THE UNIVERSITY OF HULL

The Collection Of Honeydew And The Foraging System Of The Wood Ant (*Formica lugubris* Zetterstedt Hymenoptera - Formicidae)

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by

Robert Lewis Tweed, BSc. (Hons.) (Edinburgh)

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CHAPTER 1

INTRODUCTION

The wood ant Formica lugubris Zetterstedt is an inhabitant of both deciduous and coniferous woodland in Northern England, Wales and the Scottish Highlands (Collingwood, 1964). Like all F. rufa-group ants, it builds large dome-shaped nests from forest litter, usually along the sunny edges of woodland areas. Each nest may contain up to 70,000 workers (Breen, 1979) and numerous egg-laying queens. New nests are produced by budding-off from a main nest, so that large colonies of nests often result (e.g., Cherix and Gris, 1977; Higashi and Yamauchi, 1979). Workers can move freely between the nests within a particular colony by means of a system of linking trails. Between 58% and 84% of the worker force of a nest act as foragers outside the nest (Breen, 1979), using a system of trails which emanate radially from each nest. Both the forage trails and the inter-nest trails are visible as columns of ants returning to and departing from the nest. The trails vary in both width and length, but an average trail may be approximately 200 mm wide and up to 100 m long. Heavily-used trails are often worn into the forest floor, due to the constant 24 hour traffic during the active period of May to October. Some trails follow ready-made topographical features such as ditches and grooves in rocks (Rosengren, 1971) whilst others appear simply to link the forage areas to the nest by the shortest routes.

The main diet of wood ants is insect prey and aphid-produced honeydew, accounting for 33% and 62% respectively of the total food intake of a nest (Wellenstein, 1952). Because of this large intake of forest insects (estimated at 8×10^6 insects per nest per year by Wellenstein, 1952), a great deal of attention has been focussed on the F. rufa-group ants as predators and on their potential in biological control of forest pests in man-made forests (Pavan, 1959; Gösswald, 1951, 1959; Cotti, 1963; Finnegan, 1974, 1977; McNeil, Delisle and Finnegan, 1978; Wisniewski, 1967). The intake of honeydew is no less impressive, estimated at between 300 and 500 kg per nest per year (Zoebelein, 1956) for the related F. pratensis.

Honeydew is a sweet, sugary liquid produced by many homopterans as a waste product of their ingestion of plant sap. In his review of the contribution of honeydew to the food supply of ants, Way (1963) points out that it may represent a complete food for some species of ant as it is not merely a solution of sugars, but contains many free amino-acids and amides, along with proteins, minerals and B-vitamins. However, as wood ants obviously obtain a considerable amount of protein from insect prey, the primary role of honeydew in the diet of wood ants seems to be as a carbohydrate source (Abbott, 1978; Lange, 1967). Indeed Ayre (1960) and Lange (1960) showed that a *F. polyctena* colony fed solely on a diet of honeydew/honey was unable to rear any brood, whereas a colony given insect prey in addition to honeydew/honey reared brood successfully.

A great deal has been written about the mutual benefits derived by ants and aphids, and on the behavioural and morphological adaptations of both ants and aphids which facilitate their close relationship (Nixon, 1951; Kloft, 1959; Way, 1963; Kunkel, 1973). Because aphid-attendance is so widespread among the ants, it is tempting to generalise about the ant-aphid relationship. However, as with the variety of types of territoriality seen amongst different ant species (Hölldobler, 1978), so different levels of dependence and different strategies should be expected between ant species in their relationship with aphids. Since wood ants collect honeydew above ground, especially on trees, as well as below ground, it is surprising that so little attention has been paid to their honeydew-collecting strategy.

Wood ants, when collecting honeydew, drink the very small droplets produced from the anus of aphids. This has been described in detail by Douglas and Sudd (1980). A large number of droplets is collected by each ant and stored in the crop, which is situated in the gaster: the hind section of the body consisting of part of the abdomen. The proventriculus, a valve between the crop and the gut, prevents the crop contents from passing into the gut except very slowly. Therefore, a visit to an aphid colony can provide a single ant with a load of honeydew far in excess of its own immediate requirements. Wood ants do not store honeydew, as does the honeypot ant (Myrmecocystus spp.) for example. These species have special worker castes whose crops can swell to the size of a cherry with stored honeydew (Hölldobler, 1978). Instead, wood ants widely distribute it amongst the workers by regurgitation or trophallaxis (Sudd, 1967; Gösswald and Kloft, 1960). Since not all the foragers collect honeydew; some return with insects, others with nest material and some with nothing at all (Horstmann, 1973); these energy consumers must depend for their energy source on trophallaxis with honeydew-foragers. There are two ways in which this might be done. Either the consumers meet the collectors in the trees, or the fuel might be redistributed centrally, at the nest. Because all the trails connect with the nest and all the ants communicate with the nest at some time, the latter method is clearly the most effective. This is in accord with the usual scene on a forage trail of large numbers of ants with full crops of honeydew heading for the nest, yet no ants with full crops ever leaving the nest.

Very little work has been done to study this flow of honeydew from aphid to nest, and the evidence which does exist presents a very scanty picture. Assuming that all the <u>F. rufa</u>-group ants have similar foraging behaviour, the known facts about the group allow a number of strategies to be postulated:-

1. Each ant collects honeydew for its own consumption alone.

This cannot be true, because, as already mentioned, large numbers of ants can be seen returning to the nest with full loads of honeydew. If these loads were reserves for each ant alone, then ants leaving the nest with such loads should be a common occurrence. In addition trophallaxis often occurs within the trees (Douglas and Sudd, 1980), so the collecting ants must obtain more honeydew than they can use themselves.

2. Each honeydew collector gathers a full load from aphids before taking it back to the nest where it is redistributed to other ants.

Although this strategy may be the more effective one, as discussed earlier, the occurrence of trophallaxis in the trees suggests that it might not be the only strategy used by wood ants.

3. Each honeydew collector distributes its surplus honeydew only within the tree to other ants, which are simply passing through the tree to 'refuel'. In other words, the collecting ants are acting like a petrol station for other foragers, and do not themselves return to the nest with honeydew loads.

This may be dismissed on the grounds of inefficiency. An ant which normally collected nest material for example, would have to waste a good deal of time and energy searching for collecting ants in a tree when it required more honeydew. Otto (1958) and Rosengren (1971) have both shown that ground foragers and litter collectors rarely visit trees. Otto (1958) further showed that F. polyctena workers, marked on a particular tree when attending aphids, could be found again at the same tree up to eight days later. One ant was recorded at the same branch of a tree for 29 days. Many, however, did leave the tree, a result contrary to the expected outcome of this strategy.

4. The collecting ants do not leave the trees, but pass their loads on to transporting ants whose task it is to return the honeydew to the nest.

This cannot be the whole truth either, as it does not explain the departure of Otto's marked collectors. However, there is some evidence that this strategy is used by F. obscuripes, where small workers collect the honeydew from aphids and pass it on to larger workers which in turn take it to the nest (King and Walters, 1950). Douglas and Sudd's (1980) evidence of trophallaxis in the trees suggests that this fourth strategy might also be used by F. lugubris at times. A more complex chain transport system could also be postulated in which a single load of honeydew is passed between numerous workers in a number of stages between the aphid group and the nest.

5. No one of these four simple possibilities above fully explains the known facts. A combination of several of these strategies could occur, depending on other environmental factors.

It is known that some collecting ants leave the trees. If it is assumed that these make their way to the nest, then their action on next leaving the nest must also be considered. Again, there are a number of possibilities:-

1. The ants may not return in search of honeydew, but may take up any task.
2. They continue as honeydew collectors, but go to any tree outside the nest.
3. They remain within foraging range of the sector of the nest to which they belong, but may choose any tree within that sector (Zakharov (1973) has suggested this type of 'assignment' of workers to sectors of the nest and foraging area).
4. Attending ants are faithful to one trail, but may return to any tree along the trail.
5. Attending ants return to the same tree.
6. A combination of the above strategies.

An ant which leaves the nest in search of honeydew will waste a great deal of time and energy if it walks about in random directions, climbing trees at random in the hope of finding aphids. There is relatively little dispersal of aphids between trees, and a tree with aphids in May usually continues to support aphids for the rest of the season. An efficient collector of honeydew should be able to select only those trees with aphids using information gathered by itself or other ants on previous journeys. Otto (1958) noted that 25 out of 43 ants never returned to the tree on which they had been marked, but Rosengren (1971) demonstrated that wood ants marked on a particular trail were very likely to be resighted on that same trail at a subsequent date. If collecting ants do not always return to the same tree, as is suggested by Otto's results, then they will be expected to at least use the same forage trail. Hölldobler (1971), Moglich *et al* (1974) and Moglich and Hölldobler (1975) have found that *Camponotus socius* and *Formica fusca* sometimes use a form of recruitment behaviour known as 'tandem running' to guide novice ants to food sources. Even if an ant were to change task, such information transfer could guide the worker back to an aphid group at a later time. The evidence, then, suggests that several of the possible strategies could be open to an ant when it leaves the nest.

