but not celestial cues. Although Jander (1957) demonstrated convincingly that wood ant workers can use celestial cues, these may be ignored when land mark-canopy cues are available and which, thus, have a 'higher status' in the hierarchy of orienting cues. Hence the celestial cues may be of little importance for foragers in undisturbed forests (Rosengren & Fortelius, 1986b). Wood ants store a memory picture of the canopy: this was indicated by experiments in which foragers, from both control areas and areas to be cleared in the winter, were marked in autumn and sampled in the following spring. Results showed a consistent and significant weakening of route fidelity in the cleared forest areas compared to that in the intact forest (Rosengren & Pamilo, 1977). The existence of extremely long-lasting storage of spatial information by wood ants is documented in the literature. Visually perceived land mark-canopy cues are the most obvious source of this information, but the hierarchical organisation of the orienting system made it difficult to exclude other sources of long term neural storage (Henquell & Abdi, 1981; Cosens & Toussaint, 1985).

In an evolutionary context ants and chemicals go hand in hand, looking across genera, it is clear that within the Formicidae, including the *F. rufa* group, pheromones are the primary means by which communication is mediated (Hölldobler & Wilson, 1990). Wood ants, including *F. aquilonia*, use chemical cues for a variety of purposes, such as spraying formic acid when alarmed, discerning nestmate from intruder by 'reading' a chemical fingerprint. Why, given *F. aquilonia*'s widespread use of chemicals, does it appear not to use them in navigation and orientation to carbohydrate food sources - as, apparently, do its relatives? A persistent chemical trail could, especially if combined with cleared zones on the ground, theoretically explain the topographic consistency of wood ants routes (Sudd, 1982). Although a life-long memory storage of learned olfactory cues has been well documented in ants (Jaisson, 1975), subtle habitat markings are unlikely to persist through the long rainy periods preceding winter, especially in Scottish woodlands (northern rain forest). Yet it has been reported that during both migration and foraging, wood ant workers with full crops have the habit of laying scent trails emanating from the hind gut (Horstmann, 1976; Elgret & Rosengren, 1977; Bhatkar, 1982; Lamb & Ollasion, 1994b). In *F. polyctena* at least, these chemical trails can be used for directing conspecific recruits to a source of food (Horstmann, 1976; Horstmann & Bitter, 1984). Foragers of *F. aquilonia* have the habit of dragging the gaster against the substrate whether the forager is replete or not (Cosens & Legge, unpublished data), this habit appears to be involuntary and thus distinct from the deposition of recruiting pheromone droplets by ants of other species (Wilson, 1962; Hangartner, 1969; Hölldobler & Wilson, 1990). Rosengren (1971) found that during the photophase of the day route fidelity to feeding places is mainly due to a memory of the position of trees and other large visual land marks: but the experiments, carried out in a very large open-air arena with movable 'trees' of natural size, showed clearly that foragers did not react to a shift in the position of trees during the night. Observations of groups of marked foragers in natural communities indicated that the route fidelity of foragers is retained at night (Rosengren, 1977b). Thus it seems route fidelity at night may be due to cues other than those used in the daylight. Olfactory cues come immediately to mind as an explanation, providing that pheromone trails indeed smell differently on different routes because each forager must be able to identify its own specific route among a number of alternatives. The question then arise is whether the same individual possesses an orienting mechanism for both nocturnal and diurnal foraging, which does appear to be the case since night and day foragers do not constitute clearly separate sub-populations (Rosengren, 1977b; Chapter 2).

It is difficult to exclude the possibility that a successful forager returning to the nest from a recently visited food source could provide orienting signals to alerted recruits (Cosens & Legge, unpublished data). In some ant species the recruitment mechanism is known to be based on pheromones and/or tactile stimuli, binding the recruiter and recruit in a tandem pair (Hölldobler, 1974; Möglich *et al.*, 1974). Tandem running has not been observed in wood ants. Yet a discoverer ant could direct recruits with a centripetally laid trail, or it could even provide directing visual stimuli based on a kinopsis or optomotor principle (Wilson, 1971; Rosengren, 1977a).

4.2 Aims of the study

The following experiments were designed to investigate aspects of orientation employed by foragers of *F. aquilonia.*

1. Nature of the mechanisms employed by foragers to direct nestmates towards novel food sites.

2. Whether or not orientation based on chemical trails laid by the foragers with full crops occurs in *F. aquilonia* ?
3. Whether the foragers use a hierarchial system of cues for orientation?

4.3 Materials and Methods

4.3.1 Typical behaviour of the discoverer ant

The behaviour of discoverer foragers that had made a first successful foray to a novel source were observed in 10 different experiments providing novel food source in each experiment.

4.3.1a Results

At the start of the experimental day and before the discovery of the food source, foragers ($\bar{x}$=19, SE=2.76) individually searched the foraging table where the food sites, to which they had become allegiant, had been located previously. Most of these foragers were marked veterans, and one of them typically discovered the novel food source within an hour (Table 4.1).

Table 4.1 Observations based on (discoverer foragers) focal individuals

Trial	Act-1 min	Act-2	Act-3 min	Act-4 min	Act-5 min	Act-6	Act-7 min	Act-8 min	Act-9 min	Act-10 min
1	37.5	15	5.8	4.1	23.5	4	3.8	16.32	35.7	162.7
2	46.35	18	4.9	5.3	43.8	5	4.1	21.35	48.3	149.3
3	51	23	6	6.3	39.5	3	2.3	17.9	51.6	139.4
4	45.7	31	4.2	4.7	35.5	5	5.1	18	39.8	125.3
5	50.3	12	5.3	4.9	29.6	6	3.9	21.2	-	-
6	48.7	17	4.8	3.9	31.2	4	4.2	15.89	-	-
7	45.65	-	4.9	-	41.5	3	4.8	16	-	-
8	-	-	6	-	39.3	2	5.1	17.23	-	-
9	-	-	7.1	-	43.7	3	2.9	15.3	-	-
10	-	-	4.8	-	29.5	4	3.8	15.7	-	-
$\bar{x}$	46.5	19	5.38	4.9	35.71	3.9	4	17.49	43.85	144
SD	4.51	6.8	0.84	0.87	6.96	1.19	0.9	2.19	7.36	15.79
SE	1.70	2.8	0.26	0.36	2.20	0.38	0.28	0.69	3.68	7.89

Act-1 -Discovery time
Act-2 -Number of searching ants found on the foraging table prior to food discovery
Act-3 -Initial feeding time of the discoverer
Act-4 -Homing time of the undisturbed discoverer
Act-5 -Deployment time (undisturbed): time between food discovery and the deployment of foragers onto the foraging table
Act-6 -Number of forays made by discoverer until general deployment
Act-7 -Re-emergence time of discoverer, as non-replete
Act-8 -Time of rediscovery of the food by discoverer ant
Act-9 -Homing time of the discoverer when relocated elsewhere on the foraging table
Act-10 -Deployment time of the disturbed situation

Typically, the first forager to locate a novel food source spent around 5 min (Table 4.1) at the food source, feeding and walking around the site. On the homeward journey when encountering a nestmate head-on, it vigorously vibrated its head and thorax or even its whole body. During this 'vibratory' movement both ants (discoverer and alerted) contacted each other with their antennae, with the discoverer usually assuming a higher position. This 'vibratory' display was frequently interrupted by trophallactic exchange by which a small amount of the gathered food was passed from the discoverer to the alerted forager. After communicating thus with a successful replete forager, the searching foragers began to search more confidently: but no direct movement towards the food source was observed. The discovering forager, once replete, returned to the nest along a less-than-direct route. Her homing time was around 5 min (Table 4.1). Upon arrival on the nest surface, no detectable behaviour was observed other than hungry nest mates drawn to her for food. The discoverer ant re-emerged as non-replete within 4 min (Table 4.1) and, pertinently, she was not followed by other nest mates when returning to the food as observed in *Camponotus socius* by Hölldobler (1971). This particular discoverer ant had difficulty in relocating the food, taking around 18 min and this was different from the mean homing time (5 min). She searched in the vicinity of the food source prior to rediscovery, this implied that the particular forager had knowledge only of the general whereabouts of the food but not the precise location of it. On a few occasions rediscovery of the food source occurred by a different route from the initial one, even after running along the initial route and descending back to the foraging table. Even after successfully finding the food source, she was not confident of her route. Observations like these imply that a forager is spatially aware and is able to translate distances and directions according to an accurate mental template (Cosens & Toussaint, 1985). In other words she has a sense of her position within the habitat (Jander & Voss, 1963). It was clear that foragers were deployed in significant numbers only after a food source had been discovered. After the discovery of food by a single forager (36 min, see Table 4.1) a few other foragers arrived on the foraging table in the zone where they had been fed in previous experiments (Chapter 1), and began to search. By this time the discoverer had made a few forays (4) (see Table

4.1). Subsequently the number of foragers at the bridge (which they used to access the foraging table) increased from 19 to 76 within an hour. The majority of the deployed ants made no attempt to locate the food source, rather they ran forward and backward on the bridge, frequently clustered together and sometimes they returned to the nest. Observations such as these imply that the discovering foragers had not marked the route on their homeward journey. On four separate occasions the replete discoverer ant was removed from the site, relocated and then her subsequent behaviour was monitored. She ran around the table, pausing intermittently to trophallax with other ants and finally returned to the nest after some 44 min (see Table 4.1). This was significantly different from the undisturbed discoverers' homing time (5 min). In this case where the discoverer is relocated from the food source, the deployment of foragers occurred some 2.5 h after the discoverer had returned to the nest: this delay time was significantly higher than the undisturbed deployment time (see Table 4.1). The delay may have been due to the fact that the food entered into the nest in irregular small amounts carried by the relatively unexcited foragers that had trophallaxed with the discoverer ant and had no knowledge of the actual site of the food. Hence the stimuli bought to the nest in this way may have been well below the response threshold levels required for the forager deployment. An alerting signal inside the nest provided by a properly excited ant is clearly important to initiate forager deployment (Vowles, 1955; Möglich & Hölldobler, 1975; Cosens & Toussaint, 1985) and Legge (1991) clearly demonstrated that for *F. aquilonia* the alerting and directing signals are distinct from each other.

None of the following experiments managed to show the spots observed by Lamb and Ollason (1994b) said to appear on the papers over which a large number of replete foragers had walked during a single trial extending over several days. While faecal deposits from the hind gut of foragers have been identified as a possible source of marker in wood ants (Rosengren, 1977b), the occurrence of those faecal deposits would require to be more frequent and to be left only by replete foragers if they are to act as a directional trail. The same argument applies to the material groomed from antennae and mouth parts and collected in the infrabuccal sac from which it is ejected as a dark pellet some 0.3 mm in diameter (Cosens, unpublished data). Foragers clearly use these pellets as markers of foraging activity, but they are not left with any directional intent and their sign-posting role only develops with foraging activity at a frequently visited site. In the context of the topographic tradition (Rosengren, 1977a) they would clearly act to reinforce the foragers' confidence in their route. In the experiments repeated here, only after the model tree and food source had been left *in situ* for two or three days did infrabuccal pellets ($\bar{x}$ diameter =0.27 mm, SE=0.015, N=36) become obvious. Hence it can be concluded that over time faecal and other deposits will mark well used routes (Rosengren & Fortelius, 1987), but that they are unlikely to be effective during the initial orientation (recruitment) to a novel food source. A comparative study has revealed that in many species, ants do not defecate randomly but preferably at specific locations including certain limited areas inside the nest, the peripheral nest borders, garbage dumps and trunk trails leading to permanent food sources or connecting two nest entrances. These disposal areas seem to be ideally suited to serve as chemical cues in home range orientation, and this has been demonstrated in a number of species (Hölldobler, 1971, 1974).

4.3.2 Do *Formica aquilonia* foragers follow chemical trails? (Wooden bridge experiment)

A diamond shape bridge (Figure 4.1) was constructed for the foragers to reach the sugar dish: four pieces of wood, each 100 cm long and 2 cm wide were put in place a week before the experiments and washed prior to each trial.

The traffic count on each bridge was taken for an hour. Then the bridge with highest traffic count towards the homeward direction was replaced with clean wood pieces of the same dimensions. This procedure was repeated replacing alternate bridges with new ones on an hourly basis for 3 or 5 hours. This wooden bridge experiment was performed with colony 1.

If foragers follow a chemical trail laid by replete foragers on their homeward journey to direct recruits to exploit a novel food source, when abusing these chemical trails by replacing a high homeward traffic bridge with a clean bridge, a reduction in siteward traffic on that bridge, compared to the other bridge should be observed.

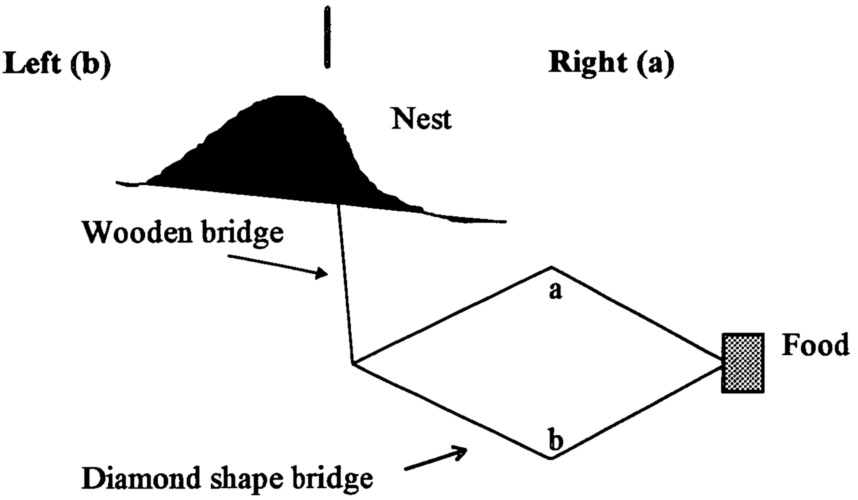


Figure 4.1 Experimental set up of the 'diamond' shape wooden bridge

4.3.2a Results

In the above experiment a reduction of siteward traffic was not observed and bridge 'b' was always the preferred bridge (Table 4.2).

Table 4.2 Percentage traffic counts on wooden bridges

	Bridge (a)						Bridge (b)					
Trial	1		2		3		1		2		3	
time (h)	+	-	+	-	+	-	+	-	+	-	+	-
1	12	10	3	4	40	80	88	90	97	96	60	20
2	9	29		3	**43**	**83**	**91**	**69**	**98**	**97**	56	17
3	**8**	**9**	**1**	**2**	36	65	92	91	99	98	**64**	**35**
4	16	19	0	2	**36**	**79**	**84**	**86**	**100**	**98**	64	21
5	**14**	**16**	**2**	**2**	42	78	86	84	99	98	**95**	**22**

Direction to site (+), from site (-)
All the traffic counts are percentages
Numbers which are bold represent the traffic count on the clean bridges
This experiment was performed with Colony 1

This may have been because the system was set up a week before the experiment, hence a previously stored topographic template may have overridden the use of chemical cues. Foragers learn to associate the location of food and nest with the possible visual cues rather than to rely on chemical cues. Old, veteran wood ant foragers do indeed maintain a surprisingly persistent site allegiance based on hierarchy of individually remembered topographic cues (Rosengren & Fortelius, 1986).

However they do not appear to depend on any chemical cues as the sole cue for orientation when being recruited to the food source. According to Wehner (1981) insects are certainly able to form visual spatial memories. The landmark map built up by the insect must allow for navigation by a temporal succession of known visual panoramas. This map does not provide the insect with a complete representation of all landmark cues within a certain distance from the nest. In many cases, the 'familiar area' map is only characterised by a few lines through the insect's habitat along which the insect awaits a certain sequence of memory pictures. More than one sequence of pictures can be memorised. So in the above experiment, foragers may have used a visual landmark map to locate the food and nest on their foraging trips. It is the horizon's skyline that most effectively determines the location of nest in most insects (Wehner, 1981).

4.3.3 Paper bridge experiment

This experiment was designed to eliminate visual cues associated with the experimental set-up: a) by covering the walls of the foraging table with white cloths and b) reducing the effective use of any previously stored topographic cues by setting up the experiment immediately before the experimental trials.

Among ants in general, trail laying and recruitment are likely to be experimentally detectable when the colony is hungry and food of relatively high quality is discovered (Wilson, 1962; Hangartner, 1969; Hölldobler, 1974; Cosens & Toussaint, 1985 & 1986; Rosengren & Fortelius, 1987). Hence the Colony was subjected to a 24 h starvation period before each experimental trial. Pertinently food deficit draws out inexperienced foragers that being less confident of topographic and other cues, are most likely to rely on a chemical trails (if present) for orientation. All the artificial trees, guide posts and possible visual material were removed from the foraging table and the entire foraging table was surrounded with white cloths and illuminated uniformly with a fluorescent tube from the ceiling. The 'diamond shape bridge' (Figure 4.1) was constructed from white paper strips 100 cm long and 2.5 cm wide since the chemical trails are laid as faecal deposits (Lamb & Ollason, 1994b) and should thus be easily seen. The experiment was performed initially without surrounding the walls of the foraging table with cloths (with visual cues). Each trial was carried out by constructing the 'diamond shape paper bridge' at the opposite end of the table and replacing the bridge with highest homeward traffic with clean paper bridges on an hourly basis. Observations were made once the first forager had located the food. When replacing the bridges all the ants on the bridges were removed. This experiment was performed with a new colony (Colony 2) and in a different location (insectry) from the wooden bridge experiment (laboratory 1) and the results are shown in Table 4.3.

4.3.3a Results

Lamb and Ollason (1994b) in their experiments managed to get the traffic count without provisioning the food source in the novel sites.

In the experimental trials reported here foragers did not deploy until food was discovered: nor did they search the paper bridges even though the colony was in food deficit for 24 h.

Two experimental days elapsed before the first forager discovered the food (48 h food deficit). Foragers were always searching on the foraging table where they had been fed in previous experiments. Food was always provided at 9.30 am.

None of these experimental trials showed that *F. aquilonia* foragers mark their routes to novel food sources using specific pheromones. If they had marked the route a reduction of traffic should have been observed on clean bridges compared to the non-clean bridges. The data clearly refute this supposition: the use of a clean bridge did not alter the traffic on either route (a) or route (b) (Table 4.3). As the foraging table was surrounded with featureless white cloth some unidentified cues (internal references) may have been used in the above experimental trials. In trial 1 (without visual cues) when replete foragers were leaving the site, they always ran half way through the bridge 'a' before finally resorted to the bridge 'b'. Observations like this imply that they used some kind of internal reference with respect to the external guide (non-chemical cue). Hölldobler (1974) conducted a similar sort of experiment with *Camponotus sericeus* in an environment devoid of visual cues and found a pheromone marked bridge is always preferred by the foragers. However, in an environment with obvious visual cues, foragers showed an equal preference for (use of) bridges with and without pheromone marked trails. The results reported here are consistent with those obtained using tree rotation experiments (Cosens and Toussaint, 1985).

Table 4.3 Percentage traffic count on bridges

4.3.1 Trial 1 with visual cues

	Bridge (a)		Bridge (b)	
Time (h)	+	-	+	-
1	32.1	40.4	67.9	59.6
2	10	40	**90**	**60**
3	**8.5**	**39.4**	91.5	60.6

4.3.2 Trial 2 with visual cues

1	38.5	35	61.5	65
2	38.5	41.5	**61.5**	**58.5**
3	**35.3**	**40.8**	64.7	59.2

4.3.3 Trial 1 without visual cues

1	62	60.9	38	39.1
2	**50**	**52.3**	50	47.7
3	35.8	54.4	**34.2**	**45.6**

4.3.4 Trial 2 without visual cues

1	12.5	25	87.5	75
2	45.1	30.2	**54.9**	**69.8**
3	30.2	38.4	**69.8**	**61.6**

Direction to site (+), from site (-)
All the traffic counts are percentages
Numbers which are bold represent the traffic count on the clean bridges
In the trial 4.3.4 instead of replacing alternate 'bridge' on 3rd hour, replaced the same 'bridge' which was used on 2nd hour

4.3.4 Rotation of a food site within a featureless foraging arena

This experiment was adopted from Möglich & Hölldobler (1975) and Legge (1991), it involved rotation of a foraging set-up on the foraging table. The experimental set-up (Figure 4.2) was made of a central pad (41 cm in diameter) with an 18 cm diameter hole in the middle through which the foragers obtain access to it. The central pad was held by four branches (12 cm in length) which attached to the top of a wooden trunk (100 cm in height) which could be rotated on a basal pad (14x14 cm^2) using the lower branches. The central pad was divided into four equal sectors labelled: ‘A’, ‘B’, ‘C’ and ‘D’, and each sector was provided with a Petri dish (1.5 cm in diameter). The Colony was unfed for a 17 h period and possible visual cues were excluded by surrounding the foraging table with white featureless cloth. The food (10% w/v sugar solution) was always positioned on sector ‘D’ throughout the experiment, and the other three positions were supplied with water. At the beginning of each trial, foragers were trained for 90 minutes (control situation) before the set-up was rotated.

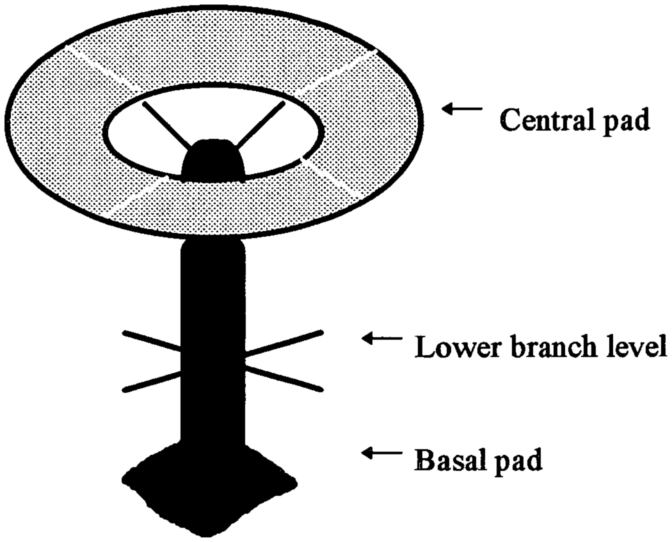


Figure 4.2 Experimental set up for the featureless foraging arena

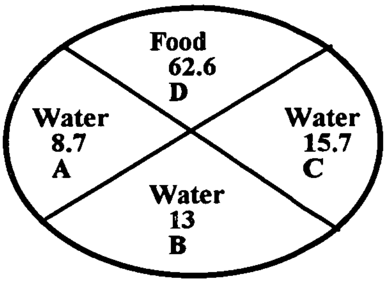
4.3.4a Results

In the control situation a significant number of foragers initially orientated into sector ‘D’ (x^2=58.3 df 3 $P<0.05$). When the set-up was rotated through 180^0 a significant number of the foragers initially orientated into sector ‘B’ which became the spatial position compared to the control situation (x^2=98.1 df 3 $P<0.05$).

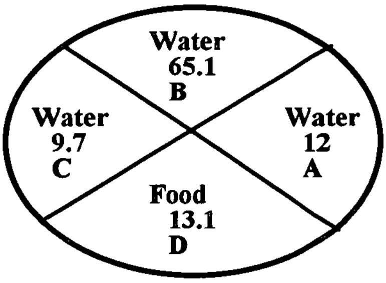
When the system was rotated through 90⑤ the foraging population was split into sectors ‘A’ & ‘C’ (x^2=0.54 df 1 $P>0.05$) (Figure 4.3; Table 4.4): there was no significant difference between the numbers of foragers at sectors ‘A’ and ‘C’. These results imply that the foragers preferred a spatially positioned sector where they expected to find food and did not orientate to the sector bearing food: it is clear that that sector had not been marked during the initial training period.

Figure 4.3 Orientation of foragers into the different sectors of the foraging arena.
Percentages of the total population based on the mean number of foragers (n=3 replicate trials) that initially orientate to the particular sector during the initial 15 min period (see also Table 4.4).

Stage 1 Control



Stage 2 The system was rotated by 180^0



Stage 3 The system was rotated by 90^0 with respect to stage 2

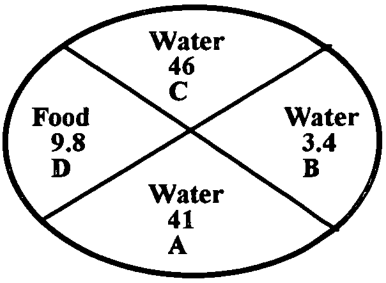


Table 4.4 The numbers of foragers at the different sectors (clockwise from training) of the foraging set-up

Stage	Spatial sector 0^0	90^0	180^0	270^0	Σ
1	D 72 (62.6)	C 18 (15.7)	B 15 (13)	A 10 (8.7)	115
2	B 114 (65.1)	A 21 (12)	D 23 (13.1)	C 17 (9.7)	175
3	C 80 (46)	B 6 (3.4)	A 71 (41)	D 17 (9.8)	174
Σ	266	45	109	44	

Numbers represent the means of three trials. Numbers in brackets are percentages.

4.3.5 Do *F. aquilonia* foragers use a hierarchical system of cues for orientation?

Demonstrating the non-use of chemical trails for recruitment to novel, static self-renewing (predictable) food sources begs the question: what cues are used by *F. aquilonia* in such orientation behaviour; particularly because the foragers display directionality in their forays. Thus an experimental design was adopted from Fourcassiè & Beugnon (1988) who, contrary to Cosens & Toussaint, (1985) with *F. aquilonia,* demonstrated that *F. lugubris* foragers apparently do rely on chemical cues for orientation in the horizontal plane. Could the behaviours of two species of closely related wood ants living in coniferous forests be different? Foraging wood ants persist in returning to sites at which they were previously rewarded (site allegiance). This persistence could be achieved through memorisation of a three dimensional route based upon idiothetic (kinaesthetic) and/or (external) cues. In this experiment an attempt was made to identify the exact nature of such cues and how they interact with, and substitute for, each other.

Both Colonies 2 and 3 were maintained in an artificial 12 h light/dark cycle at 25^{0}C were used in these experiments. The experimental set-up comprised a vertical uniform, wooden trunk 1 m high, topped by a horizontal 'cross shaped' bar forming four branches at right-angles, each 30 cm long. On the outer end of the each branch a wooden platform (75 x 75 mm^2) was attached onto which a Petri dish was placed. The use of tropographic cues was excluded by surrounding the foraging table with white cloth. Except when specified , the system was permanently illuminated from the left side by a 100 W directed light source. Prior to each experimental trial the colony was starved for 36 hours. Each trial was preceded by one hour of training during which the Petri dish on platform 'a' at spatial position 'A' (Figure 4.4.1) was provisioned with standard 10% sugar solution, the other Petri dishes were filled with an equal amount of water. Thereafter all foragers were removed from the system. There were eight 20 min or 15 min experimental periods per trial. Food was always positioned at spatial position 'A.' As soon as the foragers climbed over the line which was drawn on the vertical trunk 15 cm below the horizontal cross shaped bar, they were each followed until they reached the extremity of the one of the four branches or alternatively, turned around and returned to the nest. In order to monitor a forager's route each branch was divided into 5 equal sections these were labelled in order (1-5) from the trunk. The side of the trunk (left or right) up which they had travelled was recorded also. When recording which side of the trunk they ascended, the criterion side was that used to pass the 15 cm mark on the trunk, afterwards they might turn around and take the other side (left or right). Colony 2 was tested initially followed by Colony 3 which was housed in the observation nest (Figure 2.1) which was placed on the foraging table. There were three experimental trials with Colony 2 and two experimental trials with Colony 3. Each experimental period lasted 20 min with Colony 2 and 15 min with Colony 3, due to the large number of foragers involved in the foraging at each trial. Results of experimental trials with Colonies 2 and 3 are shown in Figures 4.4.1 & 4.4.2. Some of the replete ants were carried to the nest by the other foragers was observed in each trial with Colony 3. Then Colony 3 was trained as described, but after the preliminary training session, only the experimental period 1 (control), period 6 (chemical cues were rotated by 180^0) and part 7 (directional cues were rotated by 180^0) were performed. Results of this experimental trial are shown in Figure 4.4.3.

For the each experimental trial, the following protocol applied;

1. Side of the vertical trunk they had ascended.
2. Initial Orientation of the ant (IO)
   Branch reached immediately after arriving at the top of the trunk.
3. Final Orientation of the ant (FO)
   The extremity of the branch the ant eventually reached.

Although the same experiment was replicated, since the foraging populations from different colonies are essentially different from each other the experimental results were treated independently.

4.3.5a Results

Period 1 (Figures 4.4.1 & 4.4.2)

Have the foragers of *F. aquilonia* learnt the spatial position of the food source ?

A significantly higher number of foragers initially and finally oriented into the spatial position 'A' at the extremity of branch 'a'(Table 4.5). So the spatial position 'A' at the extremity of branch 'a' has been associated with the presence of the food.

Table 4.5 Control situation

	Foragers ascended on the illuminated left side											
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
	77	23.2	1	<0.05	82	40.9	1	<0.05	66.7	14.3	1	<0.05
	Foragers orientated onto branch 'a' at spatial position 'A'											
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
IO	62.6	63.2	3	<0.05	59	87.3	3	<0.05	46.5	54.7	3	<0.05
FO	76	125.9	3	<0.05	65	117.7	3	<0.05	56.6	115.7	3	<0.05

x^2 = Chi square df = Degrees of freedom P = Probability level IO = Initial Orientation FO = Final Orientation % Percentage value

What cues are involved in the orientation ?

In order to identify the presence of internal cues (kinaesthetic) and external cues, the directional light source was switched off and the experimental set up was washed clean with 70% alcohol and air dried. Then the experimental set-up was:

1. Uniformly illuminated from above (Period 2; Table 4.6).
2. Kept in the dark and the foragers observed in dim light (Period 3; Table 4.7).

Period 2 (Figures 4.4.1 & 4.4.2)

Table 4.6 Uniformly illuminated from the ceiling

	Foragers ascended on the left side of the trunk											
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
	68.3	10.9	1	<0.05	82.3	40	1	<0.05	-	-	-	-
	Foragers orientated onto branch 'a' at spatial position 'A'											
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
IO	51.4	75.8	3	<0.05	50	63.4	3	<0.05	-	-	-	-
FO	51.4	110.9	3	<0.05	55.2	86.2	3	<0.05	-	-	-	-

The absence of a directional light and chemical cues did not result in any significant alteration in the distribution of foragers on the tree compared to the control situation (Tables 4.5, 4.6 & 4.7; see also 4.13 & 4.14): most went to the branch with the food (branch 'a').

Period 3 (Figures 4.4.1 & 4.4.2)

Table 4.7 In the dark

	Foragers ascended on the left side of the trunk											
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
	52.7	0.12	1	<0.05	85	39.2	1	<0.05	-	-	-	-
Foragers orientated onto branch 'a' at spatial position 'A'												
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
IO	40	25.3	3	<0.05	48.9	82.9	3	<0.05	-	-	-	-
FO	50.7	68.3	3	<0.05	60	74.5	3	<0.05	-	-	-	-

These results obtained in the dark show that foragers do use internal references when orientating to food sources in accord with the idea of 'spatial awareness' as proposed by Cosens and Toussaint (1985). This point was showed too by the results of the uniformly illuminated tree in that at the tree top no directional cue was provided by the light source. When considering the side of the tree which foragers ascended to the tree top, Colony 2 was behaving differently in period 2 & 3. This difference in behaviour may have been due to the increase complexity of foraging trail of Colony 2 compared to that of Colony 3.

Directional light and chemical cues ?

The next step was to find out whether foragers use both cues independently or simultaneously when they are present. Period 4 examines the effect of a directional light in the absence of chemical cues, and Period 5 the effect of chemical cues in the absence of the directional light on the foragers' ability to orientate on the tree.

Period 4 (Figures 4.4.1& 4.4.2)

A significantly higher number of foragers ascended on the illuminated side of the trunk and initially and finally oriented in to branch 'a' at spatial position 'A' in the absence of chemical cues (presence of directional light cue).

Table 4.8 Effect of a directional light cue in the absence of chemical cues: tree washed with 70% alcohol and air dried after the training period

	Foragers ascended on the illuminated left side of the trunk											
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
	70	14.4	1	<0.05	85.6	45.5	1	<0.05	-	-	-	-
Foragers orientated onto branch 'a' at spatial position 'A'												
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
IO	46.7	43.3	3	<0.05	61.1	67.9	3	<0.05	-	-	-	-
FO	63.3	127.4	3	<0.05	76.7	143.7	3	<0.05	-	-	-	-

Period 5 (Figures 4.4.1 & 4.4.2)

Table 4.9 Effect of chemical cues in the absence of a directional light cue:
the tree was not washed clean after the training period

	Foragers ascended on the left side of the trunk											
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
	62.5	8	1	<0.05	83.5	40.1	1	<0.05	-	-	-	-
Foragers orientated onto branch 'a' at spatial position 'A'												
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
IO	50.8	65.2	3	<0.05	51.6	58.5	3	<0.05	-	-	-	-
FO	68	165	3	<0.05	59.3	88.5	3	<0.05	-	-	-	-

When Periods 4 (no chemical cues) and 5 (no directional light cue) are compared with Period 2 (no directional light or chemical cues), the distribution of foragers on the tree is essentially similar (with two colonies: Figures 4.4.1 & 4.4.2), and the same as that observed during the control Period 1.

Events observed when the directions indicated by two types of cue were opposed

Periods 6 and 7 were designed to identify if there is a preference for one of the two types of cues when both are available at the same time. In these two experiments one of the directional cues was moved while the other remained in the same spatial position and foragers were forced to choose between them.

Period 6 (Figures 4.4.1 & 4.4.2)

Table 4.10 Rotation of the chemical cues through 180^0 after training, branch ‘c’ comes into spatial position ‘A’, directional light from left side as before

	Foragers ascended on the illuminated left side of the trunk											
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
	74.7	28.3	1	<0.05	87.8	51.4	1	<0.05	68.6	16.4	1	<0.05
Foragers orientated onto branch ‘c’ at spatial position ‘A’; x^2 for chemical and spatial branches												
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
IO	53.3	36.5	1	<0.05	58.9	42.4	1	<0.05	67.8	61.2	1	<0.05
FO	60.7	50.9	1	<0.05	67.7	50.9	1	<0.05	71.1	75.4	1	<0.05

Foragers preferred the illuminated left side of the trunk when moving upwards in the vertical plane and orientating in the horizontal plane to the spatial position now occupied by branch ‘c’ in contrast to the findings of Fouracassiè and Beugnon (1988). These results clearly show that *F. aquilonia* foragers do not primarily depend on chemical cues for directional orientation in vertical and horizontal planes. Rather, they show a clear preference in their initial (IO) and final orientation (FO) for the spatially positioned branch: the location of which may be learned from a directional, visual light cue.

Period 7 (Figures 4.4.1& 4.4.2)

Period 7 examined this latter point: the system remained *in situ* and unwashed after the training period but the directional light source was rotated by 180^0 to illuminate the tree from the right side. This would cause foragers using the light cue and approaching the trunk from the illuminated side to confuse branch ‘c’ for branch ‘a’ and spatial positions ‘C’ and ‘A’ (Table 4.11).

When moving upwards foragers preferred the illuminated side of the trunk. And, in the horizontal plane they preferred branch ‘c’ in the apparent spatial position relative to the directional light cue. Thus, according to the results obtained from Periods 5, 6 and 7 *F. aquilonia* foragers rely mainly on visual cues (here a directional light) if available to them when orientating on vertical and horizontal planes: unlike *F. lugubris* foragers which apparently depend on the chemical cues when orientating in the horizontal plane. Although the two species are closely related, results obtained from the above experiment indicate a distinct difference between the two species in this regard.

Table 4.11 Rotation of the directional light cue to the right side of the tree

	Foragers ascended on the left side of the trunk											
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
	23	38.5	1	<0.05	14.1	43.8	1	<0.05	35.5	8.98	1	<0.05
Foragers orientated onto branch 'c' at spatial position 'C'; x^2 for chemical and spatial branches												
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
IO	64.8	64.7	1	<0.05	64.7	39.4	1	<0.05	84	76	1	<0.05
FO	73.6	75.5	1	<0.05	74.1	54.6	1	<0.05	87.9	82.7	1	<0.05

Period 8 (Figures 4.4.1 & 4.4.2)

Period 8 completes the sequence: the directional light cue remained as during Period 7 (from the right) and the system was rotated through 180^0 so both types of cue directed foragers to the spatial position 'C' (branch 'c') (Table 4.12).

No increase of the values of percentage maintenance of the orientation in the horizontal plane was observed compared to Period 7: values for the Periods 7 and 8 are summarised in Table 4.13. Supplementing the directional light cue with chemical cues did not alter positively the percentage maintenance of orientation in the horizontal plane as would be expected if the chemical cues have a effect, with directional cue.

Table 4.12 Overlapping of chemical and directional cues

	Foragers ascended on the left side of the trunk											
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
	33.6	12.4	1	<0.05	18.9	36.6	1	<0.05	-	-	-	-
Foragers orientated onto branch 'a' at spatial position 'C'; x^2 for 'a' and 'c' branches												
	Colony 2				Colony 3				Colony *3			
	%	x^2	df	P	%	x^2	df	P	%	x^2	df	P
IO	62.3	44.8	1	<0.05	67.8	45.6	1	<0.05	-	-	-	-
FO	68.4	61.7	1	<0.05	73.5	61	1	<0.05	-	-	-	-

Table 4.13 Orientation in the horizontal plane

(Colony 2)

Period of the experiment	Branch	Spatial position	Available cues	Number reached to the top	Final orientation	MO %
1	'a'	A	CC+DC	75	57	76
2	'a'	A	LC	74	38	51.4
3	'a'	A	None	75	38	50.7
4	'a'	A	DC	90	57	63.3
5	'a'	A	CC+LC	128	87	68
6	'a'	C	CC	122	9	7.4
	'c'	A	DC		74	60.7
7	'a'	C	DC	125	92	74
	'c'	A	CC+LC		6	4.8
8	'a'	A	None	114	6	5.3
	'c'	C	DC+CC		78	68.4

(Colony 3)

1	'a'	A	CC+DC	100	65	65
2	'a'	A	LC	96	53	55.2
3	'a'	A	None	80	48	60
4	'a'	A	DC	90	69	76.7
5	'a'	A	CC+LC	91	54	59.3
6	'a'	C	CC	90	9	7.4
	'c'	A	DC		61	67.7
7	'a'	C	DC	85	63	74.1
	'c'	A	CC+LC		3	3.5
8	'a'	A	None	87	1	1.2
	'c'	C	DC+CC		64	73.5

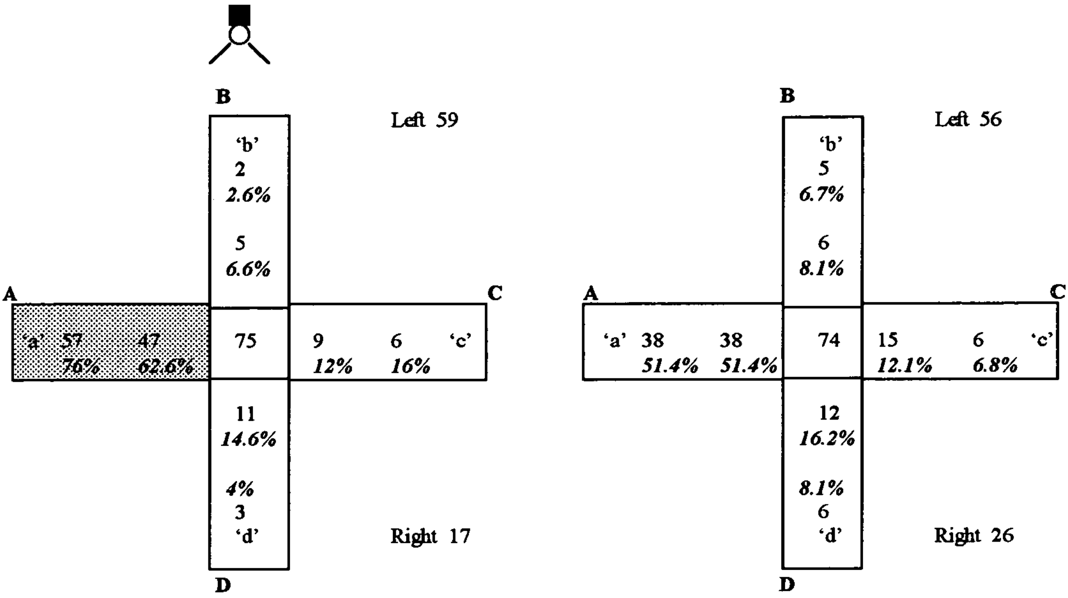
(Colony *3)

1	'a'	A	CC+DC	128	73	65
6	'a'	C	CC	118	3	2.5
	'c'	A	DC		84	71.1
7	'a'	C	DC	107	94	87.9
	'c'	A	CC+LC		4	3.7

MO	Percentage maintenance of orientation (Number of ants reach to the final part of the branch/Number of ants reach to the top of the tree X 100)
CC	Chemical cues
DC	Directional cues based on directional light
LC	Cues based on ceiling light
None	No cues

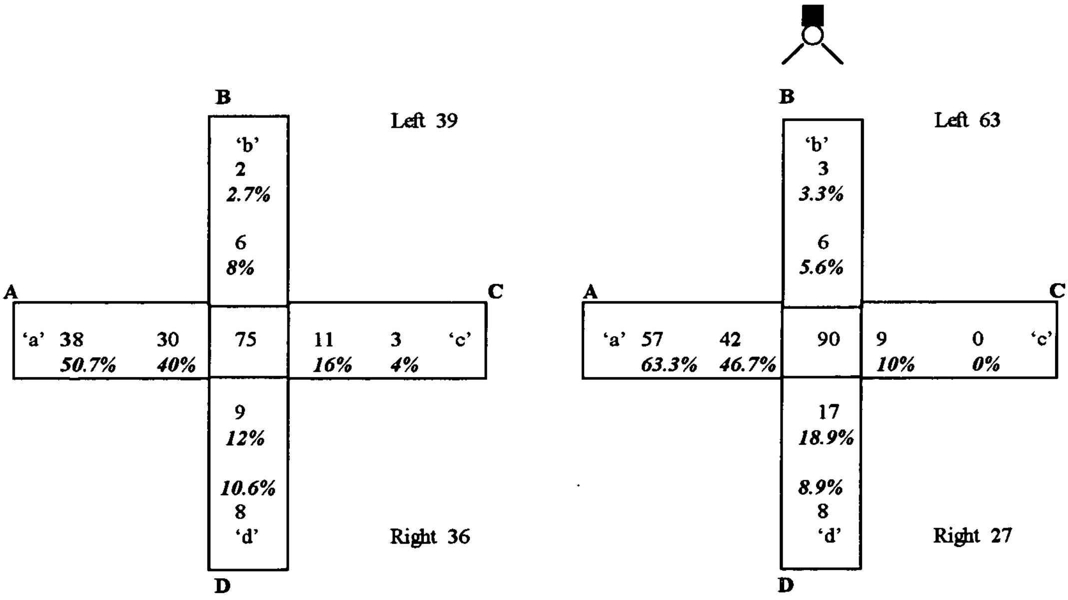
'a', 'b' 'c' & 'd' are the arms of the "cross shaped" bars

Figure 4.4.1 Orientation: distribution of foragers on different branches, Colony 2.
Food was always at spatial position A; Left & Right = side of trunk; Bold italicised numbers = % IO & FO onto each branch; Other numbers = mean numbers of foragers (N=3); shaded portion = 'chemically marked' branch; A, B, C, D = spatial positions; 'a' 'b' 'c' 'd' = branches.