It should now be clear that piecing together the existing knowledge of honeydew collection provides an unclear and often confused overall picture. The aim of this study, then, was to make as complete a study as possible of the entire process of honeydew collection in wood ants. Honeydew collectors were to be identified and marked in a natural wood ant colony and their behaviour recorded over long periods of time. Since several factors such as the aphid size and species, the aphid distribution within a tree, the nest-tree distance, the size of the tree and the time of the year might influence the strategies used by wood ants, collectors were marked on a variety of trees at different distances along the forage trails and were observed for two complete seasons. Explanations for some of the observed strategies were sought using a laboratory nest of F. lugubris. In addition, information was gathered about the initiation of honeydew collection in Spring, and its decline in Winter, and the trail system of a colony of nests was mapped on a finer scale than before over two successive seasons. This study, therefore, represents a contribution to a complete knowledge of the foraging system of a wood ant species.

CHAPTER 2

PRELIMINARY INVESTIGATIONS

The honeydew-foraging behaviour of F. lugubris was examined initially using a laboratory nest during winter 1976. Figure 1 shows the layout of the nest and foraging arenas. The two foraging tables (F1/F4 and F2/F3) were constructed from 0.25 in plywood with 5 cm high plywood walls attached to the edges and down the centre to produce the separate foraging areas. They were then varnished with matt-finish polyurethane varnish which allowed them to be cleaned with water or alcohol. The arenas were designed so that quite a long foraging distance could be compressed into the very limited available space in the ant-room. When the arenas were connected by balsa wood bridges (B1-B4), the distance between the nest bridge (B1) and the extreme end of foraging arena F4 was approximately 5.9 m. The large foraging tank connected to the nest reduced the numbers of ants reaching the foraging arenas. This facility was essential when the nest was new and the total nest population very high. Most of the ants leaving the nest by bridge B1 would merely run around within the foraging tank. A much smaller number would find the second bridge B2.

The ants were confined within the area by coating the walls of the tanks and the arenas with silicon oil

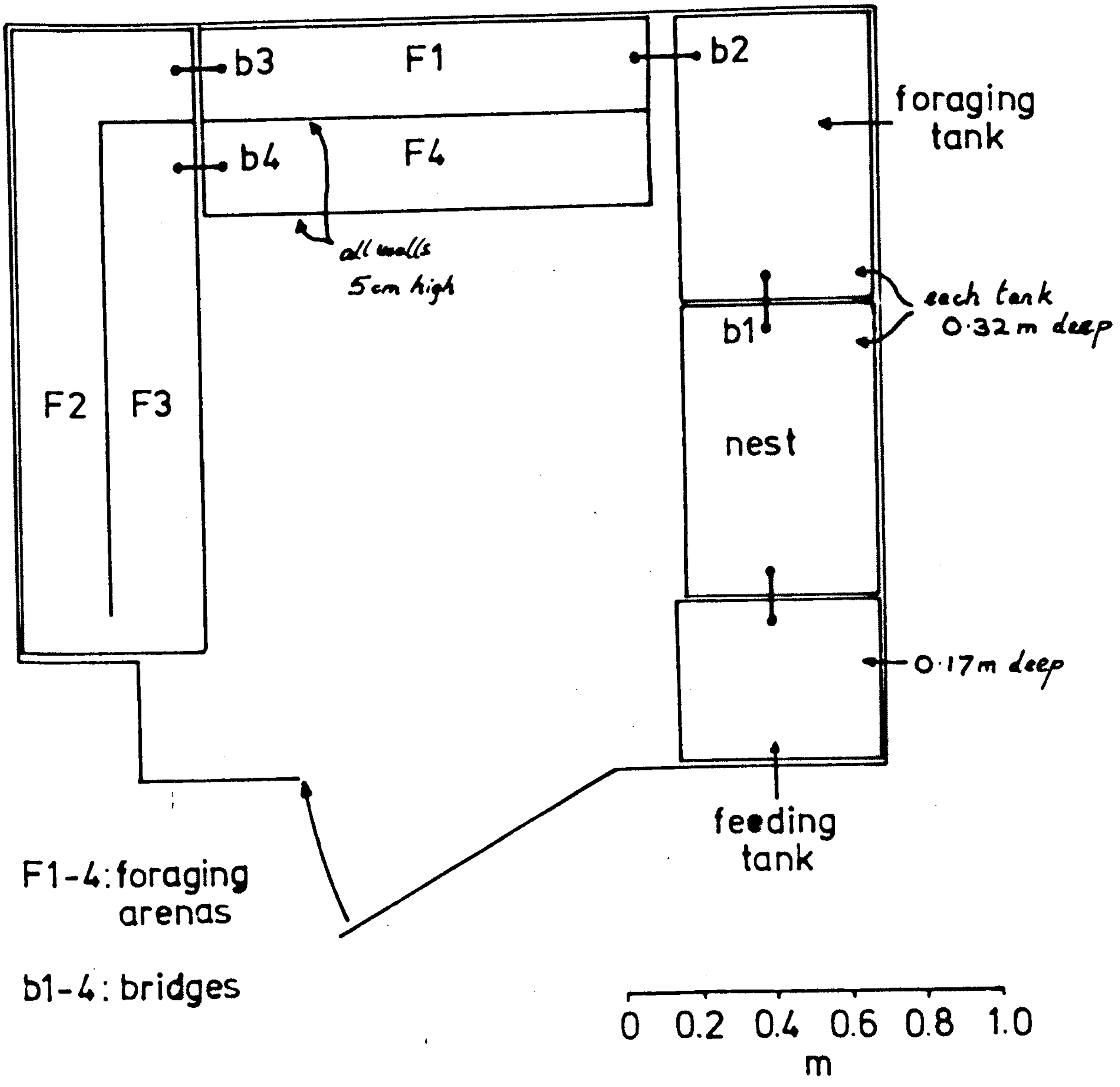


Figure 1 : Plan of experimental ant-nest and artificial foraging arenas within the laboratory : 1976

(Silicon Fluid DC550 (MS550), Hopkin and Williams, Chadwell Heath, Essex). They were fed on locusts at first, but these seemed to be too tough for them to dismember. Chopped-up mealworm larvae proved more successful. A supply of honey solution - consisting of honey and sugar dissolved in water - was also provided daily, and both the insect and liquid food was left in the feeding tank which was at the opposite end of the nest to the foraging arena. The whole room was kept on a light-dark cycle of 16 hours light, 8 hours dark, and the light was provided by two fluorescent tubes and one 100 W light bulb which was suspended directly over the centre of arena F4. A cooling device within the room was used in an attempt to keep a constant temperature in the room. This proved far from satisfactory, but the temperature was rarely outside the range of 16°C - 24°C. The nest was frequently sprayed with water to prevent it from drying out excessively. Although humidity was impossible to control, an Edney paper hygrometer in the room recorded a relatively constant humidity of approximately 80% throughout the experimental period.

Initial observations concerned the collection of sugar solution by workers. Two types of food sources were used: petri dishes containing the solution and small bottles with capillary tubes inserted in the bottom. When a petri dish of sugar solution was placed in arena F4, ants finding the dish would immediately fill their crops with solution, by drinking at the edge of the dish. Within about half an hour, there would be large numbers of ants filled with sugar solution all around the dish, but few appeared to return to the nest at this time. A great deal of food transfer also occurred around the dish. After a few days, however, some ants were found to be making regular journeys from sugar dish to nest, taking crop-loads of sugar solution which they obtained by drinking at the dish. By contrast, ants which were seen transferring food rarely returned to the nest. No behaviour which could be interpreted as being used for recruitment of other ants was observed at any point between the food dish and the nest. Although some unusual and interesting behaviour patterns occurred during these early laboratory observations, it was felt that little could be learned from the laboratory at this stage, as it was a very artificial environment for wood ants.

Unlike a dish where food is effectively unlimited and available at any time, an aphid group in a tree produces unpredictably timed output in the form of small drops. Many such drops must be collected by each ant before the crop becomes full, and only one ant can drink any one drop. A sugar dish is, therefore, a very unnatural food source and unlikely to provide much information about honeydew collection by ants.

An ant returning to a sugar dish can obtain a full load of solution within one or two minutes (i.e., as fast as the ant can drink) and can get immediate access to the solution by climbing the sides of the dish. An ant returning to a tree, however, may spend several minutes attending aphids before even obtaining a single drop of honeydew, and may often miss a drop because another attending ant reached the aphid first. In order to make a better simulation of an aphid colony, small polythene bottles (6 cm high, 2.6 cm diameter) were used. Two pieces of capillary tubing, each about 1 cm long were inserted through the wall of each bottle, about 0.5 cm from the base (see Figure 2). The area of contact between the tubes and the bottle was sealed with varnish, and the bottles filled with sugar solution to a depth of about 1.5 cm. This allowed the capillary tubes to become full of solution, but there was insufficient pressure acting on the solution to make it run out of the tubes. Ants soon learnt to drink from the ends of the tubes, but only one ant could drink from each tube at a time. The bottles, then effectively reduced the access to the solution and introduced a degree of competition into 'honeydew' collection, but once at a tube, an ant could still obtain a cropload of solution as fast as it could drink. The simulation was still not satisfactory, though there were fewer ants with full loads in the area around the food source. After a few days individual ants began to take their

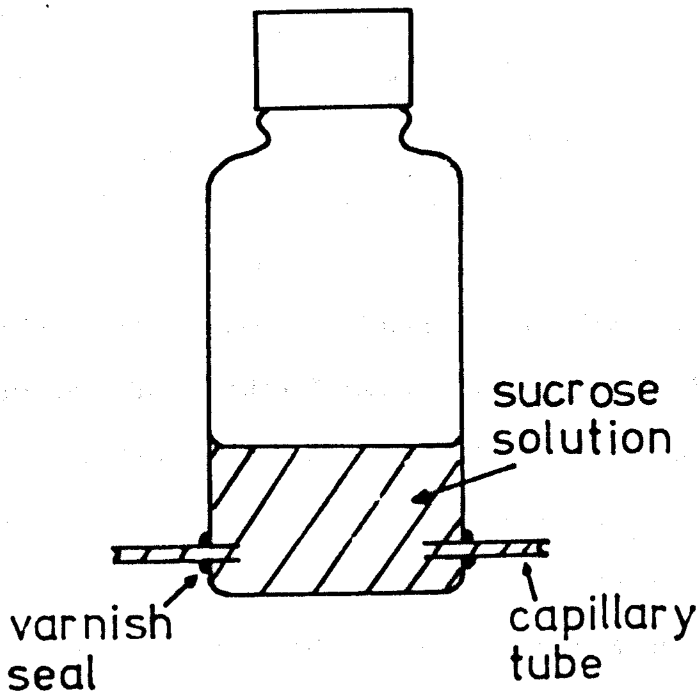


Figure 2 : Polythene bottle used in early experiments to simulate honeydew production.

loads all the way back to the nest.

At this stage it was felt that little was to be gained from study in the laboratory. It was possible that the short foraging distance (a journey of 5 m would take an ant to perhaps the first tree along a foraging trail in the wild), and the unnatural food source were making it too easy for ants to obtain food. In such circumstances, it was only to be expected that wood ants would use individual transport in order to move honeydew to the nest. There was also the danger that, owing to the limited available space, the foraging arena was treated by the wood ants simply as part of the nest, and that as far as they were concerned, the food was being provided at the nest itself. If so, typical foraging behaviour could certainly not be expected.

The collection of honeydew in the field had to be observed. Until this was done, there was no point in any laboratory work, as such work would only demonstrate what behaviour could be induced in a laboratory. If it could be shown that individual transport of honeydew occurred in the wild, only then could laboratory observations provide useful information. The following sections, therefore, deal with descriptions of the honeydew collecting behaviour of natural populations of wood ants.

CHAPTER 3

THE STUDY AREA

All the fieldwork was carried out in a section of Langdale Forest, North York Moors (O.S. Ref. SE 946936), at the edge of a steep-sided ravine which contained deciduous trees. The site was chosen not only for its large wood ant population, but also because it was in an area of forest not usually visited by the public. Throughout the period of study, human interference was never a problem.

The nearby ravine was a wooded area prior to the plantation of Langdale Forest in the 1940's, and is shown as 'Oak Rigg Wood' in the 1st edition O.S. map of the area which dates from the 1840's. Prior to forestation, the study site probably consisted of the heather moorland typical of the North York Moors. Like most of the F. lugubris ant nests in Langdale Forest, the study nests appear to have spread into the new planted forest from the existing wooded areas (Sudd et al, 1977) and are now spreading slowly inwards along the forest roads. The study area was, in fact, outside the part of Langdale Forest which was surveyed by Sudd et al (1977) and serves, therefore, as a further example of this type of spread into planted forest.

The trees in the area were Corsican pine (Pinus nigra var. maritima) and Scots pine (P. sylvestris) on the eastern

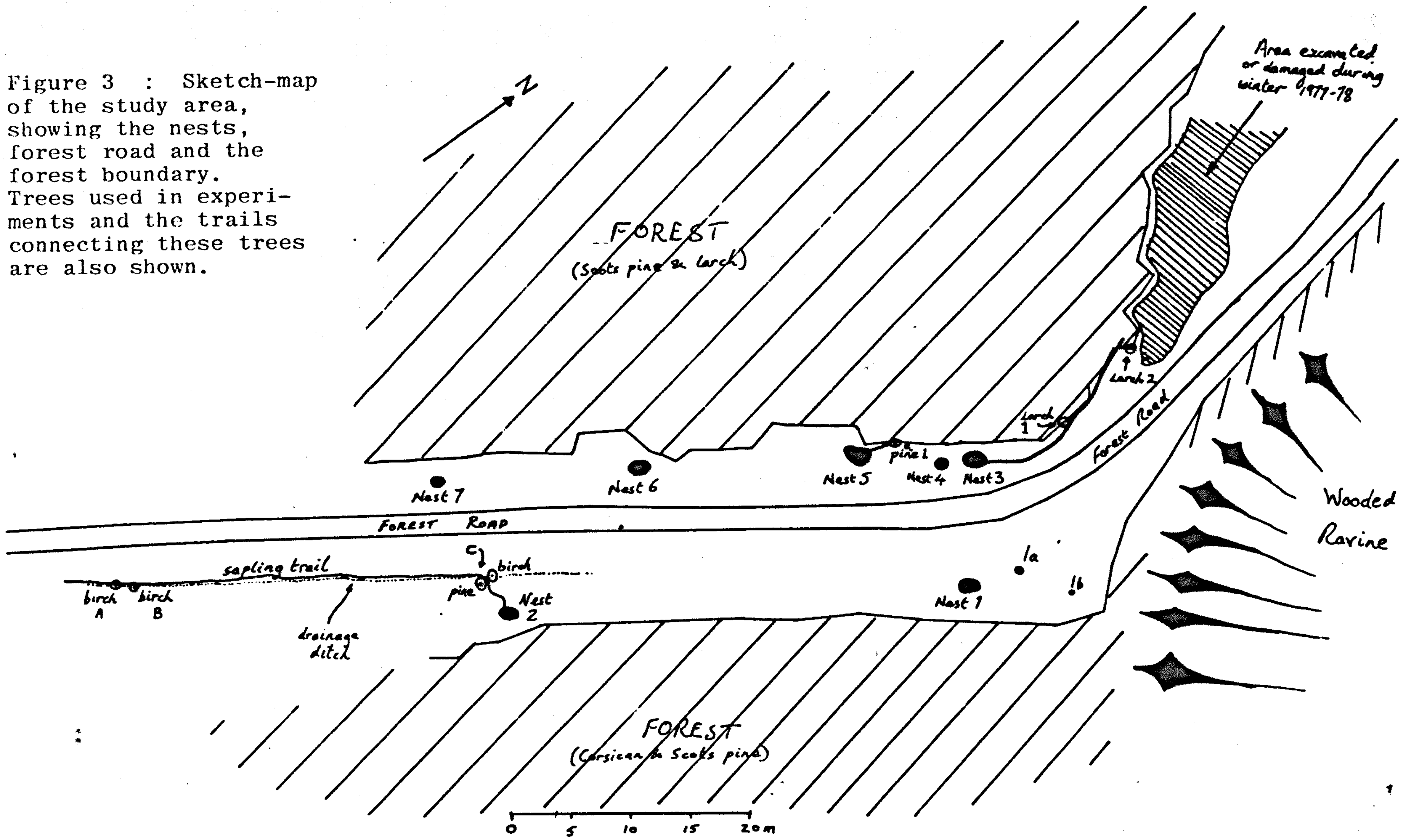


Figure 3 : Sketch-map of the study area, showing the nests, forest road and the forest boundary. Trees used in experiments and the trails connecting these trees are also shown.

side of the road (planted in 1943) and Scots pine (planted in 1944) and larch (Larix leptolepis) (planted in 1949) on the western side of the road. A map of the area is given in Figure 3, showing the positions of the nests in relation to the roads and trees.