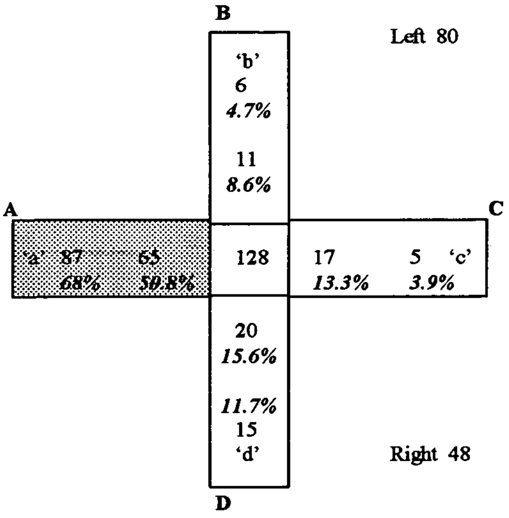
Period 1 (control)
Chemical cues & Directional light cue

Period 2
No Chemical cues
No Directional light cue, Ceiling light only

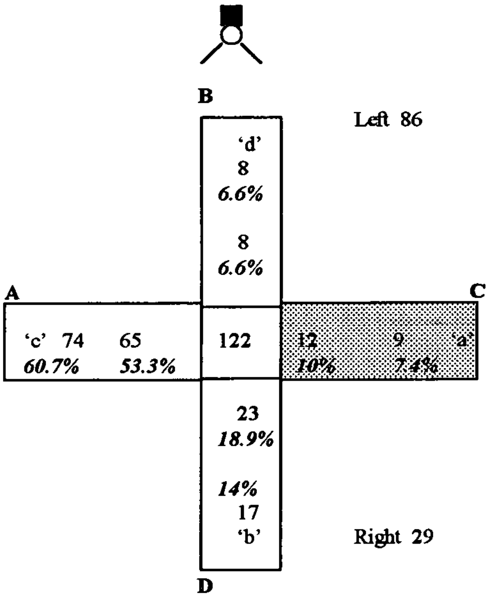


Period 3 (In the dark)
No Chemical cues
No Directional light cue

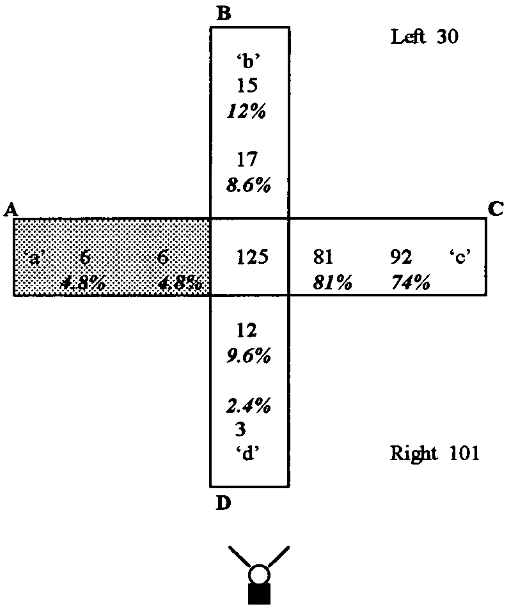
Period 4
No Chemical cues
Directional light cue only



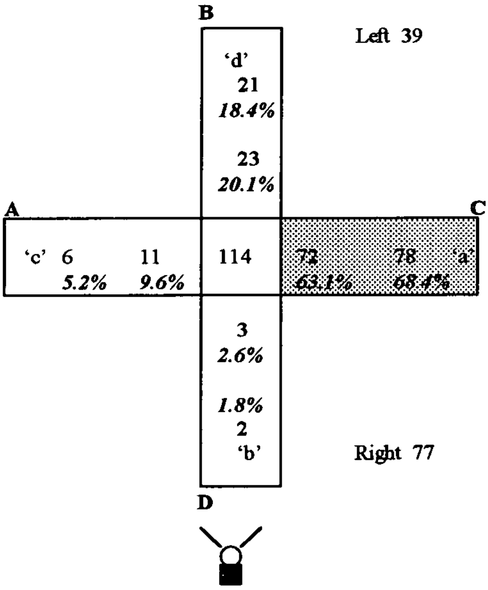
Period 5
Chemical cues only
No directional light cue



Period 6
Chemical cues rotated by 180^0
Directional light cue

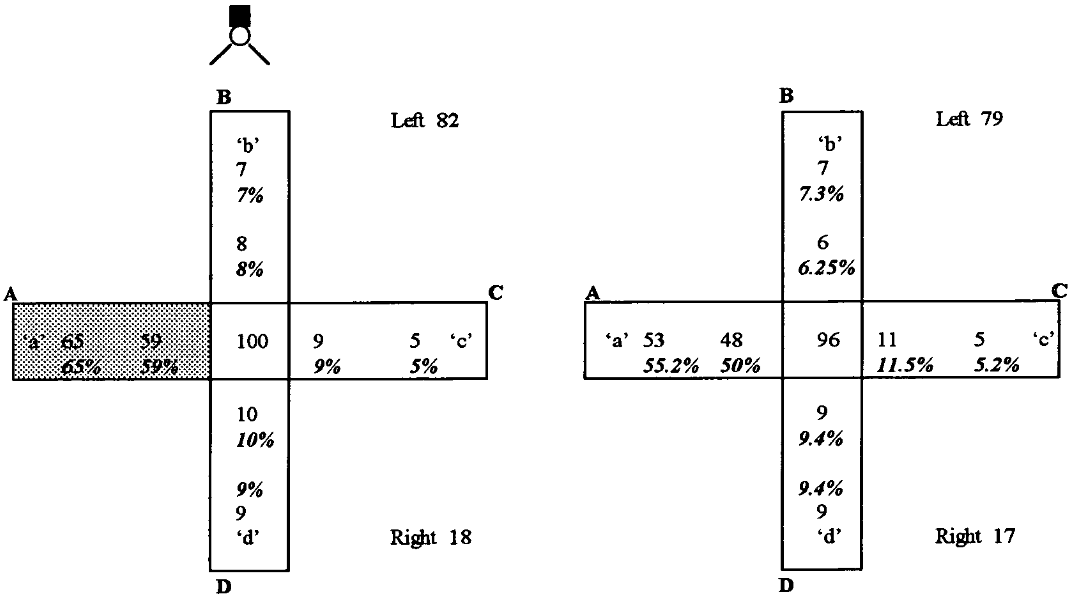


Period 7
Chemical cues
Directional light cue rotated by 180^0



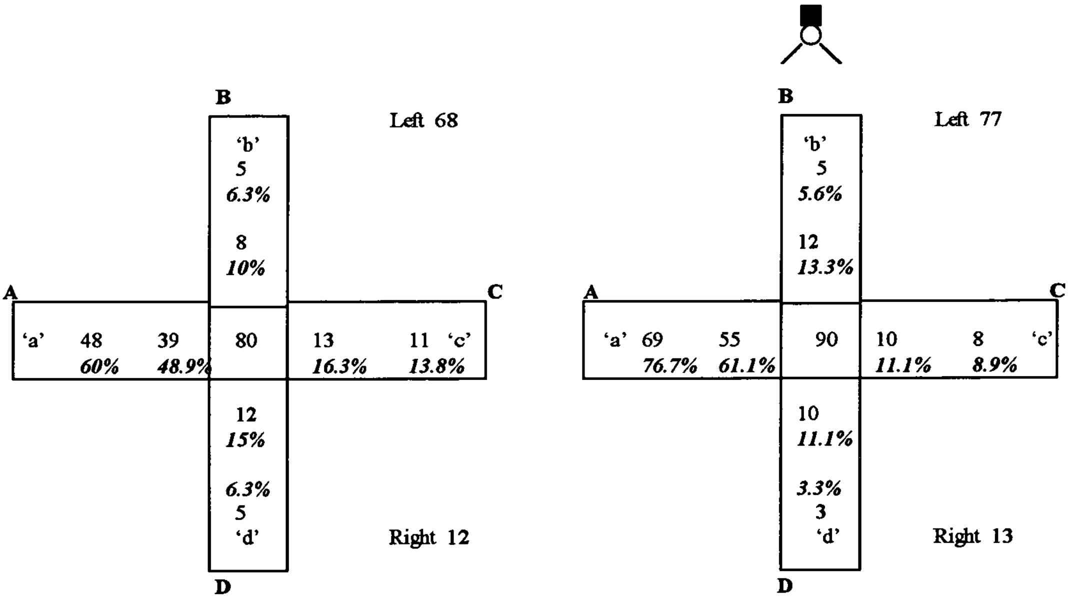
Period 8
Branch 'a' with chemical cues rotated by 180^0
Branch 'c' was washed clean, Directional light cue from Right side

Figure 4.4.2 Orientation: distribution of foragers on different branches, Colony 3.
Food was always at spatial position A; Left & Right = side of trunk; Bold italicised numbers = % IO & FO onto each branch; Other numbers = mean numbers of foragers (N=2); shaded portion = 'chemically marked' branch; A, B, C, D = spatial position; 'a' 'b' 'c' 'd' = branches.



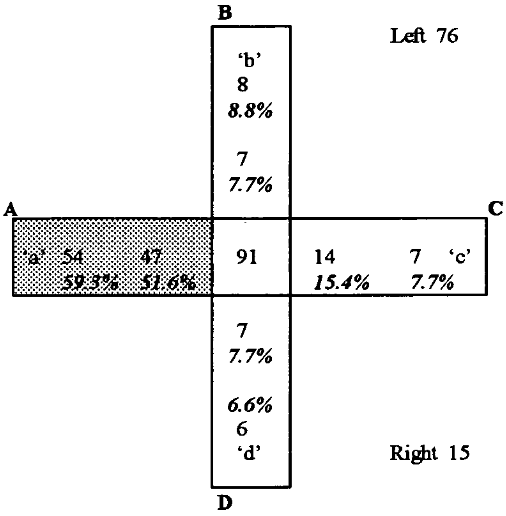
Period 1 (control)
Chemical cues & Directional light cue

Period 2
No Chemical cues
No Directional light cue, Ceiling light only

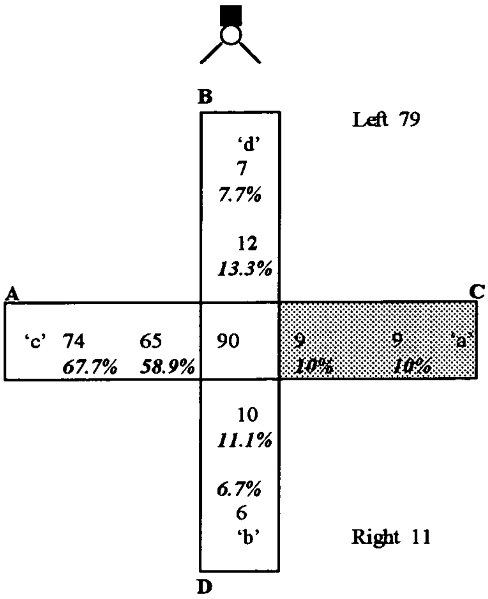


Period 3 (In the dark)
No Chemical cues
No Directional light cue

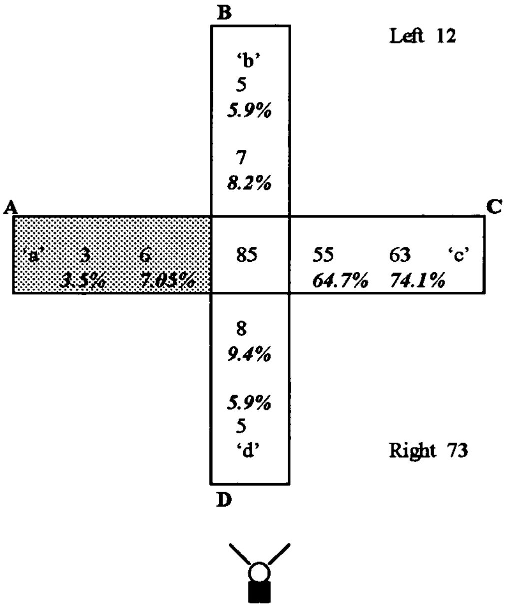
Period 4
No Chemical cues
Directional light cue only



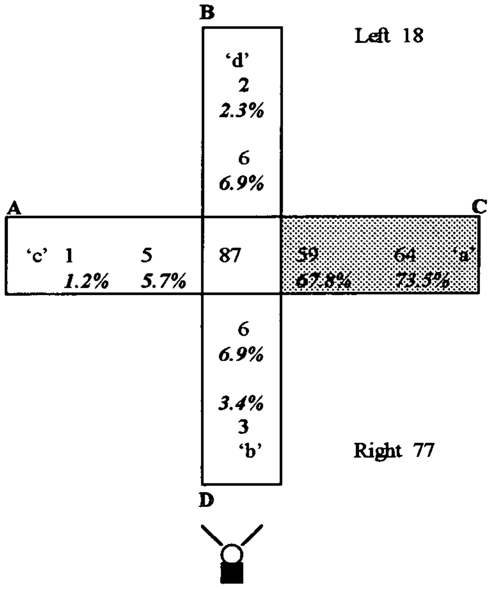
Period 5
Chemical cues only
No directional light cue



Period 6
Chemical cues rotated by 180°
Directional light cue

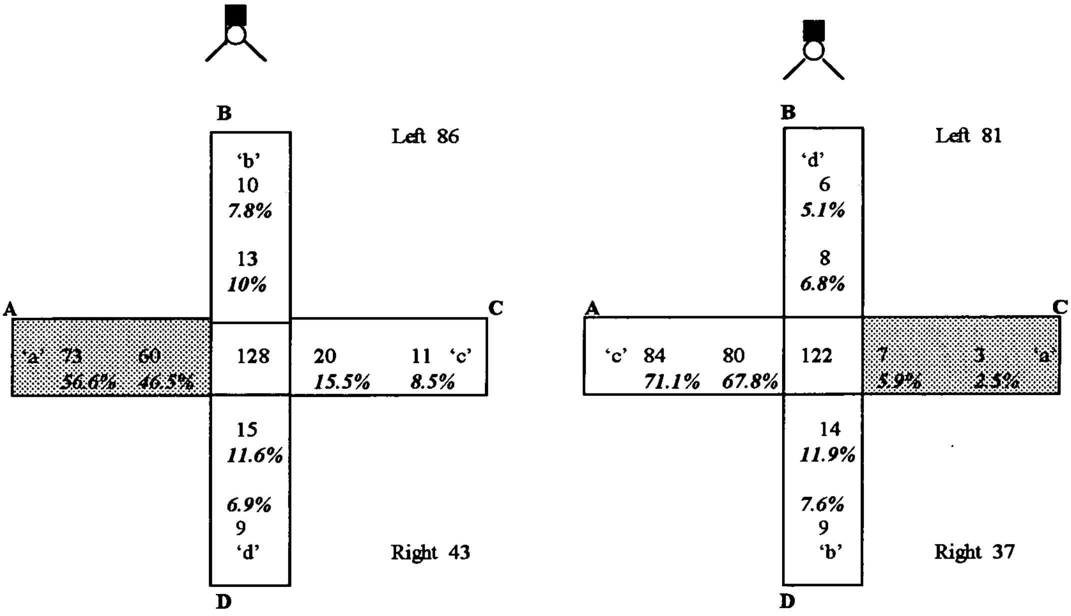


Period 7
Chemical cues
Directional light cue rotated by 180°



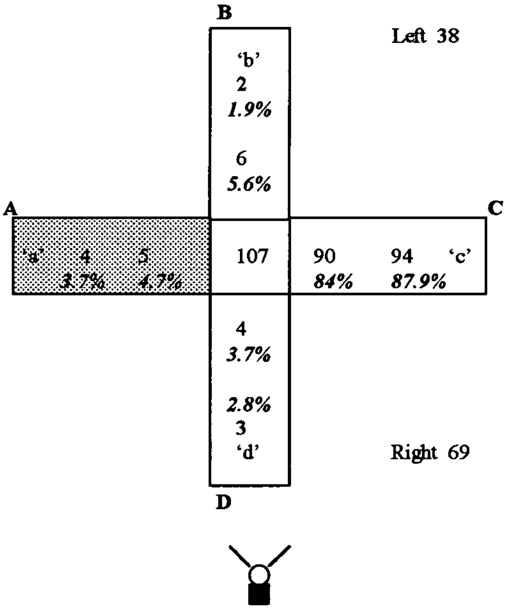
Period 8
Branch 'a' with chemical cues rotated by 180°
Branch 'c' washed clean, Directional light
cue from Right side

Figure 4.4.3 Orientation: distribution of foragers on different branches, Colony *3.
Food was always at spatial position A; Left & Right = side of trunk; Bold italicised numbers = % IO & FO onto each branch; Other numbers = mean numbers of foragers (N=2); shaded portion = 'chemically marked' branch; A, B, C, D = spatial positions; 'a' 'b' 'c' 'd' = branches.



Period 1 (control)
Chemical cues & Directional light cue

Period 6
Chemical cues were rotated by 180°



Period 7
Chemical cues & Directional light cue rotated by 180°
directly after Period 6

4.4 Discussion

Harvester ants, *Pogonomyrmex* spp. (in mesquite-*Accacia* desert, Arizona USA) feed on insect prey and fallen seeds, both of which occur randomly and in discrete patches through the desert environment. When a forager of this species was presented with a small patch of seeds, she ran back to the nest dragging her abdomen along the ground with her sting extended. Within a few seconds of her entering the nest, nestmates ran out directly to the food source clearly following a pheromone trail (Hölldobler & Wilson, 1970). The fire ant, *Solenopsis saevissima*, utilises mass recruitment techniques to direct sisters to food. A large number of ants, up to 160 individuals could be called to the food source within 15 min of a trail-laying scout ant returning to the nest (Wilson, 1962). To understand recruitment tactics of particular species, one must adopt a combined approach of behavioural and ecological aspects. In harvester ants and fire ant species, sister foragers are recruited to ephemeral food sources that require to be exploited quickly, for example before they are discovered by a competitor. This is not the case with wood ant foragers that gather honeydew from aphid aggregations; which are to be found in roughly the same locations year after year throughout the season because over-wintering eggs are laid by aphids on adjacent needles (Cosens & Toussaint, 1986). Wood ants have a comparatively long-lived foraging population with a knowledge of food sites within the woodland canopy because they repeatedly use the same routes to the aphid aggregations and veteran foragers retain information about these locations during hibernation. This ability may eventually protect their feeding sites from competitors. So it has been advantageous for the wood ants to develop a topographic tradition (Rosengren, 1977a), and passing this knowledge to the next generation of foragers is critical for the colony's survival. It is clear, therefore, that a good memory is an important component of wood ant foraging efficiency.

One forager cannot optimise the use of an aphid aggregation, therefore the colony adaptively should deploy many foragers, but without wasting effort. Ant colonies in general can achieve this goal in two ways: the foraging population at a site could be left to increase as more and more ants find the location by chance, or alternatively an ant once aware of a food site could alert her sisters and direct them to the food source. This latter method (recruitment) is common in almost every ant species. The first method is used by *Nothomyrmica macrops* the most primitive of all living ant species and found in Australia: it is a solitary hunter, returning to the nest using only visual cues and shows no form of recruitment whatsoever (Hölldobler & Taylor, 1983). There are many systems of recruitment used by ant species. The tandem running displayed by *Leptothorax acervorum* and *Camponotus sericeus* is a primitive recruitment technique (Hölldobler *et al.*, 1974). An individual returns to the nest and regurgitates food to her nest mates. She extends her sting and excretes a droplet of liquid: an action termed 'tandem-calling' behaviour; she then leads one sister to the food source maintaining a constant contact with her during the journey. In this way only one sister can be recruited at a time (Hölldobler, 1974). Other Formicine ants are seen as having more sophisticated systems of recruitment. One is known as group recruitment: in *Camponotus compressus*, a replete ant performs a waggle display that excites sisters to follow a hind gut trail that she laid on her homeward journey. This trail will be followed in the absence of the leader ant, but only for a short distance. In this way up to 30 nestmates can be recruited at a time (Hölldobler & Wilson, 1990). The most sophisticated form of recruitment is a mass recruitment, first described by Wilson (1960) in the fire ant *Solenopsis saevissima*, in which a chemical signal alone is responsible for the recruitment response and will function in the absence of a leader ant. A trail laying ant behaves in a stereotypic way: crouching close to the ground, with her sting extended; the tip of the sting is periodically touched to the ground and she leaves a series of pheromone streaks in her wake. Most of the workers within 10 mm of a freshly laid trail will follow it. There is a direct relationship between the amount of scent laid and number of responding workers. In this way the number of ants recruited to a site could be controlled (Hölldobler & Wilson, 1990). The scent trail being totally invisible and extremely species-specific, makes the study of ant trail-laying so challenging. Some species of invertebrates have learnt to follow the trails and so exploit the ants' search efforts: for example the black wood ant-beetle (*Atemeles pubicollis*) follows foragers and forces them to regurgitate honey dew (Hölldobler, 1984).