Nest number 2 was chosen for the main body of the study because one of its major forage trails, over 60 m long, linked a large number of small birch and pine saplings (between 0.25 m and 2 m high) which were growing in the area between the forest road and the edge of the plantation. Many of these saplings were infested with aphids which were visited by honeydew-collecting ants. The saplings were large enough to support considerable numbers of ants (more than 60 in many cases), and yet small enough to allow the observer to follow or identify individual ants on the tree with ease. Most wood ant trails in the area tended to spread amongst the mature pine and larch trees. Such trees, of course, would support much larger populations of aphids and, therefore, would be of greater importance to the ant nests in terms of total honeydew intake. Nevertheless, the study trail reflects a reasonably typical situation, though on a smaller and more manageable scale. With at least 35 trees attended, and with a considerable traffic flow along its length, the study trail was certainly of some importance to nest 2. It was felt that the results from this trail could be applied to any forage trail as the only difference was probably in the scale of the honeydew collecting operation.

Partly by way of a check on whether tree size affected the collection strategy used by the ants, some data were obtained from two mature larches (attended by ants from nest 3) and one mature pine (attended by ants from nest 5) on which easily visible aphid groups were attended. These trees are marked in Figure 3. Although not obviously connected to nest 2, nests 3 and 5 probably originated from the same ancestral nest as nest 2. The ancestral nest was assumed to have been somewhere in the wooded ravine. As the study area was isolated from other large colonies, very little outbreeding seemed to be possible. Neither the male or female sexual forms were ever seen to fly far from their own nests at mating times and, as a result, all the ants in this roadside colony were probably very closely related, even in nests at opposite ends which probably had communication by workers or sexual forms only on rare occasions. The only source of genetic variation was likely to have been that of the original ancestral nest and the very small number of mutations which might have occurred over the last 30 years. Brief tests of hostility to workers placed on "foreign" nests confirmed this impression (Sudd, unpublished results).

CHAPTER 4

FIELD OBSERVATIONS

Part 1 : MATERIALS & METHODS

In order to follow the behaviour and foraging activity of ants in the field over long periods, a method of individual marking was essential. Previous workers had used either mass marking by paint sprays (Rosengren, 1971; Breen, 1979) or marked individuals by picking them up and applying numbered tags (Otto, 1958; Verron and Barreau, 1974), metal rings (Kruik-de Bruin *et al*, 1977) or paint marks (Rosengren, 1971; Horstmann and Geisweid, 1978). There were many disadvantages to all these techniques which made a new marking technique essential. As the study was concerned with honeydew-collecting ants in trees, all marking had to be done in the tree under observation. Spray paints were, therefore, of no use as they would damage the tree and probably kill the aphid groups and also result in unsatisfactory marking of the ants. Most ants would receive too much or too little paint, and several ants at each marking session would probably have similar marking patterns, leading to ambiguous records of ant movements. Existing methods of individual marking also seemed unsatisfactory mainly because of the disturbance they caused to the ant. All these methods involved picking the ant up to mark it. This makes wood ants very aggressive, and even when replaced on the same branch, such ants would be unlikely to return quickly to aphid attending. Instead, personal experience had suggested that such ants would run about the tree, probably exciting other ants, and would invariably drop from the tree within a short time. Metal tags or rings were unsatisfactory in that they could be seen and recognised only at short distances, and would possibly hinder the ants' movements.

Paint marking was, therefore, used, but the techniques employed allowed ants to be marked <u>in situ</u> at an aphid group, often with no disturbance. Cellulose paint for motor cars (Holts Dupli-colour Touch-up paint) was used. Small drops of this paint dried within a minute and adhered well to the cuticle of wood ants. The enamel paints used by other workers took too long to dry and the drying time is important since the solvents used in enamel and cellulose paints induce aggressive behaviour in the marked ant as well as nearby ants. This can result in their dropping from the tree or attacking the marked ant. Application of paint with a brush was found to be of no use, since all the ants around an aphid group detected the solvent released from the relatively large amount of paint held on the brush, usually long before it was brought into contact with an ant. A special applicator was, therefore, designed and tested on ants in the laboratory. It consisted of a 4-5 cm length of very fine catheter

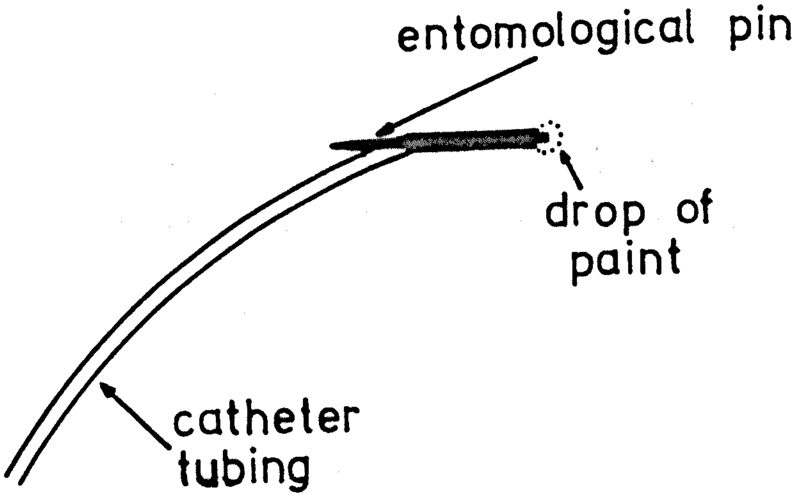


Figure 4 : Greatly enlarged diagram of device used to apply paint marks to wood ants.

tubing (0.28 mm bore) with a very fine (0.188 mm diameter) entomological pin inserted into one end so that only a very short length protruded (see Figure 4). This allowed a very small drop of paint to be held at the end of the tube, the drop being formed around the end of the tube and shaped by the small protruding pin-end.

Because a very small drop was brought towards an ant during marking, very little solvent evaporated from the applicator. With practice, the applicator could be brought into contact with an ant's gaster without it or neighbouring ants being disturbed. This was particularly true if the ants were attending aphids at the time. As long as the applicator was moved steadily, then they would ignore its presence. Some ants were, however, disturbed by the solvent evaporating from a newly marked ant. This sometimes led to scenes of aggressive and excited behaviour, but these lasted for only a short period of time. All the ants around such an aphid group would return to normal aphid attending behaviour within a minute or so of marking.

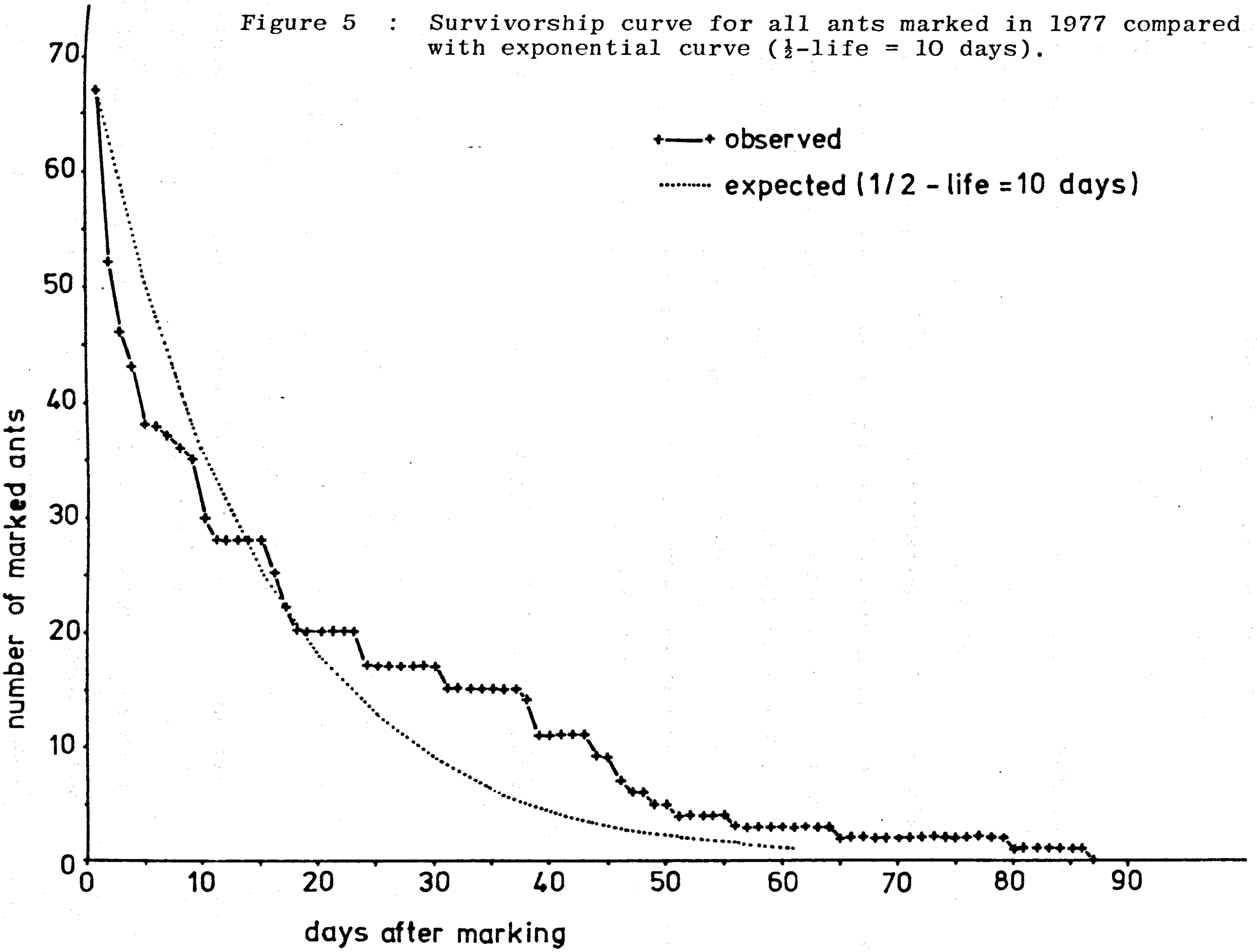
Apart from this very brief initial aggression, marking had no obvious effects on the behaviour of the ants. All newly marked ants rapidly returned to what appeared to be normal aphid attendance behaviour and usually could be seen to behave normally for many days afterwards. Ants were marked in small batches with one particular colour. To ensure that each ant was individually recognisable, even at a distance of one or two metres, only 4-6 were marked with each colour. Marking was carried out when the number of previously marked ants found in a tree dropped below about 5 or 6. Another 4-6 ants would then be marked. There were, therefore, never more than about 10-12 marked ants in a tree at any one time. This ensured that all the marked ants could be found quickly when the tree was inspected. At each marking session, the colour chosen had either not yet been used or had been used so long ago that ants of that colour were no longer being recorded. In all, 8 different colours were used - white, red, orange, yellow, light green, light blue, turquoise and silver, but colours which might be confused (e.g., white and silver) were not used on consecutive marking sessions. Each ant was marked primarily on its gaster, although marks were generally put on the legs as well, and sometimes on the thorax. Up to three separate dots of paint could be placed on the gaster, and with practice, a mark could be deliberately placed at a particular part of the gaster. Both dots and streaks of paint could be applied. A sketch of the mark pattern was recorded, and the ant given a coded number. For instance, if 5 ants were marked red, they were coded R1-R5.

Part 2 : EFFECTIVENESS OF MARKING

In general, the marking procedure proved to be very successful and it allowed individual ants to be followed and recognised for weeks at a time. The graph in Figure 5 shows the survivorship curve for all the ants marked in 1977. The X-axis represents the number of days after marking. Note that the 67 ants were not marked on the same day, but that the marking was done in batches staggered throughout the year. This graph is the combined results for all marking sessions. As can be seen, the observed plot is a close fit to an exponential curve with a half life of 10 days ($p < 0.1$ using Kolmogorov-Smirnov test), and suggests that losses of marked ants occurs at a steady rate independent of the time after marking. More ants are lost initially simply because there are more of them. So marked ants had a half-life of 10 days. This misleadingly sounds like a short time, but, for example, 22% of the ants were still being recorded a month after marking. One ant was not lost until 86 days after marking.

Several factors tended to increase the duration of mark retention. Some of the losses in Figure 5 are undoubtedly due to death, change of tree or change of task. Three of the ants were known to have moved to an adjacent tree, but are included in the graph since this shows mark retention and not

Figure 5 : Survivorship curve for all ants marked in 1977 compared with exponential curve (½-life = 10 days).



tree fidelity. Some losses, however, were due to loss of the mark. Abrasion whilst walking within the nest was probably one cause. At times, however, other workers could be seen trying to pick the paint marks from marked ants using their mandibles. Some marked ants returned to the tree with parts of their mark missing, especially if the original mark had been large. In order to prevent such losses, marks were also put on one or more legs in addition to those on the gaster. Each marked ant would then have a unique leg mark as well as a gaster mark. Although more difficult to see, leg marks were much more durable, and even if the entire gaster mark was removed, the ant could still be recognised by its leg pattern.

Part 3 : OBSERVATIONS ON A BIRCH TREE CLOSE TO THE NEST

a). Methods

In 1977, attention was initially concentrated on a birch sapling about 0.75 m high and 4.1 m from nest 2 (see Figure 3). A total of 67 ants were marked on this tree in batches throughout the summer. The tree was watched between 8th May and 5th October, 1977. The ant activity was observed for a total of 45 days during this period, throughout which the birch supported large populations of the aphid Symydobius oblongus v. Heyden. Figure 6 shows the times when this birch

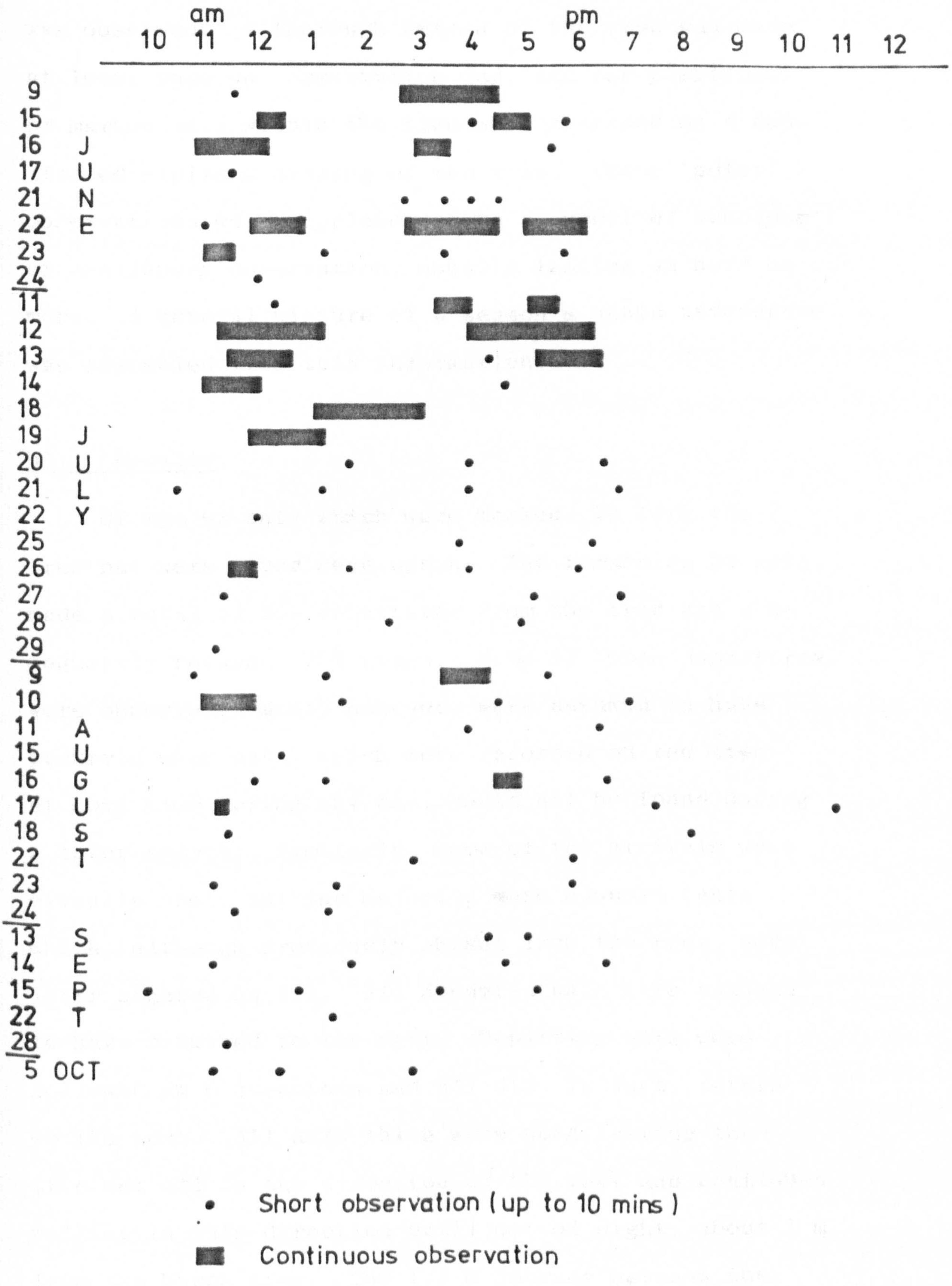


Figure 6 : Diagram showing times when birch sapling was observed during 1977.