A clear result from this experimental series was that none of these methods of recruitment involving a specific pheromone trail for guidance in novel circumstances are used by *F. aquilonia.* None of these experimental trials listed under 4.3.1, 4.3.2 4.3.3 and 4.3.4 showed that *F. aquilonia* foragers mark their routes to novel food sources using specific pheromones. If they had marked the route a reduction of traffic should have been observed on clean bridges compared to the non-clean bridges. The data clearly refute this supposition: the use of a clean bridge did not alter significantly the traffic on either route (a) or route (b) (Table 4.3). As the foraging table was surrounded with featureless white cloth some unidentified cues (internal references) may have been used in the above experimental trials. In trial 1 (without visual cues) when replete foragers were leaving the site, they always ran half way through the bridge 'a' before finally resorted to the bridge 'b'. Observations like this imply that they used some kind of internal reference with respect to the external guide (non-chemical cue). Hölldobler (1974) conducted a similar sort of experiment with *Camponotus sericeus* in an environment devoid of visual cues and found a pheromone marked bridge is always preferred by the foragers. However, in an environment with obvious visual cues, foragers showed an equal preference for (use of) bridges with and without pheromone marked trails. It is clear that *C. sericeus* will use pheromone trails while orientating in space, and equally that *F. aquilonia* does not. Rather, results of 4.3.4 implied that foragers preferred a spatially positioned sector where they expected to find food and did not orientate to the sector bearing food: it was clear that sector was not marked during the initial training period. In the experiment 4.3.5, when moving upwards foragers preferred the illuminated side of the trunk. And, in the horizontal plane they preferred branch 'c' in the apparent spatial position relative to the directional light cue. This direction may have been achieved by a compass orientation according to the light rays or basic tropho-phototaxis (Fraenkel, & Gunn, 1960). By adopting this strategy foragers can maintain a straight vertical movement enabling them to arrive at nearly the same point at the top of the trunk and so make a known angular turn in the horizontal plane. Thus, according to the results obtained from Periods 5, 6 and 7 *F. aquilonia* foragers rely mainly on visual cues (here a directional light) if available to them when orientating on vertical and horizontal planes: unlike *F. lugubris* foragers which apparently depend on the chemical cues when orientating in the horizontal plane. Although the two species are closely related, results obtained from the above experiment indicate a distinct difference between the two species in this regard. While removal of the directional light source did not seem to affect orientation in *F aquilonia,* when it was repositioned the foragers' orientation was realigned accordingly. Most probably a hierarchical arrangement of navigational cues was used by wood ants and in each instance the most stable was used and other conflicting information was discarded. Wehner and Lanfranconi (1981) found that the foragers of the long-legged dessert ant *Cataglyphis* do not navigate using scent trails but rather celestial cues as a compass: the foragers may travel 100 m from the nest during their forays. He suggested that insects, like astronomers, do not perform spherical trigonometry in the sky but they gain information about the sun's movement relative to a known landmark map. Each *Cataglyphis* forager leaves the entrance of its nest in a particular direction over periods of several days or weeks; as this orientation is governed by the landmarks around the nest, this panorama is likely to be the system of reference used by the insect to measure the different positions of sun's azimuth at different times of the day. This type of orientation may be used by *F. aquilonia* foragers when the sun (sky) is visible to them in the woodlands or the canopy pattern against the sky. Likewise, in the laboratory they may have been used the light source as a visual cue in an otherwise 'cueless' environment.

Since each colony was subjected to a food deficit prior to the trials, most of the foragers observed will have been recently deployed and will have had little knowledge of the layout of the foraging table. Henquil and Abdhi (1981) have suggested that wood ants, in particular *F. polyctena,* use chemical trails when foraging for food predominantly in the spring when the tropic zone is re-explored; and that these trails are superseded by memorised visual cues later in the season. The logic behind their suggestion is that: a) when the environment is new to foragers they are more likely to lay and follow chemical trails; and b) with experience the dependence on these chemical trails wanes. The same logic may be applied to the present experiments: as the observation period was restricted to the initial 20 and 15 min periods and novice foragers might be expected to mark the route with a chemical trail. A conflict between visual and olfactory cues is likely to be rare in nature where spatial information received through the different senses usually coincides and may be used as a double check in orientation. Although veteran foragers maintain a strong site allegiance based on a hierarchy of individually remembered topographic cues, novice foragers that have no knowledge of such cues are not prevented from laying or following chemical cues. However, neither veteran nor novice *F. aquilonia* foragers do so when successfully replete.

It is known that wood ants of the *F. rufa* group are able to recruit fellow workers from the nest and direct them to a food source (Rosengren, 1971; Horstmann 1975; Cosens & Toussaint, 1986). The nature of their recruiting and directing signals has, however, remained unclear. Standard laboratory tests of the effect of chemical trails are difficult with this particular group, because they react to visually unfamiliar situations with 'searching behaviour' (Elgret & Rosengren, 1977). If they navigate using chemical trails this response of 'searching' in visually unfamiliar situations is inexplicable. A discoverer forager which found the new food source did not mark the dish or branch with any kind of chemical, she did spend a long time walking around the dish and pad, and followed a tortuous route on her virgin journey back to the nest. The forager, by this behaviour, may become acquainted with the visual panorama around the location by specific orientation movements prior to leaving that point for the first time. *Cataglypis bicolor* turns and twists along its path, integrating a whole series of visual cues to help it locate the nest (Wehner, 1981). It would be reasonable to assume the tortuous path taken by the discoverer ant allows it to calibrate some form of internal spatial map. According to Cosens and Toussaint (1985) replete ants returning to the nest from food may stimulate nest mates to revisit the previously remembered sites. Moreover, they found that site allegiance was so strong that foragers repeatedly returned to a food source placed on an upper level branch even after another, equally rich food source had been placed, and found, on a lower level branch.

When a particular forager is deployed to forage, she has to move about in a three dimensional network of roadways composed of the woodland floor, trunks, branches and twigs where a correct turn has to be taken at each ramification. With such an intricate network of roadways a random searching to relocate the food would be inefficient since it would lead to a considerable loss of time and energy. Therefore foragers optimise their foraging efficiency by returning to the same aphid aggregation in the canopy using the same three dimensional route comprised of memorised orientation cues. When returning to an aphid aggregation, foragers must first find correct ramifications in the woodland and afterwards make the correct choice of branch. In a woodland such a foraging route may extend over 100 m and involve a well defined and visually obvious trail: chemical cues would therefore appear superfluous to an experienced forager. Moreover an average forager would take almost 1 h to traverse the 100 m and often during inclement weather, the typical volatile pheromone trail, such as that of *Solenopsis geminata*, lasting only for some 100 s (Wilson & Bossert, 1963) would seem inadequate. It can be hypothesised that pelleted material voided from the infrabuccal sac and faecal material from the hind gut were used as 'sign posts' because their effectiveness remained after several weeks in contrast to a chemical cue. Since it has been shown for *F. rufa* that the resolution of its compound eye is 0.5⑤ (Jander & Voss, 1963), pellets of 0.3 mm diameter are likely to be seen at relatively close quaters and could therefore provide a visual cue. Given that a forager will recognise the pellets, they would act as a firm indication of the colony's foraging activities at or nearby their position. An inexperienced forager presently relying upon visual cues may well deviate from the actual route when these pellets are displaced from a particular route marked by them. Indeed, this was observed in some of these experiments: when pellets at the base of the food bearing branch were washed away and some 4-week-old pellets were positioned at the base of the opposite branch some foragers deviated to that particular pellet-marked branch (personal observations).

None of the above statements clearly explain how novice foragers are directed to, or find, the novel food sources. However, inexperienced foragers show a tendency to aggregate into groups after having been deployed (Rosengren, 1977a, and observed in these experiments); and to be predisposed to be drawn along particular routes by the purposeful activity of the site-aware foragers (kinopsis) (Legge, 1991) which, thus, impose a direction to the deployment. Hölldobler (1971) found that workers of *Camponotus socius*, especially when stimulated by a 'discoverer' ant would follow readily a micro syringe, which was drawn over a glass plate while discharging small amount of Formic acid. Formic acid is a highly volatile substance, hence the ant's ability to follow a formic acid trail is apparently limited to few centimetres. Zakharov (1980) observed in the *F. rufa* group, that an experienced ant moving confidently along the route was followed by novices occurring nearby and the threatening posture of the 'observers' was assumed to be a threatening signal, other ants following suit (kinopsis based on optomotor signals). The recruitment method of *F. aquilonia* is seen as primitive because the alerting and directing signals are different and distinct (Legge, 1991). Subsequently the number on the foraging table increased and repletes engaged in trophallaxis with non repletes. This food exchange did not occur at random places on the table, but rather at branch bases, tree base, at the base of the bridge and top of the bridge. Replete ants travel from food source to the nest, stop along the way and regurgitate (trophallaxis) with naive foragers. This food exchange could act as a signal to the naive foragers: that food is available in the direction from which the replete has come, and bias the directional decisions of naive foragers. It is because this method of recruitment requires several foragers in the system having knowledge of the food that there is such a long time lag before a foraging population begins to build up at the dish compared to the advance mass recruitment in the fire ant, *Solenopsis saevissima*. In *F. rufa* (Zakharov, 1980) it has been revealed that immediately on familiarising itself with the nest site a new forager moves to the periphery of the familiar foraging area occupied by other foragers. Gradually, its foraging area approaches the nest and finally the forager completes its out of nest activities to find itself on the cupola, which brings it to the 'observer' group. It is important that 'observers' are the most experienced colony members, well known about the foraging area and they direct novices to profitable foraging patches. This could be the way that topographic traditions of the veteran foragers pass on to the naive foragers.

To orientate using visual cues, a particular animal must have a capability to perceive terrestrial cues, to store and recall the perceived cues and to manipulate these perceived memories. The acquisition of information about the environment is possible through a number of sensory channels. The visual perception consists of physical acquisition of light energy and interpretation of that pattern of energy carried out by the brain. It has been suggested that there is a link between the importance of visual cues for orientation and structure of the eye in ants (Toussaint, 1983). An ant's compound eye is composed of a number of optical units called ommatidia which enable them to perceive the environment visually. The ants that orientate using visual cues possess a following a number of ommatidia per eye: *F. rufa* 460 (Mazokhin-Porshnykov, 1975), *F. polyctena* 750 (Menzle, 1972), and *Cataglyphis bicolor* 1300 (Wehner & Menzel, 1969). For *C. bicolor* vision is crucial in the integration of a route; and *F. polyctena* depends almost entirely upon visual and topographic cues (Rosengren, 1971); while *F. rufa* depend on tactile, celestial and topographic cues for navigation (Jander, 1957). *F. aquilonia* has 700 ommatidia per eye (Toussaint, 1983); so undoubtedly *F. aquilonia* possesses a proper anatomical basis for visual orientation. There are many examples of ants having good memories for both visual and other information. If the trees surrounding a nest of *F. rufa* are clear felled during the hibernation foragers that had foraged in the previous season are disoriented and unable to relocate previously exploited food sources on emergence (Rosengren & Pamilo, 1977). This suggests that ants of *F. rufa* group are capable of long term memory of information.

The populations of *F. aquilonia* in Finland, Switzerland and the British Isles show little genetic differentiation, whereas the populations of *F. lugubris* show considerable differentiation (Rosengren *et al.*, 1979). The Central European populations morphologically identified as *F. lugubris* can be genetically divided into two groups: one of the two groups found in the Alps and the Jura mountains is genetically inseparable from *F. aquilonia* (Pamilo, *et al.*, 1992). The genetic differences within *F. lugubris* indicate that populations have evolved separately for a long time The social structure of *F. lugubris* colonies also shows geographic variation: the colonies in Finland and Ireland seem to be mainly monogynous and monodomous, whereas the nests in Central Europe and Northern Britain are polygynous and form polydomous colonies. *F. aquilonia* has polygynous and polydomous colonies in all populations so far studied (Pamilo, *et al.*, 1992). Likewise closely related species adapted to different types of habitats differ in the relative importance attached to the visual and olfactory orienting cues or they may have developed orienting mechanisms in which one type of cues can be utilised only in the presence of the another type (Rosengren & Fortelius, 1986a). The giant tropical ant *Paraponera clarvata*, another forest dweller, initially uses pheromone trails to recruit foragers, but over time the importance of the chemical trail diminishes, and ants come to rely on more stable visual cues provided by the trees (Harrison, 1988). The south of France where Fourcassiaè and Begunon (1988) worked with *F. lugubris* is substantially drier than Scotland. Such a dry climate is more conducive to volatile chemicals to persist for a considerable time compared to the Scottish woodlands. This might be the premise that two populations of wood ant, *F. aquilonia* and *F. lugubris* have undergone divergent adaptations resulting in dependant on different sets of hierarchical cues in orientation. Given that the giant tropical ant *Paraponera clarvata* shows a shift in cue dependence over a short period of time, it is not so difficult to conceive that such a shift in cue dependence is possible in wood ants on an evolutionary time scale.

CHAPTER 5

Part One

Distribution of carbohydrate and protein food in the habitat and the wood ants' searching behaviour

5.1 Introduction

Searching behaviour represents the interaction of the following factors: 1) the characteristics and abilities of an animal; 2) external environmental factors determining what resources are available and the risks involved in obtaining them; 3) internal factors such as the level of physiological need (relative to a certain kind of resource) determining what an animal, or the colony, needs at a particular time. However, the ultimate success is dependent upon a) the method used to search in relation to the availability of resources and their spatial and temporal distributions in the environment; b) their efficiency in locating resources; c) the ability of a species to adapt to long-term environmental change and the ability of an individual to respond, perhaps through learning.

The way that resources become available in time and space constitutes the major environmental constraint on searching success and is an important selective pressure on efficiency in search behaviour. According to Hassell and Southwood (1978) there are hierarchical levels of how animals perceive the environment: these include: a) resource items, for example individual prey, leaves, individuals of the opposite sex, or hosts; b) patches, which are aggregations of resource items within the foraging area; and c) habitats, which are clusters of patches. These perceived levels provide a framework for searching behaviour which involves the movements of an animal between habitats and patches to locate resource items. A resource, such as food, could be distributed in various densities and patterns, these distributions become an important environmental determinant affecting searching success and the searching behaviour itself. An animal has to employ the search mechanism that works best for a given kind of distribution.

A fundamental decision for any forager is choosing the location in which to search for food. In the case of social insects, as soon as a forager has gathered a certain amount of food it has to return to a 'central place'- a nest. At the start of the next foraging expedition, the question is where to search for additional food. On one hand the forager may choose to return to the original location and seek food there. Such a strategy is appropriate if the distribution of food is clumped or renewed at a predictable rate: so that finding one item increases the probability of finding others. On the other hand the forager may choose to search elsewhere. This strategy would be appropriate if the distribution of food is dispersed, or if it takes time to reappear in the original location: so that finding one item decreases the probability of finding another in the same patch. These two strategies are called 'win stay' and 'win shift' respectively (Olton *et al.*, 1981). In order to follow either a stay or a shift strategy the forager must remember the location of the original search zone and respond in a consistent way, either returning to the location or avoiding it.

Many studies on the organisation of insect societies have demonstrated the existence and significance of individual differences in behaviour among colony members (see Chapter 3). These individual specialisations most likely result, at least in part, from the different experiences of foragers, a perspective incorporating learning would be valuable. With regard to the foraging behaviour, variation among individuals could represent a biologically meaningful component of the colony's foraging strategy. In several species, workers consistently return to the same food sites by following routes along which landmarks are memorised (Rosengren, 1971; Rosengren & Fortelius, 1986; Beugnon & Fourcassiè, 1988). Within at least some groups of ant species, the colony-level and individual search tactics of foragers are correlated with the types of food resource they collect (Traniello, 1989). Search pattern characteristics can be under genetic influences or can be modified by individual experience through the acquisition of information about resource distribution and food profitability (Nagle & Bell, 1987).

The active movement of an animal within a patch searching for food can be described as area-restricted searching (Krebs, 1973), local searching (Jander, 1975) and area concentrated searching (Curio, 1976). This type of search is characterised by a decrease in forward movements and an increase in highly tortuous and looping movements: the adaptiveness of which is to increase the rate of resource encounters within the visited patch. According to Oster and Wilson (1978), in the Formicidae searching may involve either:- 1) Individuals alone, there is no co-operation among the ants and each forager must successfully locate, subdue and retrieve prey entirely on her own. This simple, essentially solitary, method is used by many ant species which generally are either anatomically primitive or have small colony size. 2) Facultative recruitment in which most searching is solitary, but a large prey item is procured by recruiting nestmates to help subdue and retrieve it. This technique is widespread among all subfamilies. 3) Use of trunk trails by which foragers leave the nest consistently along established routes which are recognised by odour or visual cues. The trails may have no specific end-point and individuals leave the route at random to hunt solitarily, or a trail may lead to an established foraging ground. 4) Prey specialisation in which the mechanics of searching are essentially the same as in category 2, but the species has a narrow diet and has evolved special searching tactics to locate prey. 5) Group searching: for some highly specialised ants searching is done collectively by a large number of individuals. Groups of from several hundred to several thousand search to locate food following odour trails laid by leader ants whose identity continually changes within the group. These searching categories are mutually exclusive; so far as is known, no ant species employs more than one strategy.

Wood ants employ category 3 (Holt, 1955). Foragers attend aphids for sugar rich honeydew secretions and forage for protein, chiefly other arthropods. These foods differ considerably in their distribution patterns: aphids are essentially fixed in their spatial locations and their carbohydrate secretions (honeydew) are consistent in quality and are renewed at predictable rates (Mittler, 1958; Sudd & Sudd, 1985). Insect prey, by contrast, are unpredictable in time, space, and size, and generally are not renewed with any certainty.

5.2 Aims of the study

Given the differences in the distribution patterns of food types taken by *F. aquilonia*, my experiments seek is to find out:

1 How individual experience and food resource-related modification of search patterns may contribute to a forager's search tactics {by providing carbohydrate (10%w/v sugar solution) and protein (blow fly) food? (Part 1)}.

2 Whether the recruitment of naive foragers to live protein sources is dependent on secretions of successful attackers? (Part 2)

5.3 Materials and Methods

5.3.1 Categorisation of forager types according to search persistence

Colony No. 2 was used in these experiments. Each foray by an *F. aquilonia* forager may be characterised by a travel and search phase. Foragers move straight out from the nest and travel for various distances before beginning to show local search behaviour identified as a high frequency of turning and probing. In addition to their foraging behaviour (Chapter 3), individual foragers also differ in their tendency to return to and continue to search at a location where food was found on a prior successful foray. Foragers were offered either a single pithed blow fly larva (*Caliphora* sp), or a crop load of 10% w/v sugar solution at the middle of a circle of 25 cm radius, drawn on the foraging table 1.5 m (trail length) from the mound nest. The sugar solution was offered using a syringe and a forager was allowed to feed until replete. The area of the 25 cm radius circle was covered with a transparent sheet (26 cm radius) in order to facilitate removal of odours left by foragers or the food. Each forager was individually marked whilst feeding or subduing the prey in order to follow her subsequent behaviour. After a worker had returned homeward, the transparent circle was washed clean using 90% alcohol to eliminate any search biases due to the presence of food odours or chemicals deposited by foragers. Differences in searching behaviour were quantified during the first three minutes after a forager returned to the site of a prior food find by recording a number of variables that related to the search pattern. 'Purposeful foragers' and 'Non-purposeful foragers' were categorised as the amount of time spent searching in a circular area having the locus of the food as its centre (Table 5.1). A forager was classified as non-purposeful at any time during the three minute post-return observation period if she abandoned the search.

Purposeful foragers': show a high degree of local searching in the vicinity of a prior food find during the initial 3 min post-return observation period (Table 5.1).

Non-purposeful foragers': show no search whatsoever during the initial 3 min post-return observation period (Table 5.1).

In order to quantify search persistence, a) time spent in area-restricted searching (Curio, 1976) or intensive searching (Bond, 1980), and b) initial giving up time (Traniello, 1988) were measured.

Time spent in area-restricted searching (ARS): The time spent searching within the circular area in the vicinity of a prior food find (Table 5.2).

Initial giving up (IGT) time: The time spent searching in the circular area after first returning to within 25 cm of the location of the prior food find to the first departure outside of the circular area (Table 5.2).

5.3.2 Effect of experience in carbohydrate and protein stimulated searching behaviour

To study the spatial pattern and modifiability of the search, either a single crop load of 10% w/v sugar solution or a single blow fly larva was offered to a forager at the centre of the circle. While collecting their first food load foragers were marked with a cellulose paint as before to permit subsequent recognition.

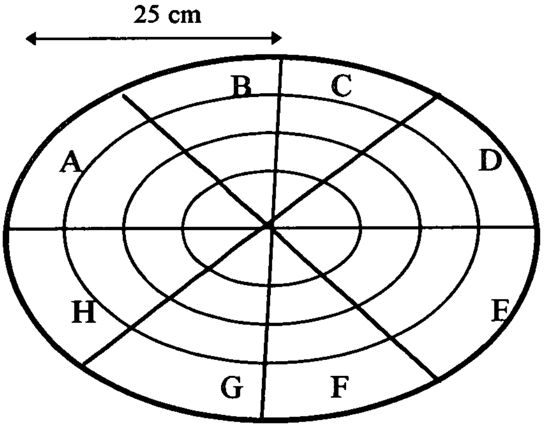


Figure 5.1 25 cm radius circle drawn on the foraging table.