was observed. A thorough search of the tree was made at least once per observation day, and the positions of marked ants within the tree were recorded on a duplicated stylised drawing of the tree. These 'point' observations were supplemented by a number of sessions of continuous observation, usually lasting an hour or more. A general picture of a season's aphid attendance was assembled from this information.

b). Results

Of the 67 ants which were marked, 14 left the tree but were never seen again. The remaining 53 ants made a total of 255 departures from the tree and subsequently returned 202 times. Some of these departures were observed. Most, however, were assumed to have occurred when ants, which were recorded on the tree at some time during the day, could not be found during a later search. Similarly, some of the arrivals were actually seen, but the majority were assumed (ants which, although previously absent from the tree, were later sighted on it). All departed ants were assumed to have returned to the nest. Departing ants were followed on 6 occasions and all did, in fact, return to the nest. All ants which were seen leaving the tree set off in the direction of the nest and continued walking in this direction until out of sight, about 1 m from the birch tree. The 4.1 m journey between the tree and the nest took between 4 and 10 minutes depending on air temperature (c.f. Holt, 1955). Most ants leaving the tree had full loads of honeydew which were, in the majority of cases, collected directly from aphids. A fully laden ant was easily distinguishable because its gaster was so dilated that the sclerites were forced apart and the transparent membrane between them was tightly stretched. Collecting honeydew from *S. oblongus* was a slow process, because this small aphid excretes such tiny droplets. The mean time spent in the tree by collecting ants was 178 minutes. However, there was a very large variation in time spent at the tree (S.D. = 306 minutes). Some ants stayed for several days at a time apparently waiting for honeydew drops to be produced: one ant marked in June was seen at the same aphid group for 5 consecutive days. *Formica rufa* and *F. polyctena* are also known to remain overnight at aphid colonies on oak trees (Horstmann and Geisweid, 1978). Honeydew-collecting ants walked around an aphid group, stroking the aphids with their antennae. An aphid which was ready to produce a drop would raise its abdomen and exude and hold a small droplet of honeydew at the tip of its abdomen. Some ants seemed attracted by this abdominal raising movement of the aphids and would quickly move to the aphid and drink the droplet. Other ants, however, would not respond to the aphids' actions and these ants appeared to come across honeydew drops purely by chance. This aspect of honeydew collection has been dealt with in greater detail by Douglas and Sudd (1980).

For a large part of the year, there was very little behavioural interaction between the ants on the trees or on the trail between the tree and the nest. When an ant had obtained a full load of honeydew, it would simply leave the tree, walk to the nest, and return to the tree again at a later time with an empty crop. However, during July 1977 (approximately between 11th and 19th July, although exact dates cannot be given), there was a sudden appearance of food transfer occurring between ants within the tree. By marking the regurgitating and accepting ants, it became clear that one group of ants always accepted and the others always regurgitated. The accepting ants were found to obtain almost all their honeydew from regurgitating ants. These acceptors also attempted to obtain droplets from aphids, but when they met other ants at aphid groups, they began palpating them with their antennae, generally around the head, and moved their mouthparts towards those of the other ant. Sometimes the solicited ants would refuse to give up any food, but on other occasions they would begin regurgitating their crop contents in response to the accepting ant's behaviour. Six acceptor ants were marked and followed. They were found to be able to collect honeydew very quickly. Table I shows

Ant Number	Time taken to collect a full crop of honeydew between arrival at and departure from tree	Number of acceptances during loading time
W3	33 min	9
W3	33 min	7
W3	26 min	9
B5	35 min	2

Table I   The Collection of honeydew by two known 'acceptor' ants on birch sapling : July 1977.

the times spent in the tree by two such ants on four occasions: in this time, each ant arrived at the tree with an undilated gaster, collected honeydew from other ants and left with a full crop. The loading time varied between 26 and 35 minutes. By comparison, marked ants which repeatedly regurgitated to the acceptor ants stayed on the trees for much longer periods than usual, since they were giving up partial loads of honeydew almost as quickly as they collected them. These ants were never seen regurgitating if their gaster was fully dilated. Three such ants were unable to leave the tree for two complete days during this time. The regurgitating ants ('collectors') rarely moved from their particular group of aphids whilst the accepting ants ('transporters') moved throughout the tree from ant to ant and from aphid group to aphid group. This difference in movement is shown in Table II. All the collectors show a very low number of location changes (less than 0.2 per hour) whereas the transporters made frequent location changes (between 0.9 and 22.5 changes per hour). Table II also shows that no transporters were seen to regurgitate, but always accepted loads, whilst the opposite was true for collectors. It was perhaps surprising that despite the large number of behavioural interactions shown by a transporter whilst collecting a load, once it had collected a full crop of honeydew, it would return its complete load to the nest without any further interactions in the tree or

Ant Number	Total time spent observing ant (min)	Number of acceptances	Number of regurgitations	Number of locations visited within tree	Number of locations visited per hour
		TRANSPORTER ANTS			
B5	35	2	0	2	3.43
B5	7	3	0	1	8.57
B5	8	3	0	3	22.50
B5	42	8	0	5	7.14
B5	30	5	0	1	2.00
B5	66	4	0	1	0.91
W3	33	9	0	NOT RECORDED	-
W3	26	9	0	1	2.31
W3	33	5	0	3	5.45
W3	33	7	0	2	3.64
W3	19	5	0	4	12.63
B3	5	1	0	1	12.00
B3	13	1	0	1	4.62
B2	15	4	0	1	4.00
B1	13	1	0	1	4.62
		COLLECTOR ANTS			
W4	>1 DAY	0	2	1	<0.04
W1	>1 DAY	0	1	1	<0.04
W1	APPROX 5HRS	0	1	1	APPROX 0.20

Table II Honeydew collection in birch sapling, July 1977. Acceptances, regurgitations and movements within tree recorded for 'collector' and 'transporter' ants.

(Note: A location was defined as a branch if that branch had one or less aphid groups, or as an aphid group if the branch had more than one aphid group).

on the trail. Transporting ants did not obtain all their honeydew second hand from other ants. Aphid drops were occasionally obtained, and all the transporters did attend aphids. One such ant (B5 in Table II) was observed for 42 minutes, and in that time it obtained 1 drop of honeydew from an aphid, but attended aphids on 38 occasions. Eight partial loads were obtained from other ants, and a total of 27 ants were solicited.

During this short period in July, then, the observations suggested that some ants were using a form of chain transport whereby 'collector' ants were obtaining the small and infrequently produced drops of honeydew from the birch aphids and storing these as partial loads in their crops. A second group of 'transporters' collected these partial loads from the collector ants and returned their quickly obtained loads back to the nest. It is interesting to note that Douglas and Sudd (1980) reported fragmentary evidence of a similar kind: they identified "short-stay" ants which were more mobile than others and for which exchange was recorded more frequently.

Before any generalisations can be made about the collection of honeydew by wood ants, it must be realised that this birch could be said to be rather atypical. It was very close to the nest - 4.1 m along the forage trail - and within the same order of distance as used in the laboratory experiments. The tree was also very small and in any case the wood ants visited other species of tree such as pine and larch where they attended other species of aphid. Observations were, therefore, followed up on mature larch and pine trees and on birch trees much further from the nest.

Part 4 : OBSERVATIONS ON PINE TREES

a). Methods

It is extremely difficult to study the behaviour of wood ants on mature trees, mainly because most of the honeydew production and collection is in the upper branches. Nevertheless, a mature pine tree (*Pinus sylvestris*) was found in the study area which allowed some observations to be made. Although this tree was 10 - 12 metres high, there was one aphid group on a branch at about chest height. This group was visited by about 10 - 20 ants at any one time, but most ants arriving at the tree continued walking up the trunk past the base of this branch, and were impossible to follow when they moved higher than about 2.5 m up the stem. The aphid group which was observed was near the end of the third-lowest living branch on pine 1 (see Figure 3). The branch joined the stem about 2 m from the ground and the aphids formed a large colony on the twigs, about 1.5 m from the connection of the main branch with the stem. In order to find this aphid group, an arriving ant would have to select the correct branch, take the correct sub-branch (the seventh from the stem end), and then the correct sub-sub-branch. The aphids were identified as <u>Cinara pini</u> Linnaeus, and the tree was 2.4 m from nest 5.

The ants on this branch were observed for 10 days, between 15th June and 19th July 1977. Fifty-three ants were marked during this period. Unlike the marking experiment on the birch tree, no attempt was made to provide the ants with unique individual marks. As the tree was so large and the number of ants on the tree so much greater than on the birch, 4 - 6 recognisable marked ants would soon have been lost. Individual recognition was, therefore, sacrificed for the sake of replication of results. Group-marked ants arriving back at the tree were watched in order to discover whether they found their way back to their original aphid group.

b). Results

Casual observation of marked ants seen leaving the aphid group suggested that they all returned to nest 5. Attention, however, was concentrated on ants arriving back at the tree. Of 23 returning ants, only 1 found its way back to the original aphid group with no 'mistakes'; i.e., it did not walk along any branches or sub-branches which would have taken it elsewhere in the tree, but made all the correct turns necessary to lead it to the aphids. Three ants reached the aphid group after having taken at least one wrong turning at some point within the tree. Six ants reached the correct branch but did not reach the aphid group, and 13 ants simply carried on walking up the stem past the third branch before being lost from sight.

It was not possible to obtain any other data for ants on this tree, owing to its size and the very low traffic flow during the observation period. Only 23 returns were seen out of 53 marked ants over 10 days.

Part 5 : OBSERVATIONS ON LARCH

a). Methods

Two Japanese larch trees (Larix leptolepis Gord) were found suitable for study, as each supported at least one easily visible group of aphids. These aphids, identified as Cinara kochiana Börner, were much larger than the pine and birch aphids. The fully grown apterae were almost as large as a small wood ant worker. The biology of this aphid will be discussed in a later chapter. The honeydew output from these aphids seemed to be much higher than from either the birch or pine aphids. They formed much larger but more compact groups, mainly on the undersides of the thick parts of the branches, though some groups were found on the stems of larches. In general, larch trees with C. kochiana were heavily visited by wood ants, and it was clear from casual observation that nests with access to larch trees were obtaining a large proportion of their honeydew from these aphids.

b). Larch Number 1

The first larch tree to be studied was close to a major trail, 8.6 m from nest 3 (see Figure 3). It was unusual in that the third-lowest branch drooped onto a forage trail, so that most ants used this branch instead of the stem to ascend and descend the tree. Some ants, however, left the forage trail and ascended, as is normal, via the stem. The aphid group which was studied was one of three which were easily visible, and was situated on the fourth branch up the stem, approximately 0.25 m along the branch from its junction with the stem. It was quite a large group, taking up about 6 cm length of branch, and was very heavily attended with between 20 and 30 ants at any one time. Another aphid group was found at the junction of the stem and the lowest branch. Ants which climbed the tree via the stem had to walk past this group on the way up the tree. A third extremely large group was found on the trunk at a height of about 2.5 metres.

The ants on this tree were observed on 8 days between 19th July and 11th August, 1977. The ants were mass marked as on the pine tree, although in this case it was possible to recognise a number of individuals. The times of arrival and departure from the aphid group were recorded for those ants which had unmistakable marks, and records were kept of all arriving ants in order to discover whether or not they found the aphid group at which they had been marked.

c). Results

Fifty-two returns were recorded and, of these, 42 (80.8%) returned to the aphid group which they had previously left. The mean time spent at the aphids before leaving with a full crop of honeydew was 24.6 minutes (S.D. = 9.6 min.), and most loads were obtained from aphids alone. Very few exchanges of food were recorded, and even those ants that were seen to accept loads of honeydew from other ants obtained most of their loads from aphids. One ant was watched for its entire 31 minutes visit at the aphids and was seen to accept 3 times out of a total of 9 attempts. These acceptances were very short, lasting only a couple of seconds. By comparison, each food exchange on the birch trees lasted between 30 seconds and 180 seconds.

The time between leaving the tree and returning again was recorded for 10 ants. This was fairly constant with a mean of 41.5 minutes (S.D. = 11.3 min.). Thus, on average, 37% of the total trip time was spent at the aphid colony. This is very similar to F. rufa workers attending oak aphids, which spend on average 29% of their trip time ('Umlaufzeiten') at oak aphids (Horstmann and Geisweid, 1978). Several departing ants were checked to ensure that they were actually taking their loads of honeydew to the nest. This was verified, and indeed, one ant was seen leaving the nest and was followed back to the larch tree again. No marked ants were seen to walk past the larch tree during the entire observation period.

Individual transport of honeydew collected from aphids appeared to be the general rule. A certain amount of food exchange was seen, but could not be shown to be evidence of chain transport. The output of honeydew was much higher than on birch, and the fact that an ant could obtain a full crop of honeydew in only 25 minutes from an aphid group already attended by 20 - 30 other ants probably had something to do with the lack of chain transport. It was probably as easy if not easier to obtain honeydew from aphids as from other ants. Vowles (1955) suggested that trophallaxis in ants was initiated by the donor ant (i.e., an ant with a load of honeydew induced another ant to accept part of its load). In the case of the ants on the birch trees during July 1977, the behaviour of the 'transporter' ants suggested that it was they (the acceptors) who were initiating the trophallaxis. On larch, the small amount of trophallaxis which was observed was perhaps more likely to have been induced by the donors, since the supply of aphid-produced honeydew as so readily available.

d). Larch Number 2

A second larch was studied in order to compare with the results just described. This larch was 16.8 metres from the nest and was accessed by the same forage trail as larch number 1. Ants attending an easily visible aphid group were mass marked at the aphid group, and marked ants returning to the tree were followed in order to discover to which group they returned. Observations were made on 4 days between 25th July and 28th July, 1977. Of 23 returns, 13 reached the original aphid-group, representing an aphid-group fidelity of 56.5%. Unfortunately, the traffic flow on this tree was rather low and no other results could be obtained.

Part 6 : OBSERVATIONS ON BIRCH TREES 35 M FROM THE NEST

a). Methods

In 1978, observations were made of ants attending aphids on two birch saplings about 35 m from nest 2 (see Figure 3). These saplings were accessed by the same trail as the first birch, studied in 1977 (see Part 3). The two saplings (A and B), which were 35.4 m and 34.8 m respectively from the nest, were chosen to discover whether the nest-tree distance affected the honeydew-collecting strategy. Individual marking was used: 26 ants were marked on birch A; 20 ants were marked on birch B. Birch A was observed on 11 days between 23rd May and 23rd June, 1978, whilst birch B was observed on 12 days between 13th July and 11th August, 1978. The methods used were the same as for the 1977 birch, except that the tree fidelity figures are for ants which were recorded back on the tree after they were actually seen leaving in the direction of the nest, or which were seen returning from the nest, whether or not they had previously been seen leaving. Ants which were missing from the tree (or which reappeared) but whose departure was not actually seen were ignored. The figures are, therefore, more reliable as they do not include ants which may have simply wandered about the trail before returning, or ants which were missed during checks for marked ants.

b). Results for Birch A

Fourteen of the marked ants were seen leaving Birch A with full loads of honeydew on 28 occasions, heading in the direction of the nest. On 20 occasions they were recorded back again on birch A at a later date. In other words, 71.4% of the departing ants returned to the same tree again. Six ants were seen leaving the tree on 10 other occasions, but were followed in order to ascertain whether they did, in fact, reach the nest. All of them did reach the nest without stopping anywhere along the trail or exchanging food with other ants. On 9 occasions, these ants were later recorded back at birch A. So of the departing ants known to have reached the nest, 90% returned to the same tree again. Assuming, then, that all the ants seen leaving the tree did, in fact, reach the nest, we can conclude that the ants on birch A had a tree fidelity of 76.3%.

The mean journey time between the tree and the nest was 50.4 minutes (S.D. = 10.6 min.), varying between 35 min. and 65 min. By chance, one marked ant was seen leaving the nest and heading for the tree. It reached birch A 77 minutes later. The mean walking speed of these ants was calculated as 0.72 m per minute (S.D. = 0.16 m min.^{-1}).

The exact time spent actually on the tree was known for only 2 ants. These spent 30 and 31 minutes respectively at the tree before leaving with full crops of honeydew. However, 17 ants were known to have spent more than 1 hour on the tree, 12 spent at least 2 hours on the tree, and 4 were still on the tree after 5 hours. It was suspected that 5 ants had spent more than a day at the tree, because they were seen on the tree in the evening, and were at or near the same place the following morning, and stayed there without leaving all day. Three of these ants probably stayed for 2 days continuously and 2 were thought to have spent 3 consecutive days in the tree (c.f. Horstmann and Geisweid, 1978). There was, therefore, a very wide variation in the time taken to obtain a full crop of honeydew. Since there was no evidence to suggest that a chain transport system was at work on this tree (see later), this wide variation in times was not a result of a donor/acceptor division. However, this birch was observed during the first two months of the season, when the aphids are still growing. Output of honeydew was therefore very low throughout these observations. Though no data was obtained to demonstrate the point, it was noted that the long-stay ants remained at the same groups of aphids throughout their stay, whereas the short-stay ants moved about the tree. Clearly, during a time when honeydew output is low, an ant will collect honeydew more quickly if it visits several groups of aphids than if it remains at only one. It is, therefore, difficult to understand why some of the ants attend only one aphid group. It is true that these aphid groups are protected continuously by such ants, but since other groups were left totally unattended for hours at a time, this would seem to be an unlikely explanation for the phenomenon.

c). Results for Birch B

The results obtained for this sapling were very similar to those for birch A. Eleven journeys made by 8 ants were followed all the way to the nest in order to confirm that loads of honeydew were taken back to the nest and not exchanged *en route*. As with birch A, all these ants did, indeed, return to the nest without any trophallaxis along the way. Ten returns to birch B at a later date were recorded for these ants, representing a tree fidelity of 90.9%. For all ants seen leaving the nest, whether followed to the nest or not, a tree fidelity of 88.4% was obtained (13 marked ants made 43 departures and 38 subsequent returns). By chance, 5 ants not actually seen leaving the tree were observed leaving the nest and all of these returned to birch B.