Searching behaviour was recorded following the collection of either a protein or carbohydrate reward and the return from the nest to the reward site. To characterise search pattern the average length of the search path (target distance) of a searching forager from the reward site was measured by marking the forager's position using numbered applicator pins on a duplicate circle at every 18 sec of the 3 min post-return observational period. The distance (cm) between the positions of each applicator pin (target distance) was measured using metric tape after the forager had been given a food load at the end of the observation period. This procedure (marking the forager's position on a duplicate circle) caused minimal disturbance to the searching forager. To measure the effect of experience in searching behaviour in response to protein and carbohydrate food, a series of 6 consecutive rewards of a given food type were offered; target distance was measured after the first, third and sixth reward and compared using t-Test two sample assuming equal variances.

5.4 Results (Part One)

54.3% of foragers (N=151) showed purposeful searching and 45.7% showed non-purposeful searching when they were given carbohydrate (sugar solution). 45.5% foragers (N=148) showed purposeful, while 27.7% showed non-purposeful, searching after the protein reward (Table 5.1). Although 26.4% foragers (N=148) did not return to the site where they were previously rewarded with protein.

Table 5.1 Differences in searching behaviour during the first three minutes after a forager returned to the site of prior food find (Purposeful and non-purposeful foragers).

Type of food	Number of foragers tested	'purposeful foragers' (persistent searching)	'Non-purposeful foragers' (non persistent searching)
Carbohydrate	151	82 (54.3%)	69 (45.7%)
Protein	148	68 (45.5%)	41 (27.7%)

39 (26.4%) foragers out of 148, laden with blow fly did not return to the patch. All 151 foragers replete with sugar solution returned to the patch where food was previously found.

Table 5.2 Differences in searching behaviour during the first three minutes after a forager returned to the site of prior food find (Initial giving up times (IGT) and time spent in area restricted searching (ARS) for protein and carbohydrate food in seconds). Each individual was tested only once for protein and carbohydrate food and different individuals were tested for each type of food

IGT(PRO) Seconds	IGT(CHO) Seconds	ARS(PRO) Seconds	ARS(CHO) Seconds
24	27	24	45
23	31	26	63
25	38	28	34
30	32	31	71
29	45	29	32
30	32	31	97
28	26	29	109
26	37	30	128
27	32	27	31
29	49	26	74
30	33	30	111
25	37	30	68
31	43	31	41
23	25	24	52
35	63	36	32
24	69	25	45
32	38	37	131
28	34	29	76
41	26	41	116
27	31	28	52
25	37	26	104
29	49	30	98
31	26	31	109
31	31	38	139
32	37	32	38
28	32	29	52
23	40	23	56
22	33	22	75
22	45	22	47
30	32	31	35
34	55	35	39
30	67	30	30
30	39	30	49
27	44	28	58
	41		32
	31		39
	25		52
	33		50

PRO - Protein, CHO - Carbohydrate
Initial giving up times (IGT) and time spent in area restricted searching (ARS) for protein and carbohydrate food were measured only for the purposeful foragers).

Above results indicated the differences in food type produce differences in the degree of persistence shown by foragers that had contacted food of each type.

The results obtained indicated that foragers showed different degrees of search persistence in response to collecting each type of food (Tables 5.3, 5.4 & 5.7). The initial giving up time (IGT) was significantly greater for the carbohydrate compared with protein (t= -4.92, df 70, P<0.05) (Table 5.3). Foragers that had fed with sugar solution showed a significantly higher area restricted searching effort (ARS) compared to the foragers that had fed with protein (t= -6.54, df 70, P<0.05) (Table 5.4).

Table 5.3 Two sample t-Test: assuming equal variances for initial giving up time data in Table 5.2.

	IGT(PRO) Sec	*IGT(CHO) Sec*
Mean	28.17	38.04
Variance	16.59	121.69
Observations	34	38
Pooled Variance	72.14	
Hypothesised Mean Difference	0	
df	70	
t Stat	-4.92	
P(T<=t) one-tail	2.75×10^{-06}	
t Critical one-tail	1.67	
P(T<=t) two-tail	5.51×10^{-06}	
t Critical two-tail	1.99	

PRO - Protein, CHO - Carbohydrate, Sec - Seconds

Table 5.4 Two sample t-Test: assuming equal variances for time spent in area restricted searching (Data from Table 5.2)

	ARS(PRO) Sec	*ARS(CHO) Sec*
Mean	29.28	66.03
Variance	19.4	1053.29
Observations	34	38
Pooled Variance	565.89	
Hypothesised Mean Difference	0	
df	70	
t Stat	-6.54	
P(T<=t) one-tail	4.19×10^{-09}	
t Critical one-tail	1.67	
P(T<=t) two-tail	8.39×10^{-09}	
t Critical two-tail	1.99	

PRO Protein, CHO Carbohydrate, Sec Seconds

Table 5.5 The average length (cm) of the search path (target distance) of a searching forager for carbohydrate and protein food. Each forager was tested only once and different individuals were tested for protein and carbohydrate.

Carbohydrate						Protein					
1st (cm)	out of circle	3rd (cm)	out of circle	6th (cm)	out of circle	1st (cm)	out of circle	3rd (cm)	out of circle	6th (cm)	out of circle
99.3		81.9		69.3		20.1		189.3	*	303	
180		119		99		289.2		303.6		323.9	*
108.7		99.8		89		178.6		201.1		183.4	
89.3		69.7		59.3		129.3	*	189.8		129.5	
98.2		59.3		51.2		141.8		171.9	*	149.4	*
101.3		48.6		39.3		183.6		163.4		183	*
89.3		79.1		58.1		191		129.6		179.3	
78.3		69.3		49.8		112.3		119.3	*	121.6	
91.3		59.3		61.3	*	118.6	*	176.1		187.3	
101.6		81.3		73.5		239.5		151.3		139.6	
93.5		85.3		69.1		148		181.4	*	160.1	*
89.3		76.1	*	69.3		201.6	*	176.3		118.9	
78.9		37.3		29.1		183.2		169.6		59.8	*
59.3		59.8		49.3		151.4	*	139		129.3	
37.8		61.3		59.1		139.3		181.3		123.1	
99.3		39.4		29.9		121.6		139.6		181.6	*
39.5		40.1		38.6		143		117.3		136.9	*
91.3		81.3		59.3		117.5		211.8	*	171.8	
79.4		67.6	*	60.1		99.9	*	139.6	*	139.6	
99.1		77.1		65.6		203.6		118		169.7	
89.3		76		60.1		181.3		89.3	*	181.3	
91		73.4		57.1		89.5		116.7		139.6	*
79.5		69.5		59.3		132.6	*	129.3	*	148.4	
86.3		58.6		39.1		149.3		181.3	*	156.3	*
101.4		81.3		70.6		131.9		118.6		106.3	
89.3		79.3		59.3		106.6		100.6	*	111.6	*
102.6		69.9		48.6		108.9		91.9		98.6	*
89.8		71.8		41.3		117.1		123.6		119.9	
99.1		59.8		52.5		195.8		220.8		216.9	
78.1		45.9		37.1		226.7		187.9	*	192.4	*
87.3		72.8		57.7		216.1		216		181.8	
79.6		69.8		37.3		197.3		206.3		271.3	*
89.3		71.9		69.1		211.3		217.8	*	229.6	
93.1		80.3		59.6		105.6		209		189.7	
91.3		69.6		39.6		181.7		201.3		199.6	*
79.6		53.7		41.3		149.3		186.7	*	179.8	*
89.3		37.1		40.2		169.5		179	*	189.3	

Out of circle; out of circle search by foragers. * Indicates foragers which showed out of circle search while searching within the 25 cm target area.

The target distance for carbohydrate food searching was significantly lower than that for protein (t= -7.37, df 72, $P<0.05$) (Table 5.6). When considering the six consecutive carbohydrate rewards, the target distance for the 3rd reward was significantly lower than that of the 1st reward (t= 4.74, df 72, $P<0.05$) (Table 5.7). Similarly, the target distance for the 6th reward was significantly lower than that of the 3rd reward (t=3.48, df 72, $P<0.05$) (Table 5.9).

Table 5.6 Two sample t-Test: assuming equal variances for the 1st reward (Carbohydrate and Protein). Data from Table 5.5

	1st(CHO) (cm)	*1st(PROTEIN) (cm)*
Mean	89.74	156.32
Variance	458.74	2559.02
Observations	37	37
Pooled Variance	1508.88	
Hypothesised Mean Difference	0	
df	72	
t Stat	-7.37	
P(T<=t) one-tail	1.14×10^{-10}	
t Critical one-tail	1.67	
P(T<=t) two-tail	2.28×10^{-10}	
t Critical two-tail	1.99	

There was a significant difference in target distance (cm) in first reward for carbohydrate and a protein (t= -7.37, df 72, $P<0.05$)

Table 5.7 Two sample t-Test: assuming equal variances for the 1st and 3rd reward (Carbohydrate). Data from Table 5.5

	1st (cm)	*3rd (cm)*
Mean	89.75	68.47
Variance	458.74	286.73
Observations	37	37
Pooled Variance	372.74	
Hypothesised Mean Difference	0	
df	72	
t Stat	4.74	
P(T<=t) one-tail	5.23×10^{-06}	
t Critical one-tail	1.67	
P(T<=t) two-tail	1.05×10^{-05}	
t Critical two-tail	1.99	

There was a significant difference in target distance (cm) in first and third rewards for carbohydrate (t=4.74, df 72 $P<0.05$)

Table 5.8 Two sample t-Test: assuming equal variances for the 1st and 6th reward (Carbohydrate). Data from Table 5.5

	1st (cm)	*6th (cm)*
Mean	89.74	55.38
Variance	458.74	235.33
Observations	37	37
Pooled Variance	347.03	
Hypothesised Mean Difference	0	
df	72	
t Stat	7.94	
P(T<=t) one-tail	1.01×10^{-11}	
t Critical one-tail	1.67	
P(T<=t) two-tail	2.03×10^{-11}	
t Critical two-tail	1.99	

There was a significant difference in target distance (cm) in first and sixth rewards for carbohydrate (t=7.94, df 72, $P<0.05$)

Table 5.9 Two sample t-Test: assuming equal variances for the 3rd and 6th reward (Carbohydrate). Data for Table 5.5

	3rd (cm)	*6th (cm)*
Mean	68.47	55.38
Variance	286.73	235.33
Observations	37	37
Pooled Variance	261.08	
Hypothesised Mean Difference	0	
df	72	
t Stat	3.48	
P(T<=t) one-tail	0.42×10^{-4}	
t Critical one-tail	1.67	
P(T<=t) two-tail	0.84×10^{-4}	
t Critical two-tail	1.99	

There was a significant difference in target distance (cm) in third and sixth rewards for carbohydrate (t=3.48, df 72, $P<0.05$)

Table 5.10 Two sample t-Test: assuming equal variances for the 1st and 3rd reward (Protein). Data from Table 5.5

	1st (cm)	*3rd (cm)*
Mean	156.31	166.09
Variance	2559.02	2008.79
Observations	37	37
Pooled Variance	2283.90	
Hypothesised Mean Difference	0	
df	72	
t Stat	-0.88	
P(T<=t) one-tail	0.19	
t Critical one-tail	1.67	
P(T<=t) two-tail	0.38	
t Critical two-tail	1.99	

There was no significant difference in target distance (cm) in first and third rewards for protein (t= -0.88, df 72, $P>0.05$)

Table 5.11 Two sample t-Test: assuming equal variances for the 1st and 6th reward (Protein). Data from Table 5.5

	1st (cm)	*6th (cm)*
Mean	156.31	167.65
Variance	2559.02	2868.69
Observations	37	37
Pooled Variance	2713.85	
Hypothesised Mean Difference	0	
df	72	
t Stat	-0.94	
P(T<=t) one-tail	0.18	
t Critical one-tail	1.67	
P(T<=t) two-tail	0.35	
t Critical two-tail	1.99	

There was no significant difference in target distance (cm) in first and sixth rewards for protein (t=0.94, df 72, P>0.05)

With respect to protein food, the target distance for 1st and 3rd reward or 1st and 6th reward did not show significant difference (t= -0.88, df 72, P>0.05) and (t=0.94, df 72, P>0.05) (Tables 5.10 & 5.11). Foragers showed a large number of out of circle searching visits from 25 cm target area with respect to the protein food, compared to that of the carbohydrate food. The above data clearly support the hypothesis that foraging behaviour may result from ecologically correlated behavioural predispositions and resource-related experiential processes.

Part Two

Recruitment to protein food

5.5 Introduction

Protein sources contribute 33% of the food requirements of wood ants (Sudd, 1970; Skinner, 1980b). A single ant can successfully call her sisters to any point in space where their help is required. Unlike sources of honeydew (carbohydrates) produced by aphids, insect prey (protein) is not renewed in a predictable manner and it is randomly distributed both in space and time. The ephemeral nature of protein food requires that once it has been discovered, it must be exploited as quickly as possible and certainly before the other competitors. So it is reasonable to expect a different type of recruitment behaviour to be involved from that used to exploit the spatially stable food sources. Ants possess several glands in the body that secrete different chemicals and are physiologically well equipped to convey twenty or more documented signals in olfactory communication. Minute gradients of odorant molecules can be detected with an ant's sensitive antennae, which endlessly sweep the air (Wilson, 1984). These chemicals can convey alarm, aggression, or alert nestmates to the position of food where help is needed to exploit it quickly.

Small prey (1-3 mm) is captured by a single forager: grasped in the mandibles and taken back to the nest. Larger prey (5-10 mm) which cannot be dealt with by a single forager demands co-operation of several depending on the size of prey, which is usually taken back to the nest whole. The capture of a prey item involves a considerable element of chance. The ant has to be in close proximity before an attack can be initiated, typically by stumbling across the prey in an opportunistic manner. Therefore in the field, success rate against small prey may be low. Conversely, in the laboratory success rate of attacks on blow fly maggots was 100%, all the maggots supplied were attacked and dragged back to the nest during the spring. Owing to their fairly large size, slow mobility and greater susceptibility to attack, blowfly maggots were used in the experiments that were repeated 11 times.

5.6 Materials and Methods

5.6.1 Minimum reactive distance

A single live maggot (*Caliphora* sp.,) was placed on the foraging table and the distance at which a forager show its first observable response to the maggot was measured.

5.6 1a Results

Foragers did not respond to the movement of maggots beyond 4 cm ($\bar{x}$=4, SD=1.98, N=41).

5.6.2 Recruitment to the live prey

A few (4) live maggots, contained in a 3 cm diameter Petri dish, were placed in the middle of a cardboard circle of 15 cm diameter with 12 inner circles drawn at 1 cm distances to the Petri dish. The behaviour of foragers was monitored using a closed circuit video camera and video monitor when the first forager reached the outer margin of the cardboard circle. Using video recordings the number of ants within 1 and 4 cm circles from the maggots were counted at 10 s intervals for 3 mins. Paths followed by the excited foragers were also recorded for some individuals.

5.6.2a Results

There was a considerable interval (t=60 s) before the first maggot was attacked (Figs. 5.2, 5.3). For example on one occasion at t=40 s, an individual was observed at the 4 cm circle from the Petri dish (prey) but no attack response occurred. At t=50 s three foragers were found individually within the 4 cm circle and one of them walked into the Petri dish and tried to grasp a maggot using its mandibles.

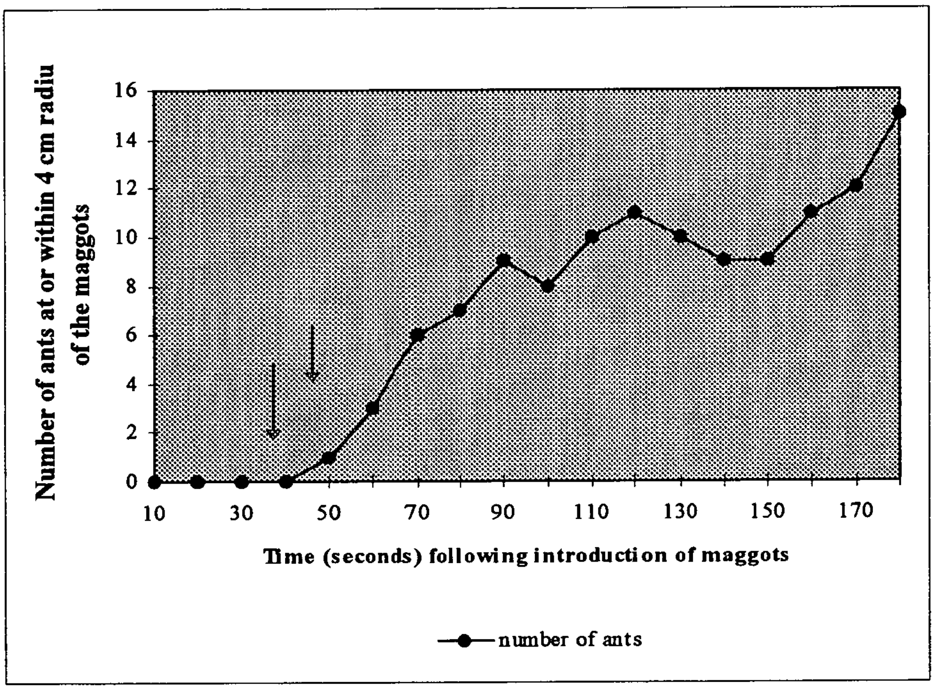


Figure 5.2 Response of foragers to live prey on the foraging table (first 3 min period), after being starved of protein for 3 weeks. The arrows indicate the points where glandular secretions were emitted by attacking foragers.

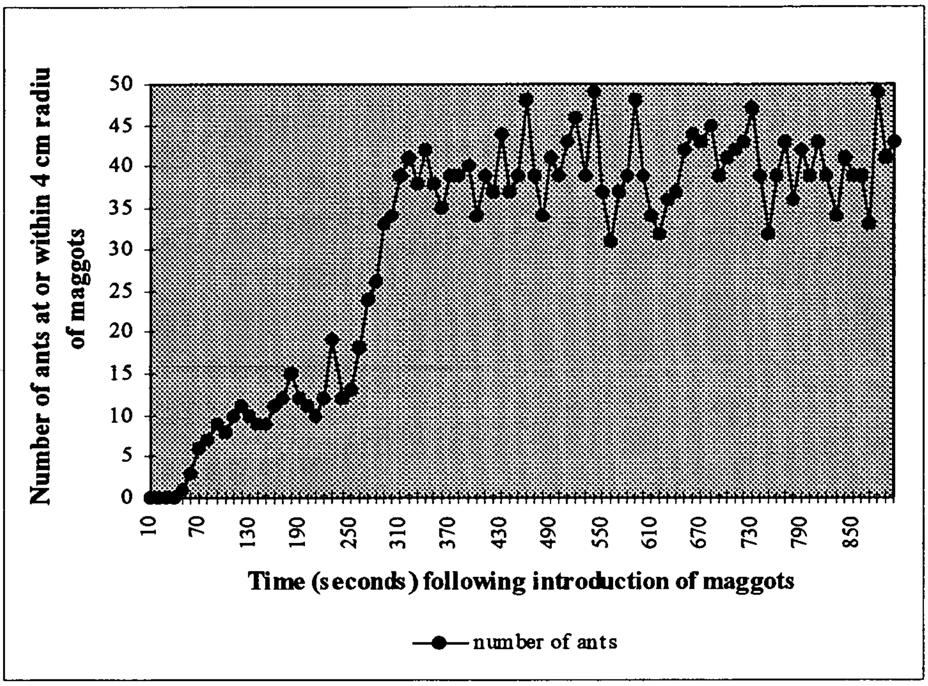


Figure 5.3 Response of foragers to live prey introduced on to the foraging table after being starved of protein for 3 weeks (an extension of Fig. 5.2).

Then, in response to the subsequent movement of the maggot the forager squirted a secretion (possibly formic acid) and thereafter the running speed of nearby foragers increased and they rapidly discovered the maggots. This increased running speed may be a response to the squirted secretion by the first forager which attacked the prey. Ants within 15-20 cm were recruited to the maggots in this way, foragers seemed to locate the prey by following a gradient of the secretion released by the first few attackers (Fig. 5.4).

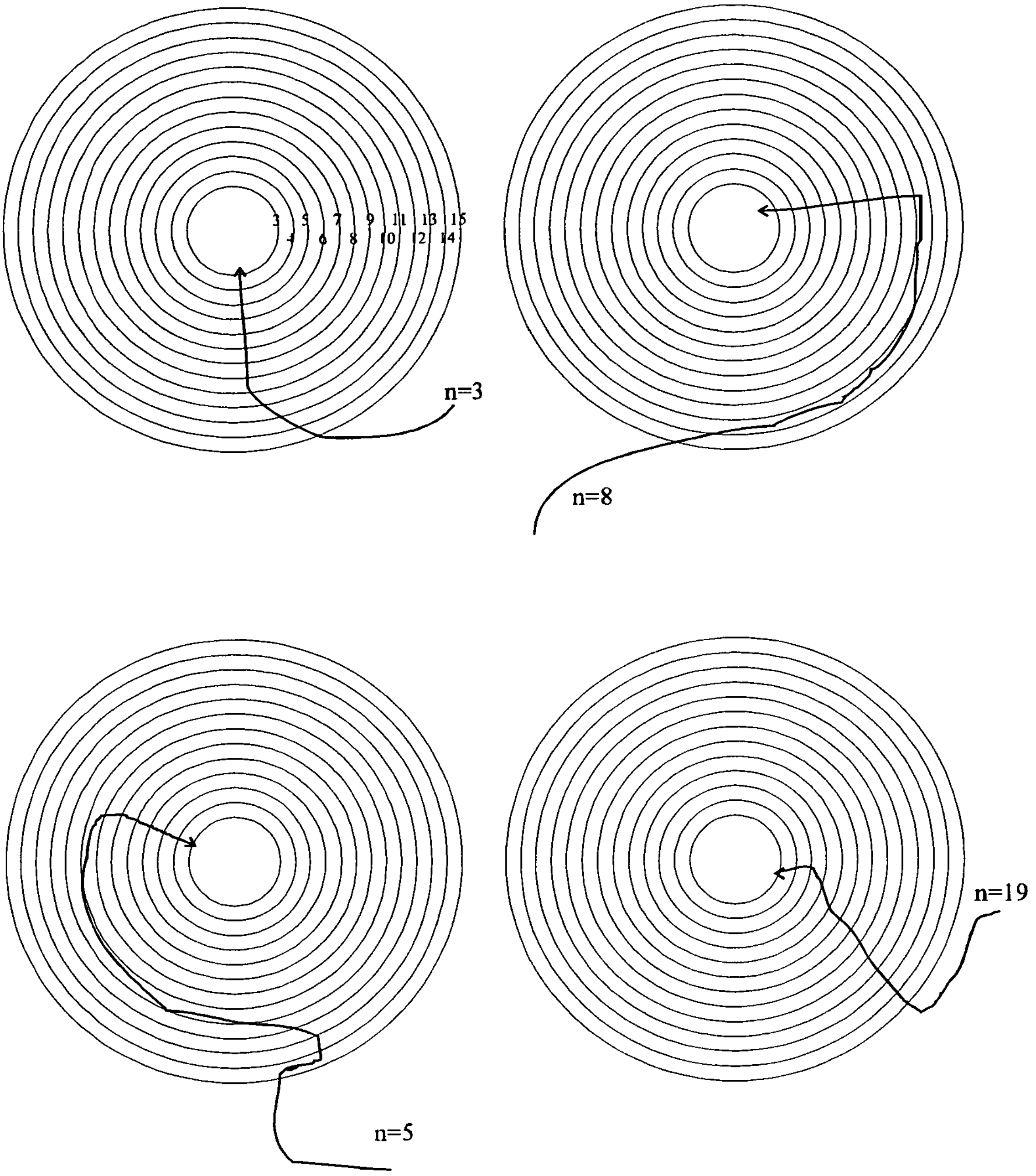
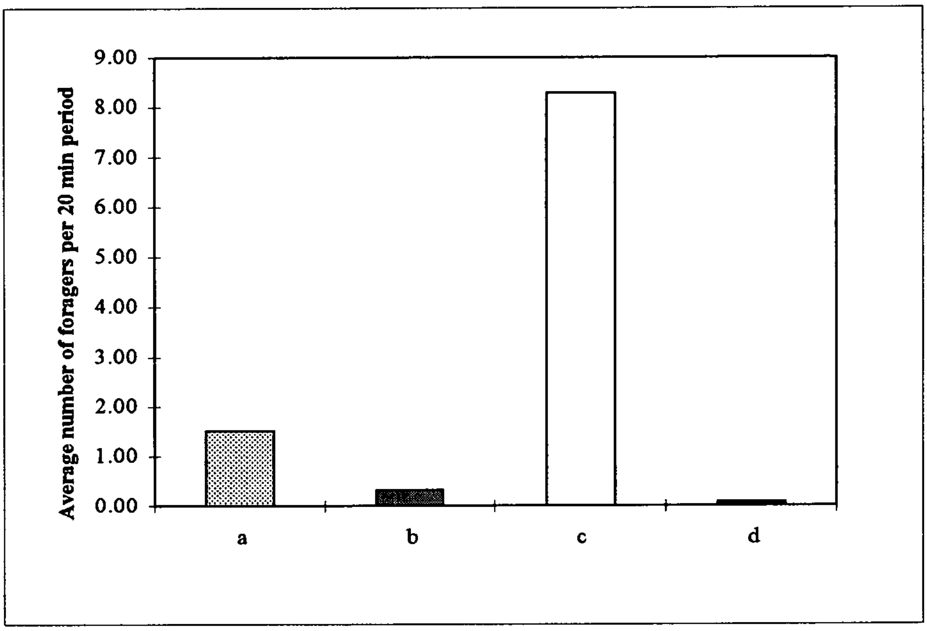


Figure 5.4 Typical tracks of 4 individuals recruited to maggots following the release of gland secretions by a previous attacker. n = number of previous attackers at site

5.6.3 Do foragers recruited to maggots follow the glandular secretions of previous attackers?

Four 100 ml beakers: a) with two maggots, b) with two ants, c) with two maggots + two ants and d) an empty control, were wrapped in two layers of butter muslin such that their contents would be captive and not be visible to searching foragers but any odour from within the beakers would be readily detectable. The four wrapped beakers were placed together on their sides in the middle of the foraging table and the number of ants subsequently searching at the openings of each beaker were counted at 20 s intervals for a 20 min period, This procedure was repeated 8 times.

5.6.3a Results



'a' Two maggots, 'b' Two ants, 'c' Two maggots + Two ants and 'd' Control
Figure 5.5 Average number of ants visit to the opening of four containers with various contents (see text).

Observations in Fig. 5.5 suggest that the combination of ants and maggots was particularly attractive to foragers. This attractiveness strongly supports the idea that foragers actively recruit nestmates to live prey.

5.7 Discussion

Foragers of *F. aquilonia* differ in the extent to which they will continue to search in the vicinity of a site where food was previously found. The type of food encountered strongly influenced the tendency of a worker to search the site of the find, but foragers given one reward of either protein or carbohydrate food showed purposeful or non-purposeful search patterns independent of the food type. Hence purposefulness of searching is not depend on a food type. The foragers' site allegiance may be the reason for their return to the prior protein find site and not because they expect to find other prey items at the same site. The results indicated (Tables 5.2, 5.3 & 5.4) that foragers showed a greater degree of search effort in response to the food type which should have a greater pay off, if greater effort is allocated. It is reasonable to assume that the foragers responding to a stable food type (carbohydrate) by returning to the site of the prior find and continuing to search the area will have a higher probability of foraging success than those that show a temporarily limited search. Likewise, foragers that have found insect prey will have little success in locating additional prey of the same type in the same area because of the uncertainty of insect prey in time and space.

It appeared that foragers may be predisposed toward developing search persistence depending upon the type and frequency of food contacted. The data obtained in this experiment showed that search accuracy was significantly increase as a function of repeated reinforcement with carbohydrate food (Tables 5.4, 5.7, 5.8, & 5.9). This observation was contradictory to the findings of Traniello (1988) with *Formica schaufussi* in which search accuracy did not increase with repeated reinforcement of either food type (carbohydrate or protein). *F. schaufussi* was a common north temperate open-field ant that nests in soil and has generalist food habits. Workers tended aphids for honeydew secretions and feed on plant sap directly, and also forage for a wide range of arthropod prey (Traniello, 1987).

Information on the spatial distribution of stable food such as honeydew obtained from aphids should be retained for longer periods of time than information on the location of ephemeral insect prey. Honeybee foragers were able to reduce the travel time and distance by storing in memory the configuration of the land marks around their nests and by building 'mental maps' of the environment (Cartwright & Collett, 1987; Wehner & Menzel, 1990). In several ant species, foragers consistently return to the same food sites by following routes along which land marks were memorised (Rosengren, 1971; Hölldobler, 1976). In seed harvester ants *Messor* *pergandei* and *Pogonomyrmex rugosus*, handling time per seed was decreased with foraging experience (Rissing, 1981). In *F. schaufussi*, short-term experience did not appear to control search pattern (Fourcassié & Traniello, 1993), although the control of search orientation resulted from a forager collecting one resource load and then searching for another appeared to involve responses mediated by behavioural predispositions (Traniello, 1987; Fourcassié & Traniello, 1994). However, in *F. aquilonia* such short-term experience did appear to be involved in the modification of searching behaviour with respect to a stable carbohydrate food source. Learning ability (experience) of *F. aquilonia* foragers, parallel to the stability of resources, could be the reason for this modification of search pattern in response to consecutive rewards. Orientation during search is one mechanism by which movement may be adjusted according to the distribution of food resource-dependent search tactics involving patterns of locomotion that increase the chance that a stable resource will be efficiently located. Likewise, the search pattern generated in response to protein food allows a forager to avoid scanning redundantly in the area of prior find, where the possibility of locating additional prey, which are unpredictable in time and space, is low.

The resource related differences in searching behaviour could be explained by considering two phenomena which are not mutually exclusive. 1) The foragers' reactive distance. For *F. aquilonia* foragers the distance of detection of carbohydrate food, when undisturbed, is extremely short (less than a few millimetres). Protein food, on the other hand, is discovered at greater distances (few centimetres) probably because volatile chemicals are produced by larval arthropods. Given this difference in the distance over which perception of protein and carbohydrate foods is achieved, the protein stimulated search pattern does not need to be narrowly centred around a prior site, as does the carbohydrate stimulated search pattern. Foragers should also require less time to scan a given area to find potential insect prey than for carbohydrate food sources. 2) Spatial memory (Cosens & Toussaint, 1985, 1986) also play a major role in differences in search persistence. In the laboratory set up foragers collecting sugar solution stayed 2.5 min (on average) feeding and another 1.5 min (on average) for scanning the site after first finding of food. Whereas foragers given a blow fly larva immediately returned to the nest after seizing it. Foragers which gather carbohydrate food thus may be able to store a more detailed picture of the food site surroundings than foragers collecting protein that were often found disoriented after seizing the prey. As a consequence foragers gathering sugar solution may develop an enhanced ability to subsequently locate a rewarding site. Data obtained for consecutive carbohydrate rewards support this supposition. Natural selection should favour search behaviour that maximises the rate of resource arrival at the colony (nest). The resource-related preparedness of searching *F. aquilonia* foragers allows the rate of resource harvesting by the colony to be adjusted to the probability of finding additional food. The searching *F. aquilonia* forager may also be responsible for the differences in individual foraging specialisations and colony level searching strategies.

CHAPTER 6

Time and energy budgets of wood ants

6.1 Introduction

The foraging animal must make decisions such as where and when to forage, which food items to include in a foray, when to give up a particular diet or foraging area, which mechanisms to employ in a foray and so on. The optimality approach to these decisions assumes that animals should tend to make such decisions so as to maximise foraging efficiency. As a consequence of looking mathematically at the foraging systems of animals, optimal foraging models have been developed which assume that the fitness of a forager can be measured in terms of some 'currency' such as food, energy or time; and that natural selection has resulted in individuals that forage in such a way to maximise the currency. MacArthur and Pianka (1966) and Emlen (1966) raised the topic of 'optimal foraging theory'. These authors perceived this as a question of finding which components of a time or energy budget increase and which decrease, as certain activities are enlarged. Most subsequent work in this mould has concentrated on foraging, and especially predation by individuals (Kamil & Sargent, 1981 for review). All these authors concur that the animal's 'goal' is to maximise its net energy gain per unit time throughout its life. However, most of the optimality models do not consider the animal's motivational state for feeding, but rather assume that the animal is permanently hungry and always feeds at a maximum rate. It is clear that energy is not the only constraint on an animal's foraging behaviour: physiological limitations, the risk of predation, the animal's dietary requirements, competition, food handling ability, mate-finding obligations and other necessary but non-foraging activities all have effect. Another important constraint is time. However, one can expect that natural selection will design animals in a way that their available time and energy is put to a maximum use. It seems reasonable, therefore, to expect that animals will treat time and energy as valuable resources and will budget accordingly. Interactions between time and energy are important in many aspects of animal behaviour. The animal has to budget for each type of activity and for the consequences particular to each of them. In such circumstances trade-off is inevitable. In addition to minute by minute considerations, animals take a more global account of their time and energy budgets. In nature, foragers encounter complex situations whose solutions may demand the sacrifice of some measure of foraging success in order to achieve other goals as well. Ultimately the trade-off is calculated by natural selection during evolutionary time in terms of fitness. A fundamental tenet of 'optimal foraging theory' is that the animal chooses a foraging pattern, or 'strategy', that will increase its life time fitness in that no animal's 'aim' is to prolong its own life time but rather to be successful at breeding within the life time it has. Obvious problems arise when attempting to relate such optimal foraging theories to the highly eusocial insects like ants which separate their reproductive individuals from sterile worker castes. In such cases an individual's effort cannot enhance her own reproductive success, only that of her queen(s). As the members of a colony are genetically related, the workers do increase their inclusive fitness by helping the reproductives (Carrol & Janzen, 1973; Bernstein, 1975). For an individual worker in such a system the constraints on optimisation of her foraging are somewhat different from non-eusocial animal. Costs to her own metabolism, incurred whilst acquiring food, are not the total costs to the reproductive unit which must be considered to be the entire colony. The energetic costs of all members of the colony for the duration of a foraging trip must be measured against the total profit from that trip (Emlen, 1966). The outcome of optimisation is not a individual gain but a gain of colony as a whole. If, however, individual foragers are able to minimise their own costs for a standard reward, it will eventually reduces the colony's cost. The assumption here is that once the foragers leave the nest their effort is independent of activity within the nest. Therefore some aspects of the conventional approaches to optimal foraging do still apply to decisions made by the foraging individuals as they exploit the environment outside the nest.

Orians and Pearson (1979) introduced the term central-place foraging to describe cases in which the foraging animal brings food back to a fixed location, a nest (the 'central place'). Although the central-place foraging concept was originally developed for the prey and predator type of system, it is reasonable to consider the wood ant social foraging system under this category. A foraging cycle for a central-place forager consists of a journey from the central-place (nest) to the foraging area, a time spent collecting food (handling) and a journey back to the central place. The efficient exploitation of available food is a vital requirement of all animals. How much food a forager can collect depends not only on how quickly it can find food but on how much time it has to spend finding and carrying to it nest. Some ants probably keep the time they spend in searching and in transport as small as possible by living near their food (Sudd, 1970). Wood ants use their ability to return to the same spot, but also may remain overnight with their aphids on trees many yards from the nest (Ökland, 1934). Perhaps this is because honeydew is not produced very fast early in the day and the ants will not go home till they have a full crop. Wood ants often down-load (by trophallaxis) their gathered honeydew to nestmates they meet at the foot of the tree, so that it may be carried home by a relay system. The optimality theory is a valuable tool in the quantitative study of adaptations. It has been used to generate hypotheses and organise data relating to foraging behaviour (Krebs, 1978; Pyke *et al.*, 1977).

6.2 Objectives of the study

The main aim of this study was to address how the wood ants budget the available time when collecting honeydew from aphid aggregations. Owing to the long foraging trails of wood ants, it would be advantageous to employ some sort of relay method to decrease the acquisition time. In this chapter, it was hypothesised that two distinct forager types exist which facilitate effective transportation of honeydew to the mound nests: a) Gatherers which collect honeydew droplets from individual aphids, and b) Transporters which collect from Gatherers and transport honeydew back to the nest in a relay system. This division of labour would reduce the cost of travelling with respect to value of the food gathered and at the same time helps to defend food sites from alien ant colonies through continuous occupation of a site.

This hypothesis was tested in two ways;

1. Providing restricted access to a food source ('model aphid aggregation') and non-restricted access to a food source to the same colony in the laboratory, foray intervals of foragers fed from two types of food sources were compared using two sample t-

test assuming equal variance. If there was a bottleneck created by restricting the access at the food source, (like slow production rate at the aphid aggregations) foragers must respond to this: reducing their foray intervals by down loading on the way to the nest (involving relay system).

2. Due to the complexity and length of foraging trails in the field quantification of individual foray intervals was not feasible. Hence by assuming journey time ((t_r) travel between nest and aggregation) was constant: the time required to become replete at the aphid aggregation by gathering honey dew droplets (t_g) and become replete by trophalaxing with semi-replete foragers at aggregation were compared. This particular comparison was done by comparing, observed production rate ***R'*** (mean crop load of a replete forager(V_{max}) x departure rate at the aggregation) and actual production rate ***R*** (volume of the honey dew droplet x production rate of honeydew at the aphid aggregation). If there is a big difference between ***R*** and ***R'***, in other wards ***R'*** is higher than ***R*** there would be a additional stored crop (Gatherers) where, foragers could have trophallaxed and obtained full crop before departing the aphid aggregation.

6.3 Parameters relevant to foraging at aphid aggregations

At aphid aggregations, honeydew is produced at a certain rate and should be immediately collected by the foragers (Gatherers) and stored in their crops: it will otherwise be lost. When the foragers have collected sufficient to become replete they leave the site and return to the nest, or pass their loads to another forager (Transporter).

If R (mm^3/min) is the rate of honeydew droplet production/unit time by the aphid aggregation and all of the honeydew is collected by the foragers; and nV is the volume gathered/unit time, where n is the number of foragers at the aphid aggregation and V the amount of honeydew collected by an individual: then $R = nV$.

If the number of foragers (n) at the aphid aggregation is constant, then the amount of honeydew (V) collected per unit time is also constant. Assuming R is a fixed rate, when n is increased V will tend to decrease: hence there should be a V_{max}. corresponding to an optimal number of foragers, n_0. (Dreisig, 1988).

Other relevant constraints which operate on gathering honeydew are the time required to run between the nest and aggregation, t_r, and the time required to become replete at the aggregation site by gathering honeydew droplets, t_g , and/or by trophallaxis. The total volume of honeydew passed by trophallaxis at the aphid aggregation = $n_t v$, where v = volume of honeydew passed by one bout of trophallaxis; n_t = number of trophallactic bouts per unit time observed at the aphid aggregation. t_x = duration of a bout.

6.4 A mechanism by which a forager achieves the functional goal of maximising net reward per unit time

Table 6.1 List of abbreviations

Abbreviation	
Fi_n	Foray interval (non-restricted access food)
Fi_r	Foray interval (restricted access food)
$l_n t_x$	Length of trophallactic bout (non-restricted access food in the laboratory)
$l_r t_x$	Length of trophallactic bout (restricted access food in the laboratory)
n	Number of foragers present in the aphid aggregation
n_o	Maximum possible number of foragers at aphid aggregation
n_t	Number of trophalactic bouts per unit time
$n_t v$	Volume of honeydew passed between two foragers at a time
$n_{tc} t_x$	Total time required to get replete from already replete individuals in the laboratory
$n_t t_x$	Total time required to get replete from semi repletes in the field
Nrt	Travel time of non replete forager from nest to non-restricted food (laboratory)
R	Rate of honeydew production at aphid aggregation
R_t	Travel time of replete forager from non-restricted food to nest (laboratory)
t_x	Duration of trophalactic bout in the field
t_n	Time spent within the nest (non restricted food: laboratory)
t_g	Patch residence time
t_r	Travel time of a forager
T_f	Foray time
V	Volume of honey dew carried by the replete individual on her departure
V_{max}	Maximum possible crop load
v	Volume of honeydew transferred by the trophalactic bout

It has often been pointed out that fitness will not necessarily be maximised by maximising energy. The animal's goal while foraging may be to avoid starvation (Houston *et al.*, 1988; Stephens & Charnov, 1982) or the animal may have to combine foraging with some other activity such as defending territory (Kacelnik *et al.*, 1981). The main aim here was to find the policy that maximises net reward over repeated series of foraging trips. It is therefore worth looking at a single foraging period to find the policy that maximises the rate of food input to the central place (nest). Travel time is of course one of the parameters involved.

Given that a droplet of honeydew from *Symydobius oblongus*, an aphid on silver birch, has an average volume of 0.03 mm^3 and an average replete wood ant crop capacity of 5 mm^3 (Cosens unpublished data); a forager requires to gather some 167 droplets to maximise her load. Assuming that the rate of honeydew production per aphid aggregation is a constant and that a forager, one of a fixed population, fills her crop by gathering droplets, she would require to remain at the aggregation for a relatively fixed time (t_g) (patch residence time). Her running time (t_r) between nest and aggregation is also essentially constant. Thus her total foray time (T_f) will be;

$$T_f = t_r + t_g \qquad (1)$$

While (t_r) is fixed, a forager may reduce her time at the aggregation (t_g) by filling her crop by trophallaxis with a few semi-repletes (Gatherers). Thus, this forager (the Transporter) will have a total foray time;

$$T_f = t_r + n_{tc}t_x \qquad (2)$$

Where (n_{tc}) is equal to the number of trophallactic bouts required to fill the crop and (t_x) is equal to duration of trophalactic bout in the field. This value will be less than when a forager becomes replete by gathering droplets at the aphid aggregation. The time spent by a forager at the aphid aggregation may be (t_g) which includes handling time, waiting time and crop filling time or ($n_{tc}t_x$) which involves negotiating trophallaxis;

$$T_f = t_r + t_g \qquad (3)\ \text{(Gatherers not involved)}$$

$$T_f = t_r + n_{tc}t_x \qquad (4)\ \text{(Gatherers involved)}$$

$$\text{Therefore: } t_r + n_{tc}t_x < t_r + t_g \qquad (5)$$

Hence, if $t_r + n_{tc}t_x$ is [(T_f (5)] operating in the wood ant foraging system foragers would maximise net reward over series of foraging trips (Carriers involved) by reducing time spent at aggregation (t_g).

6.5 Materials and methods

6.5.1 Laboratory experiments

Owing to long foraging trails (up to 100 m) and long waiting time at aggregations to fill crops it is difficult to quantify (T_f) in the field. Hence a model 'aphid aggregation' (Fig. 6.1) was constructed on the foraging table (Abernethy, 1990) providing the real constraint operating in the field (long waiting time to fill crop). The experimental set up was placed at the same distance and height where foragers had fed during previous experiments. This 'aphid aggregation' gave access to the unlimited sugar solution by means of 3 (4 mm) bore nozzles (middle nozzle was always prevented access by blocking with air tight bung) working on a simple siphon principal from a 50 ml open syringe reservoir. The non-air tight bung and a mesh prevented ants from drowning in the reservoir. The ratio of reservoir surface area to total nozzle surface area is large enough for the surface tension at the nozzles to prevent any overflow. The distance between mound nest and 'model aphid aggregation' was 2 m and its height above the level of the foraging table was 0.5 m. However, these distances are not comparable with the lengths of foraging trails observed in the field. On the 11th day upon finding the 'model aphid aggregation', foragers (19) were yellow marked during a 5 min period (9.40-9.45h) in order to identify a cohort. Then each nozzle was scanned at 5 min intervals between 9.45-11.45h. On the following day (12th) unmarked foragers (21) found at each nozzle were marked pink during a 5 min period (9.50-9.55h) and sampling was performed as before. The behaviour of uniquely marked individuals (within these marked cohorts) was monitored for their actual foray numbers (the frequency of consecutive visits by these particular foragers to one or other of the nozzles). From these data the foray intervals were derived. The duration of the typical bout of trophallaxis within the laboratory set up (l,t_x) was measured for 15 bouts on the foraging trail (Table 6.2).

These results were compared with the foray intervals obtained for individuals using a non-restricted access food source at the same distance and height as the model 'aphid aggregation'.

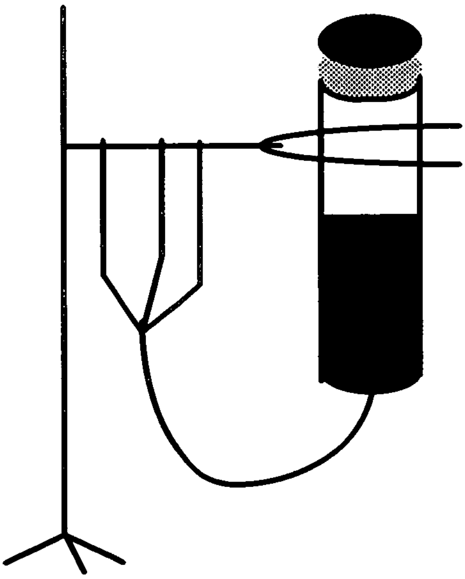


Figure 6.1 Model 'aphid aggregation'

For this set up the mean travel time of non replete ants from the nest to food (Nrt), the mean travel time of replete ants from food to nest (Rt), duration of the trophallaxis bout ($l_n t_x$), time spent within the nest by the replete forager (t_n) were obtained (Table 6.2). When using the restricted access food source ('model aphid aggregation') some of these parameters were altered due to a change in behaviour: the majority of individuals did not travel back to the nest after becoming replete, rather they engaged in trophallaxis near the site or on their way back to the nest with siteward-bound foragers (relay system?). This behavioural change must have been related to one of the two possible constraints that occur in the field: that is the long waiting time at the food site due to limited access. The other constraint, a long foraging trail, was not examined in this experiment. Now, assuming that foray interval ($Fi_{nr} = T_f - t_g$) was comparable to the $Nrt + Rt + l_n t_x + t_n$ of a average forager: it is reasonable to compare foray intervals obtained during the early part of the day (9.00-12.00h: when foragers were most active) as a valid index of foray times (T_f). Where $t_r = Nrt + Rt$ (Travel time of a forager ($\boldsymbol{t_r}$) = Travel time of a non-replete forager to non-restricted access food (***Nrt***) + Travel time of a replete forager to non-restricted access food source to nest (***Rt***)). In other words if the foragers operate through a relay system to compensate for the long waiting (t_g) time at the 'model aphid aggregation, significant differences in foray intervals (*Fi*) would be expected because due to the limited access at nozzles patch residence time (t_g) tends to increase and trophallaxis bouts become more common such that sitebound foragers become replete from such bouts ($n_{tc}t_x$) rather than from the nozzles. This behaviour may operate at any point on the short foraging trail but typically occurs on or near the tree. Hence foray intervals obtained with either the restricted access food ('model aphid aggregation') or the non-restricted access food must accord with: ($t_r + n_{tc}t_x$) or ($t_r + t_g$) respectively. These two types of foray interval were compared using two sample t-test assuming equal variances. The null hypothesis was that there was no difference between the foray intervals observed when using restricted and non-restricted food sources.

6.5.1a Results

Table 6.2 Parameters obtained with restricted and non-restricted access food sources

Parameters		$\bar{x}$ (min)	SD	N
Travel time for the non-replete forager from nest to food (food) (Nrt)		4.5	0.7	31
Travel time for the replete forager from food to nest (Rt)		2.5	0.4	31
Length of trophallaxis bout ($l_n t_x$) (non-restricted access food)		1.5	0.5	16
Length of trophallaxis bout ($l_r t_x$) (restricted access food source)		3.2	0.2	15
Time spent within the nest (t_n) (non-restricted access food)		8.2	5.2	21
Foray interval obtained for non-restricted access food (Fi_n)		16.8	1.03	10
Foray interval obtained for restricted access food (Fi_r)		9.6	4.3	18
Feeding time of a average forager (non-restricted access food source)		2.5	0.35	47
Feeding time of a average forager (model aphid aggregation)		3.7	1.63	17
Rate of trophallaxis near the nozzles (restricted access)	min^{-1}	4.2	0.93	14
Rate of trophallaxis near the sugar dish (non-restricted access)	min^{-1}	0.7	0.28	14
Volume collected between 9.45-11.45 am (non-restricted access food)	mm^3	5.9	0.68	5
Volume collected between 9.45-11.45 am (restricted access food)	mm^3	5.6	0.38	7

Nrt and *Rt* values were obtained only for the non-restricted access food

Table 6.3 Mean number of foragers observed at nozzles for 5 min sampling period

Day	Amount of food collected for 2h period (mm^3)	*Mean number of foragers observed at nozzles for 5 min period (N=25)	Standard deviation (SD)
11	5.0	18	2.9
12	5.2	17	2.2
14	6.0	16	2.0
15	5.8	16	1.9
20	5.7	16	2.8
22	6.0	16	4.2
25	5.5	14	2.6

* obtained from 5 min samples between 9.45-11.45 am.

Mean volume of food collected on each of 7 days: $\bar{x}$ =5.6 cm^3, SD=0.38, N=7

Mean number of foragers at a site for each 5 min period: $\bar{x}$ =16, SD=1.2, N=7

Table 6.4 Mean number of foragers observed at non-restricted access food source for 5 min sampling period

Day	Amount of food collected for 2h period (mm^3)	*Mean number of foragers observed at non-restricted access food source for 5 min period (N=28)	Standard deviation (SD)
01.08.96	5.9	12	1.7
02.08.96	6.0	11	1.5
04.08.96	4.9	12	1.8
07.08.96	6.1	12	1.2
12.08.96	6.8	13	1.4

* obtained from 5 min samples between 9.45-12.00 PM.

Mean volume of food collected on each of 5 days $\bar{x}$ =5.9 cm^3, SD=0.68, N=5

Mean number of foragers at site for each 5 min period $\bar{x}$ =12, SD=0.92, N=5

Foray intervals for some of the individuals at the model aphid aggregation were less than 1 min due to replete individuals engaging in trophallaxis with other foragers nearby and immediately returning to the nozzle. The foray intervals which were less than 1 min are not included in the analysis, rather they were considered as extended forays (see Table 6.5).

Table 6.5 Time spent feeding by foragers at a restricted access food source (6.9.96)

Forager	Time (min) spent feeding to replete for successive visits												mean
W	5	3	2	2	3	2	3	5	2	3	4	3	3.1
Y													
Yleg	7*	5	10*	6									7
Wmoon	2	3	2	5									3
Ymoon	5	3	2	6									4
Wdash	2	3	1	2	2								2
wdum	6	7	5	10*									7
Ydash	2	3	5										3.3
Ydum	2	3	2	4									2.8
Green	3	2	2	3									2.5
Gside	3	5	2	3	4								3.4
Gmoon	5	6	11*	5									6.8
Celtic	2	3	2	3									2.5
Greeny	3	5	2	4	1								3
Gface	1	3	5	1	2								2.4
Dash	3	2	6	3	2								3.2
Smile	4	2	3	5	2	3							3.2
Blue	5	2	3	1	1	3	2	5					2.8

Overall mean $\bar{x}$=3.65, SD=1.63, N=17, '*' extended forays

Table 6.6 Individual foray intervals (mins) between 9.00 to 12.00 with non-restricted access food

	01.08.96	02.08.96	12.08.96	Mean	SD
WV	17 18 15 16 17 17	16 17 18 16 17		17	0.90
WO	16 14 16 15 16 17	17 16 15 16 16 17 16	17 16 16 17 16 16	16	0.78
GR	15 16 17 15 16 14	15 16 15 17 16 16 15	16 16 15 16 17	16	0.83
JADE	17 18 18 17 19 18	15 16 16 16 17		17	1.18
GYLE	12 15 16 17 16 17	17 17 16 17 17 16	15 17 16 17 16 16	16	1.23
GIS	17 16 15 9 16 15	18 18 17 17 16 17	17 16 17 19 17 18 17	16	2.06
WYR	20 19 20 21	21 20 19 19 19 21	19 19 18 19 18 19	19	0.96
HAP	14 15 16 16 16 17	15 16 16 16 16 15 16	16 17 16 17 17 16 16	16	0.76
WAG	19 18 17 19	19 19 18 19 19	18 18 19 17 17 16 17	18	1.00
GAN	15 16 18 17 17 18	16 17 16 16 17 16 16	17 16 17 17 18 18	17	0.87

Overall mean $\bar{x}$=16.8, SD=1.032, N=10

It was clear that foray interval (**Fi_n**) with the non-restricted access food source was consistent 17 min (SD=1.032, N=10: Table 6.6) and almost equal to [mean travel time of a non replete forager from nest to non-restrict access food (*Nrt*) + mean travel time of a replete forager from non-restricted access food to the nest (*Rt*) + length of trophalactic bout with non-restricted food (l_nt_x) + time spent within the nest (t_n)] = (4.5+2.5+1.5+8.2) = 16.7 min (Table 6.2). The mean foray interval (Fi_r) of 9.6 min (SD=4.3, N=18) obtained with the 'model aphid aggregation' (restricted access food source; Table 6.6) was significantly lower than 16.7 min obtained with the non-restricted source (t = -5.1, df 26, $P<0.05$, Table 6.7). Nevertheless, the volumes of food transported into the nest over the two hours between 9.45 and 11.45h from the non-restricted and restricted access food sources, respectively, were 5.6 and 5.9 mm^3 (Tables 6.3 & 6.4) which were not significantly different. These observations implied that when there was a long waiting time to fill their crops, foragers may organise themselves to maximise their ability to satisfy the colony requirements at a same rate as when there was no waiting time. This organisation may have been involved the subdivision of the foraging effort into gathers and transporters and the increased use of trophallaxis (Table 6.2) between these sub populations of foragers (relay system). This approach effectively overcomes the bottleneck caused by the waiting time by allocating fewer foragers (Gatherers) at the aphid aggregation at any time in the field. The Transporters can fill their crops within a few minutes by trophallaxing with replete foragers ($n_t t_x$) even without knowing the actual position of the aphid aggregation, merely the route to the tree. It was observed in the laboratory that replete individuals from the 'model aphid aggregation' engaged in intense trophallaxis at different points on the route back to the nest (tree trunk, tree base, on the bridge and so on) and when non-replete returned to the food source directly.

Table 6.7 Two sample t-test: assuming equal variances for the foray intervals obtained for different individuals

	Restricted access food	*Non-restricted access food*
Mean	9.6	16.8
Variance	18.5	1.03
Observations	18	10
Pooled Variance	12.9	
Hypothesised Mean Difference	0	
df	26	
t Stat	-5.10	
P(T<=t) one-tail	1.3 ⓽ 10^{-05}	
t Critical one-tail	1.7	
P(T<=t) two-tail	2.5 ⓽ 10^{-05}	
t Critical two-tail	2.1	

t = -5.10, df 26, $P<0.05$

6.5.2 Behaviour of colour-marked foraging cohorts at the 'model aphid aggregation'

The mean number of foragers observed at each nozzle of the 'model aphid aggregation' was 16 (SD=1.2, N=7: Table 6.3) although the maximum accessible number at the two nozzles was 9. When recording the number of foragers at the nozzles, all the foragers surrounding the nozzle including foragers engaged in multiple trophallaxis were counted (n). The low value of standard deviation (1.2) implies that the number of foragers at the 'model aphid aggregation' at a particular time did not vary significantly. The behavioural patterns of yellow and pink marked foraging cohorts were highly predictable over several days (Fig. 6.2, 6.3 & 6.4). However, by day 25, the number of yellow and pink marked foragers reduced and the number of unmarked foragers increased (Fig. 6.5). This may be explained by considering the turnover rate of the foraging population (1-1.5 months). The predictability of the behavioural patterns of colour-marked foraging cohorts implies that there must be a finely tuned organisation within the foraging system: in other words Gatherers always represent the same sub population of individuals in the foraging population. The next question to arise is: do the Transporters represent another sub population of the same foraging population? Unlike the Gatherers, Transporters do not reach the aphid aggregation in a predictable manner. The small number of foragers (16 Gatherers) observed at the 'model aphid aggregation' is much less than the large number of foragers observed on the foraging trail and the tree trunk. Hence sampling of potential Transporters away from the 'model aphid aggregation' was not possible with any reliability. However, the variance of 18.5 obtained for the mean foray interval of 9.6 min of Gatherers observed at the 'model aphid aggregation' was very high compared to that for the unlimited access food source of 0.94 and mean foray interval of 17 min. The implication of this is that the Gatherers may have transferred their loads ($n_{tc}t_x$) indiscriminately to Transporters, and the altered behaviour could be explained by considering that the long waiting time at the aphid aggregation had created an unexpected food deficit within the nest. As a consequence of this food-deficit a large number of potential foragers were deployed from the nest.

Figure 6.2 Behavioural pattern of foragers on three successive days at each nozzle of the model aphid aggregation over 2 h period

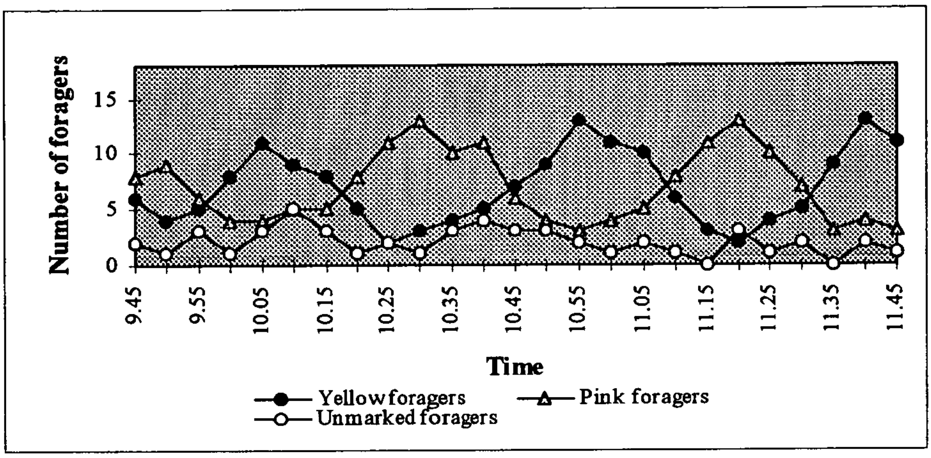


Figure 6.2a Behavioural pattern on day 14

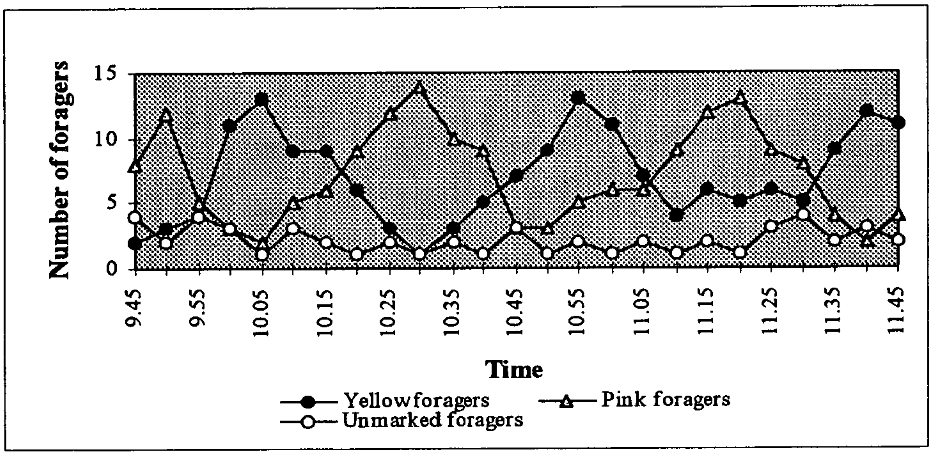


Figure 6.2b Behavioural pattern on day 15

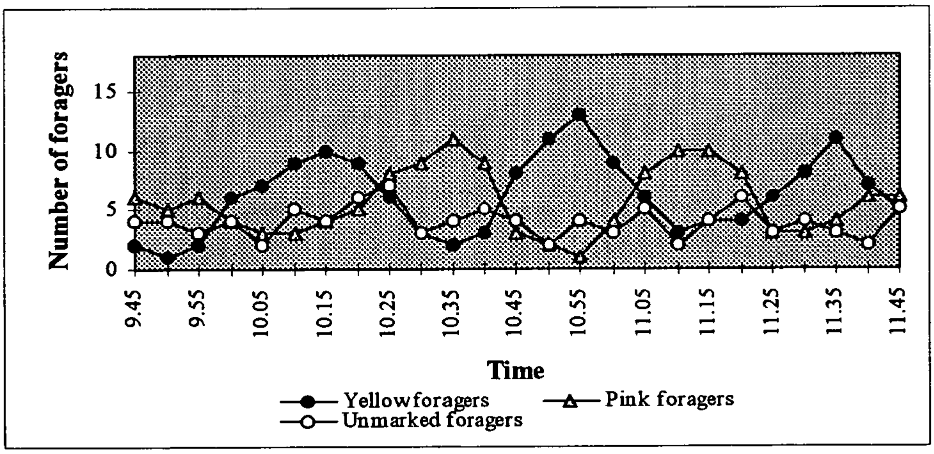


Figure 6.2c Behavioural pattern on day 20

But the limited access at the 'model aphid aggregation' may have caused these deployed foragers to negotiate trophallaxis with nest-bound repletes and so creating a relay system of Gatherers and Transporters. Another significance of the observed high incidence of trophallaxis may be to direct these novel foragers towards a food site (Cosens & Toussaint, 1986), as well as to speed up the acquisition of food. However, it has been suggested that foragers are able to transfer information about the accessibility to the food and so deploy only sufficient numbers to maximise efficiency (Cosens & Toussaint, 1985 & 1986). The colony hunger may have overridden this response to the accessibility of food and the foragers organised themselves to maintain the input food to the nest despite the bottleneck at the food source.

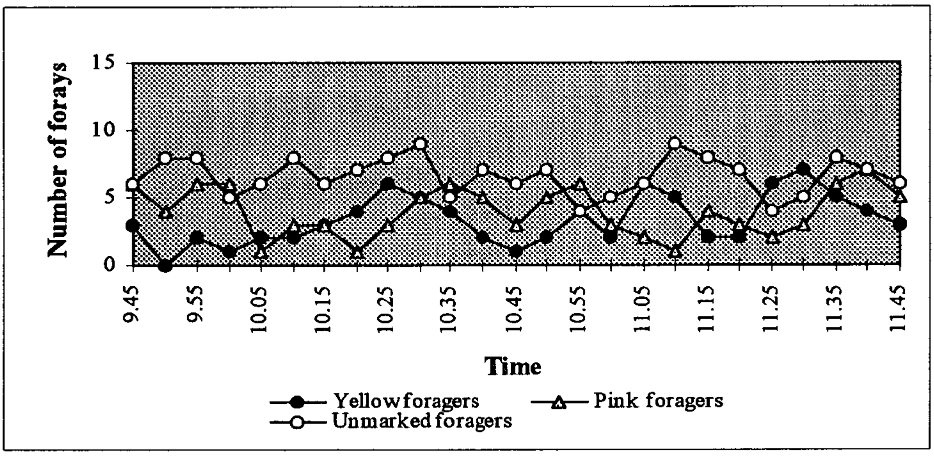


Figure 6.3 Behavioural pattern at day 25

6.5.3 Field experiments

Using a CCTV camera (Panasonic Colour Model WVP-200E) and video recorder (Model NV-100), ants which were foraging at a aphid aggregation (*Cinara picae*) on a small spruce tree were filmed at Loch Ard Forest, Aberfoyle. Whilst filming, the number of aphids forming a particular aggregation, the number of foragers (n) present at the particular aggregation (counted every 10 min), the mean duration of a foray site-visit (t_g), the arrival and departure rate of foragers for ten 10 min intervals and the number of trophallactic bouts for six 10 min periods (n_t) were recorded and their duration (t_x) (Table 6.9). Using an appropriate magnification factor (obtained by measuring a head width ratio of 15 foragers taken from the foraging trail and 15 forgers from the video film), the mean volume of honeydew carried by replete foragers was calculated (see Chapter 1). It was assumed that mean volume of honeydew carried by the replete forager was equal to the maximum possible crop load V_{max}: no reason for an individual to carry less volume other than maximum possible volume after being travelling long distance in the field. It was also assumed that all the honeydew produced at aphid aggregation was collected by foragers and production rate was equal to the amount carried by the replete foragers departing the aphid aggregation. The production rate at aggregation was also estimated from the volume of honeydew droplet produced by a aphid. These production rates obtained from two methods were compared.

Two aphid aggregations (A1 and A2) were selected for the analysis on the first visit to the field (10.10.96). By the second visit, one week later (17.10.96) A2 had subdivided: some aphids had moved downwards on the trunk by 30 cm, these relocated aphids were subsequently considered as A3. The number of aphids per aggregation had also reduced and this reduction continued: some aphids were observed dispersed on the bases of pine needles and this subsequent relocation (laying over wintering eggs?) may have been the cause (Table 6.8). A forager's journey time ((t_r) travel between nest and aggregation) was constant: the time required to become replete at the aphid aggregation by gathering honeydew droplets (t_g) was relatively constant and longer than becoming replete by trophallaxis (nt_x). Hence it was reasonable to assumed foragers organised as Gatherers and Transporters to maximise the harvesting of the available honeydew: $(t_r) + (nt_x) < (t_r) + (t_g)$.

6.5.3a Results

Table 6.8 Number of aphids observed at each aggregation during 3 consecutive visits separated from one week interval

Date	A1	A2	A3
10.10.96	39	58	---
17.10.96	30	16	38
23.10.96	18	10	19

A1, A2 & A3 are aphid aggregations

The mean crop load (maximum possible crop load V_{max}) carried by the replete foragers on departure from the aphid aggregation was 5.5 mm^3 (N=16). If we assumed all the honeydew produced at the aphid aggregation is collected by foragers, the production rate must be equal to the amount carried by the replete foragers departing the aggregation per unit time ($\boldsymbol{R'} = nV$).

Therefore **production rate** is equal to the **(replete crop load)** x **(departure rate)**:-(Data obtained from the Table 6.9)

Observed production rate of A1: 5.5 x 0.59 x 60 = 19.47 cm^3h^{-1}
Observed production rate of A2: 5.5 x 1.10 x 60 = 36.30 cm^3h^{-1}
Observed production rate of A3: 5.5 x 0.47 x 60 = 15.51 cm^3h^{-1}

Table 6.9 Parameters related to field observations

	Aggregation 1	Aggregation 2	Aggregation 3
Number of aphids	39	59	38
Number of foragers (n)	$\bar{x}$=23.4 N=12 SD=0.99	$\bar{x}$=35.7 N=8 SD=1.67	$\bar{x}$=24 N=14 SD=1.11
Number of ants per aphid (n_0)	1.69	1.6	1.58
Observed production rate (mm^3min^{-1}) (*R'*)	3.25	6.05	2.59
Actual production rate (mm^3min^{-1}) (*R*)	0.429	0.638	0.418
Observed duration of patch residence time (t_g') min	$\bar{x}$=41 N=5 SD=13.6	$\bar{x}$=42 N=6 SD=6.77	$\bar{x}$=50 N=7 SD=12.5
Calculated duration of foraging visit (t_g)	40	31.3	48.5
Arrival rate (ants min^{-1})	$\bar{x}$=0.56 N=10 SD=0.54	$\bar{x}$=1.2 N=8 SD=1.4	$\bar{x}$=0.52 N=7 SD=0.75
Departure rate (ants min^{-1})	$\bar{x}$=0.59 N=10 SD=0.88	$\bar{x}$=1.1 N=8 SD=2.1	$\bar{x}$=0.47 N=7 SD=1.5
Number of trophalactic bouts min^{-1} (n_t)	$\bar{x}$=5.35 N=6 SD=0.44	$\bar{x}$=5.2 N=6 SD=0.70	$\bar{x}$=6.95 N=6 SD=0.28
Length of the trophallactic bout (t_x) (min)	$\bar{x}$=0.42 N=20 SD=0.39	$\bar{x}$=0.49 N=23.SD=0.37	$\bar{x}$=0.56 N=19 SD=0.57
The mean crop load carried by the replete forager (mm^3) (V)	5.5		
Amount exchange in the trophalactic bout (mm^3) (v)	$\bar{x}$=0.92 N=8 SD=1.29		
Time spent on collecting honeydew from semi replete foragers (min) (nt_x)	5.5/0.92 x 0.42 (2.5)	5.5/0.92 x 0.49 (2.9)	5.5/0.92 x 0.56 (3.3)

With a mean diameter of a honeydew droplet of 0.398 mm, the calculated volume of a honeydew droplet ($4/3\pi r^3$) is 0.033 mm^3. The group of 10 aphids produced 35 droplets ($\bar{x}$=34.6, SD=6.9, N=7) in each 10 min period. Therefore the production rate of honeydew is equal to 21 droplets aphid^{-1} h^{-1} (0.033 x 21 = 0.69 mm^{3} aphid^{-1} h^{-1}). The actual production rate of droplets (***R***) at the aggregations must be equal to **(number of aphids)** x **(the production rate aphid^{-1})**. Therefore:-(Data obtained from the Table 6.9)

Actual production rate at A1 → 0.69 x 39 = 2.69 cm^{3}h^{-1}
Actual production rate at A2 → 0.69 x 58 = 4.00 cm^{3}h^{-1}
Actual production rate at A3 → 0.69 x 38 = 2.62 cm^{3}h^{-1}

The observed volume of honeydew transported each hour from the aphid aggregation was much larger than the production rate of honeydew droplets by the aphids. This difference in volumes implied that foragers not only collect honeydew droplets directly from aphids but collect also from Gatherers (semi-repletes) that constitute an additional stored source. The high rates of trophallactic exchanges at aggregations, (Table 6.9) tree trunks and foraging trails support this supposition.

The mean duration of a foraging visit ((t_g) patch residence time) may also be obtained from the number of foragers present at the aphid aggregation/mean of the arrival and departure rates (Table 6.9). Therefore the calculated mean duration of a foraging visit for:-

	Calculated (min)	Observed (min)
A1 → [23/(0.56+0.59)/2]	40.0	41
A2 → [36/(1.2+1.1/2]	31.3	42
A3 → [24/(0.52+0.47)/2]	48.5	50

6.6 Discussion

When the foragers were provided with non-restricted access food source in the laboratory their foray intervals (***Fi_n***) were relatively consistent (Table 6.6) and almost equal to the 17. That is $Nrt + Rt + l_n t_x + t_n = 16.7$ (4.5+2.5+1.5+8.2): Table 6.2). However, restricting access to the food resulted in a long waiting time at the aggregation (t_g) to get replete. Foragers perceived this constraint and adopted an optimal behaviour. In this situation, it was reflected in lower foray intervals: (***Fi_r***) = 9.6 observed at the 'model aphid aggregation' (Table 6.2) by transporting gathered honeydew via a relay system to the nest (involving Gatherers and Transporters). Foray intervals were not easy to obtain in field situations due to the length of the foraging trails (up to 100 m) and often these trails go unseen beneath moss covers.

According to the above observations it can be inferred that individual foragers made decisions to maximise the net rate of reward during a foraging bout. This goal was achieved to a large extent by minimising time spent at the aggregation $(t_r + t_g)$ through a relay system $(t_r + n_t t_x)$: because travel time t_r was constant. The foragers may use the time spent at an aphid aggregation (patch residence time (t_g)) in the rule defining optimal behaviour: that is either to collect honeydew droplets directly or to depend on trophallaxis with semi repletes to obtain a full crop (5.5 mm^3) and to return to the central place (nest) in the shortest time. Observed and calculated durations of foraging visits were similar: this time (t_g) spent at an aphid aggregation was much longer than the time (nt_x) spent obtaining a full crop-load by collecting honeydew from semi repletes (Table 6.9). This difference implied that foragers arrived at the aphid aggregation to collect honeydew droplets, but a long waiting time induced them to negotiate the optimal behaviour. Hence foragers' patch residence time (t_g) was not (nt_x), but nt_x + initial handling time. Finally it could be argued that the hypothesis that the foragers optimise their net reward per unit time was valid. Foraging behaviours of organisms are likely to represent evolutionary compromises based on various selection pressures: yet economic decisions may provide maximum gain for the ant species which travel along foraging trails more than 100 m long because the efficiency of foraging represents a significant component of biological fitness.

CHAPTER 7

7.1 General discussion

In social insect societies the factors motivating the observed behaviours are not clearly discernible because the natural environment is not controllable. However, behaviours are 'natural' only when they are not isolated from each other or the natural environment: indeed there is always the risk, especially with social insects, that behaviours produced by isolated individuals under experimental manipulations may be abnormal. Even if the individual behaviours are discernible in this way, piecing them together in order to get an overall picture is very difficult. All of the work undertaken in this study was based on an environment where the ants could engage in their natural social activities and they were not isolated from each other. Only one aspect of their social activity: foraging was subjected to artificial manipulation creating an experimentally controlled situation.

The organisation of 50,000 or more ants is not a easy task. Individual behaviours and roles seem to play a large part of this organisational structure. A division of labour enables specialisation and a greater efficiency for carrying out these roles. The foraging population is the most susceptible part of the colony to mortality through predation, and, therefore, it would be advantageous if foragers represent a small proportion of the energetic investment of the colony. Porter and Jorgensen (1981) have shown that in *Pogonomyrmex owyheei* the foraging population comprises older workers that retain relatively small energy reserves and represent a 'disposable caste'. However, this was not true for *F. aquilonia*: immediately after the long starvation period a large number of newly eclosed individuals were recruited to the foraging population and have been observed in these experiments (these newly recruited individuals are lightly pigmented and were often carried by veteran foragers back to the nest after becoming replete). There was a relationship between the number of foragers outside the nest and the duration of starvation: that is the smallest population of workers forage sufficient to satisfy the immediate requirements of the colony. According to Heinrich (1979) in a hungry hive of bees, a greater proportion of newly eclosed workers forage compared to a satiated colony. Foraging populations of both ants and bees seems to be regulated by the colony hunger and it influences the behaviour of potential foragers. In a hungry colony a returning replete ant is more likely to influence prospective foragers compared to the well fed colony. This will stabilise an appropriate number of foragers to supply colonial requirements, simultaneously minimising loss of investment resulting from mortality due to the high risk foraging task. It has been shown in marking experiments with *F. aquilonia*, that only a relatively small number of the potential foragers actually forage on any particular day (Chapter 2, Table 2.6).

Within an experimental day, the foraging population at a particular site was represented by a heterogeneous group: foragers that make a high number of forays (high raters) and foragers that make low number of forays (low raters). When the performance of any one forager was compared across several days, she was seen to maintain a similar foraging rate (Figs. 2.6, 2.7, 2.8 & 2.9). This was particularly true for high raters: in some low raters the frequency of forays tended to increase as the days progressed although the majority of them maintained a constant performance. The novel foragers when recruitng to the foraging population make fewer forays hence individuals that tended to increase foray frequencies may be the newly recruited members. Individuals in this study had shown a high degree of fidelity to profession as well as to a particular spatial region of the nest. The role of ‘a worker’ is subdivided many times over to give each individual ant particular tasks to carry out and be responsible for within a given nest location. The individual foray frequencies and foray intervals over days seemed less variable for individuals (Figs. 2.6-2.9) than between individuals: this may result from the foragers’ allegiance to certain spatial regions within the colony. In contrast to newly recruited foragers, veteran foragers maintain strong site allegiance (Tables 3.13 & 3.25). It would be expected that since foragers return to the same rewarding site, they would use the same learnt route to get there: this practice explains route fidelity. The relative stability of Scottish woodlands has favoured predictions based upon the experience of foragers, and a foraging strategy of returning to previously rewarded sites would be prudent by reducing search time. A forager searching for new food sources will, at an individual level, be uneconomical compared with a forager visiting a ‘known’ source of food in a stable habitat. The plasticity of this allegiant strategy was observed only when the quality of food was altered: if a food source was extinguished or if the colony need could not be satisfied with the existing resources. The preferred site was often the first site located (Fig 2.2). Should a resource run dry, then foragers explore elsewhere and upon locating an alternative, subsequently switched their allegiance. In the laboratory discovering an alternative site after the known site ran dry took 7-10 days. In the wild with a more complex environment this time may be extended perhaps causing severe detrimental effects to the colonies. This outcome may not differ from the effect of clear-felling practised in Scottish woodlands in present days. As the preferred food sites of *F. aquilonia* are the first located sites: maximisation of the net energetic yield of the colony as a whole may conflict with the optimal foraging as measured at the individual level. Site allegiance was a constant property of certain individuals of the colony's foraging population. A key component of the wood ants' foraging system was the mechanism whereby the colony kept a large proportion of its foraging population distributed on the most profitable food sites (Chapter 3, Fig. 3.1) whilst its members showed strong site allegiance. Wood ants discriminate food sources without making comparisons among honeydew (carbohydrate) sources as suggested by Lamb and Ollason (1993). The newly recruited (naive) foragers more often show transient behaviours (Tables 3.13 & 3.25) in their foraging repertory than veteran allegiant foragers. The daily recruitment of a small number of foragers has also been observed in these experiments (Tables 3.3, 3.6 & 3.7). In other words there was a continuous turn over in the foraging population (Fig 2.17). These naive foragers represent the behaviourally flexible members of the foraging population and were used to trace novel food sites likely to occur in the habitat. By adhering to this strategy, (recruiting daily proportions of uncommitted foragers to the foraging population) wood ant colonies are able to overcome the behavioural inertia (dogmatic approach to the environment) associated with site allegiance and the possible lack of flexibility at times of dramatic change such as clear-felling, which seriously disrupts the topographic tradition.

Although significant differences were observed in the foragers' level of activity, there were no specific foraging populations operating during the day and night. The observed gradual declining activity when the colony was subjected to a 17.5:6.5 light:dark cycle (Figs. 2.10 & 2.12), and which did not begin immediately after lightout, suggested some sort of endogenous nature of their activity pattern. However, that the rhythmicity was reduced in constant dark (Fig. 2.13) and completely lacking in constant light (Fig. 2.14) suggested the foraging rhythms of wood ants were entrained by light-dark cycles. This extended foraging habit enabled them to obtain a broader selection of prey and protection of food sites from alien ant colonies than would be obtained from concentrated foraging at the same time each day.

The food of the *F. aquilonia* is patchily distributed over a large area. Such a distribution demands that long distances are travelled and considerable powers of orientation are required. For orientation, information concerning spatial position must be available, that is some kind of 'cue' is required. Different ant species depend on different cues depending upon circumstances. Recruiting signals are evidently of immense importance in opportunist species utilising ephemeral sources of clumped food but may play a smaller role in territorial species living in stable habitats and using spatially persistent, renewing resources. Almost all the ant species have alternative means of orientation, that is they can use several different cues (Rosengren & Fortelius 1986b). Despite the knowledge that animals may use alternatives on eliminating one cue, the orientational abilities of ants still cannot be wholly explained in terms of cues that are understood to be available. In this particular study despite elimination of all the obvious cues, orientation was still achieved (Chapter4, Figs. 4.4.1 & 4.4.2 Period 3) so it can also be argued (with the knowledge of other researchers Rosengren 1971, 1977a, 1977b, Rosengren & Pamilo 1976, Rosengren & Forttelius 1986b) this orientation was achieved through the animal's learning capacities. When beginning foraging a naive forager experiences a certain spatial sequence by moving from one point to another: finally she may be able to build up and use a familiar area map in such a way that particular points within the foraging range can be visited in arbitrary, rather than fixed, sequences. This ability was clearly shown during the night when in complete darkness and without obvious visual cues foragers managed to find the allegiant food site. My own field observations revealed that aphid aggregations were not found at precisely the same location on several consecutive visits spaced between one week: although they were found on the same tree (Chapter 6). These observations imply that wood ant site allegiance was to the particular tree but not to the exact point on that tree. After locating a particular tree, foragers may follow the faecal deposits or pellets from the infrabuccal sacs: in the field, as well as in the laboratory, foragers continuously groom their antennae and mouth parts. In this study no evidence was found for pheromone laying or following, even for recruitment of naive foragers to novel food sites after a long starvation period: rather foragers showed high dependency on the spatial position of the food sites (Chapter 4, Figs 4.3 & 4.41, 4.4.2 Periods 1-8). The proposed hypothesis of local enhancement (sign posting) of random foragers may be effective over small distances found in the laboratory but would not be useful over long distances unless there was some form of channelling of foraging activity. It has been well documented that wood ant foraging trails are well defined in woodlands (Elton, 1932; Kiil, 1934; Otto, 1958: Dobrzanska, 1958; Rosengren, 1971). Hence the sign-posting or local enhancement hypothesis could be modified in the following way. Rosengren (1971) said that recruiters were often sent along these well-defined paths. If trophallaxis encourages the inexperienced forager to forage then it may well use a well-defined path nearby. These main trails may not necessarily lead directly to the new site but will enable a large number of foragers to be directed away from the immediate surroundings of the nest. A successful and purposeful forager, after unloading in the nest, may be followed along the well-defined route thus bringing the aspect of random searching to an area much closer to the desired site. Subsequently, excited inexperienced foragers need only know and remember the positions of trophallaxis bouts with returning replete foragers and need not follow her. The route confirmation decision of a naive forager eventually comes through the increasing number of trophallaxis bouts along the route. It has also been shown that replete foragers returning from a 'restricted access' site do not encourage foragers out even when the colony was hungry (Cosens & Toussaint, 1985). This indicates that perhaps communication of accessibility is also transmitted. This could be done through the 'readiness' of the replete forager to take part in trophallaxis. During the normal foraging day the level of trophallaxis was fairly low: so it was reasonable to assume that the motivation of the trophallaxis 'acceptor' was related to its own or colony hunger. Whereas the readiness of the 'donor' varied with the quality or accessibility of the food source (amount of effort needed to collect food). Thus by merely altering the motivation of acceptors and readiness of donors to engage in trophallaxis it is possible to have a system whereby the colony 'selects' to send its foragers to the most economical site. Unlike the honeydew sources produced by aphids, insect prey is not renewed in a predictable manner and is randomly distributed both in space and time. This ephemeral nature requires that once prey has been discovered, it must be exploited as quickly as possible and certainly before the competitors. This criterion requirement was fulfilled by *F. aquilonia* foragers by employing different effort to collect prey, from collecting spatially stable honey dew. That was following formic acid signals squirted by successful attackers of the insect prey (Chapter 5, Figs. 5.4 & 5.5).

A fundamental decision for any forager is choosing the location in which to search for food. In the case of social insects, as soon as a forager has gathered a certain amount of food it has to return to a nest. At the start of the next foraging expedition, the question is where to search for additional food. The answer to this question must depend on the nature of the distribution of food: that is clumped and renewed predictably or dispersed in a random manner. The type of food encountered strongly influenced the tendency of a worker to search the site of the find, but foragers given one reward of either protein or carbohydrate food showed purposeful or non-purposeful search patterns independent of the food type (Table 5.1). In this study the existence and significance of individual differences in behaviour was observed: these differences resulted, at least in part, from the different experiences of foragers. Foragers of *F. aquilonia* differ in the extent to which they will continue to search in the vicinity of a site where food was previously found (Tables 5.2, 5.3 & 5.4). The differences in food type produced differences in the degree of purposefulness shown by foragers that have contacted food of each type. Foragers showed a greater degree of search effort and modification of search behaviour in response (Table 5.5) to the food type which should have a greater pay off, if greater effort is allocated. Likewise, the search pattern generated in response to insect prey allowed a forager to avoid scanning redundantly in the area of prior find, where the possibility of locating additional prey, which were unpredictable in time and space, was low. Hence the protein stimulated search pattern does not need to be narrowly centred around a prior site as does the carbohydrate stimulated search pattern.

A foraging cycle of a central place forager consists of a journey from the central-place(nest) to the foraging area, a time spent collecting food (handling) and a journey back to the central place. The maximisation of the net rate of reward during a foray depends on how quickly a forager can find food and how quickly that gathered food is transported to the nest. Owing to the long foraging trails it was hypothesised that two distinct forager types exist to facilitate an effective foraging effort: a) 'Gatherers' that gather droplets of honeydew from individual aphids, and b) 'Transporters' that collect from Gatherers and transport honeydew back to the nest (Chapter 6). Evidence was found that foragers make decisions to maximise the net rate of reward for a foray by minimising the time spent at the aphid aggregation: through a relay system. The foragers may use the time spent at an aphid aggregation either: to collect honeydew droplets directly from aphids, or to engage in trophallaxis with semi-replete sisters to obtain a full crop and so return to the nest in the shortest time.

There was no age polytheism found in wood ant foraging populations although a sort of work polytheism was observed. Individual foragers showed a high degree of allegiance to a particular region of the nest (spatial fidelity zones) and performed duties accordingly (Chapter 2).

Foraging rhythms of wood ants were likely to be entrained by light:dark cycles. There was continuous turn over of the foraging population: duration of particular foraging cycle was approximately 1.5 months. This may be the way they maintain topographic traditions within the colony over a long time. Veteran members of the foraging population are highly restrictive in behaviour compared to naive members. The colony's strategy to compensate behavioural inertia associated with the restrictive behaviour of veterans was to deploy a proportion of naive foragers to the active foraging.

No evidence was found to support chemical orientation in foragers. The results presented here(Chapter 4) were evidence of extremely long-lasting storage of spatial information in wood ant foragers. Visually perceived objects were the most obvious source of wood ants' hierachial organisation of orienting system. The clear-felling practised in Scottish woodland disturbs the topographic scenario and aphid aggregations which may cause disorientation in foragers.

Foragers showed a large degree of search effort and modification of search behaviour in response to a stable food type (carbohydrate) which has a great pay off, if great effort is allocated.

Foragers reduced search time whilst visiting known sites (allegiant sites) and also made decisions to maximise the net rate of reward for a foray by minimising the time spent at the aphid aggregation through a relay system.

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