The mean journey time between birch B and the nest was 40.6 min. (S.D. = 28.9 min.). However, most ants took between 22 min. and 45 min. to make the 35 m journey, and the mean figure is distorted by one ant which took 120 min. to reach the nest. This journey was made on a very cool day after heavy overnight rain. If this figure is ignored, the mean journey time is 31.8 min. (S.D. = 8.1 min.). The nest-tree journey time was known for two ants: 28 min. and 32 min.

respectively. The mean walking speed (ignoring the very slow ant) was 1.15 m per minutes (S.D. = 0.24 m per min.), very much faster than the figure for birch A. Birch A was observed in late spring - early summer, whereas birch B was observed during July and August. Holt (1955) showed that the activity of wood ants was dependent on air temperature and this probably explains the significant difference between the walking speeds for the ants from the two trees, ($p < 0.001$; Mann-Whitney U test).

No information was obtained to suggest that any ants stayed on birch B for more than a day. The mean time spent on the tree was 48.4 min. (S.D. = 22.8 min.), varying between 25 min. and 83 min. No long day-time visits were recorded, unlike the results for birch A. The much shorter visits on birch B are probably a reflection of the increased honeydew output by Symydobius oblongus, as a result of both increased aphid numbers and increased aphid size between July and August. Indeed some ants on birch B were obtaining loads of honeydew as fast as those on larch trees.

Part 7 : CONCLUSIONS

The fidelity of wood ants to particular trees during the summer is very high, irrespective of tree species, tree size, aphid type or nest-tree distance. Table III sums up the tree fidelity ratings of wood

Tree	Tree-nest distance	Number of departures by marked ants	Number of returns by marked ants	Tree fidelity
Birch (1977)	4.1m	255	202	79.2%
Birch 'A' (1978)	35.4m	38	29	76.3%
Birch 'B' (1978)	34.8m	43	38	88.4%

Table III Tree fidelity of wood ants attending aphids on birch trees close to and far from the nest.

ants to the birch trees, and shows that distance has no significant effect on the fidelity of ants to particular trees ($X^2 = 0.25$, df = 2, $p > 0.80$). Even a 35 m journey between the tree and the nest did not prevent each ant from taking its own load of honeydew all the way to the nest. Such a journey represented a great investment in time and (presumably) energy. In mid summer, at least one hour was required in order to move a single load of honeydew from the aphids on birch B to the nest and for the ant to return to the tree again. At no time was any food exchange seen on the trails, showing that no form of chain transport was used once the honeydew left the tree. A form of chain transport was shown to have occurred within the birch in 1977, although it was not seen in any other tree in either 1977 or 1978. However, even in the birch in 1977, all the interactions occurred within the tree itself. As soon as a transporter ant had left the tree, it made no further exchanges until it entered the nest.

Although there were at least 15 other saplings known to support large numbers of aphids between the nest and the 1978 birches, marked ants were never seen returning to any other trees but their original tree at which they had been marked. They did not simply return to the first aphid-infested tree they came across, but actually made their way to a particular tree. The fidelity figures, however, do not demonstrate

100% faithfullness to a particular tree. Of course, this may be partly due to loss of marks and death, but at least two ants, one from birch A and one from birch B were known to have changed to different trees. These were, however, adjacent to the original birch in each case. Although regular checks were made on all the saplings along the 50 m of this forage trail between April and late June, no marked ants were found on any other tree. In other words, it would appear that any ants which are not faithful to a particular tree do not drift far from their original tree.

Although the fidelity of wood ants to a particular tree is very high, the fidelity to particular aphid groups varies considerably. Table IV shows the branch and aphid group fidelities for those trees for which the appropriate data was obtained. The branch fidelity is the percentage of returning ants which went to the branch which they had left on the previous visit. Similarly, the aphid-group fidelity is the percentage which returned to the aphid group they had previously left.

There is a significant difference between the returns to both branches and aphid groups for different trees ($X^2 = 21.0$, df = 3, $p < 0.001$ for branch returns; $X^2 = 54.6$, df = 3, $p < 0.001$ for aphid group returns). This large variation in fidelity figures is probably a result of the different tree sizes and the positioning

Tree	Aphid Species	Nest-tree distance	Number of returns by marked ants	Branch fidelity	Aphid-group fidelity
Birch	*Symydobius oblongus*	4.1m	202	46.0%	28.7%
Scots Pine	*Cinara pini*	2.4m	23	43.5%	17.4%
Larch	*Cinara kochiana*	8.6m	52	80.8%	80.8%
Larch	*Cinara kochiana*	16.8m	23	56.5%	56.5%

Table IV Branch and aphid-group fidelity of wood ants attending a variety of aphid species on different trees (1977).

and structure of the aphid groups. S. oblongus in birch forms groups which are not particularly big, but there can be many groups on each branch. They are usually spread generally throughout the tree. In any case, the branches of the birch saplings are short and the distance between branches is very small. An ant returning to a birch tree has a high probability of finding an aphid group on almost any branch, and need not choose the branch which it had been on at the last visit. Ants attending birch aphids usually move through several aphid groups and may visit aphids on more than one branch during any one visit at the tree. There is, therefore, no reason to expect that an ant returning to a birch tree should return to the aphid group it last attended. As Table IV shows less than half the ants returned to the branch which they had been on prior to leaving on the previous visit. Even fewer (29%) returned to the aphid group they had last visited. Otto (1958) provided some data on the fidelity of F. polyctena attending S. oblongus on birch. If the dashes in his Tables 10 - 12 symbolise that an ant had left the tree, then 3 of his 43 marked ants made 31 returns to the same branch out of a total of 40 returns to the birch - a branch fidelity of 77%. There is, unfortunately, no way of knowing how typical these 3 ants were of his F. polyctena foragers.

Cinara pini on mature pine trees forms quite large clusters, but they all feed on the small twigs.

The aphid groups are distributed quite sparsely through the trees. Of course, the branches of mature pine trees are very large and the distance between branches is very much greater than on birch saplings. An ant returning to a mature Scots pine, therefore, has a difficult task finding a particular aphid group. It must select the correct branch and then negotiate a complex maze of smaller branches and twigs if it is to find the aphid group. More than half the returning ants reached the correct branch of the pine which was studied, but fewer than 1 in 3 of these then managed to find the aphid group. It is possible that as a result of the distribution of *C. pini*, the navigational limits of *F. lugubris* were reached. A large amount of time seemed to be wasted by ants simply wandering about the branches, apparently searching for aphids.

Cinara kochiana on larch forms very large clusters on the underside of the thick parts of the main branches, usually within one or two metres of the junction with the stem. Sometimes there are several clusters to a branch, but on mature larches, the living branches are quite far apart, so the overall distribution of clusters is quite sparse. A wood ant returning to a larch must first choose the correct branch. Larches in planted forests tend to have large numbers of dead branches, especially around the bottom few metres of stem. However, once the ant has selected the correct branch, it need only walk along it in order to reach the aphids. Table IV shows that no ants which chose the correct branch failed to find the aphids. It also shows that they are much more faithful to C. kochiana clusters than to any other species of aphid. This is probably because C. kochiana are very attractive to wood ants, since they produce large amounts of honeydew. Their honeydew may be more attractive because of its composition, and the relatively sparse distribution of the aphid clusters and the ease with which they can be found, provided the correct branch is selected, probably has an additional influence on the fidelity. By comparison, C. pini has lower honeydew output and is therefore unlikely to be as attractive to wood ants. On mature pines, C. pini is much more difficult to find even if the correct branch is selected. Learning to find a particular aphid group is therefore less likely and more difficult on pine than on larch. The aphid group fidelity on larch is similar to that found for F. rufa on oak - 81% (Horstmann & Geisweid, 1978). This may reflect a similarity in the colony structure of Cinara kochiana and Lachnus roboris.

It must be noted that the many pine saplings along the trail connecting nest 2 to birches A and B were very heavily visited (see later). As even the stem of these saplings was often as thin as a sub-branch of a mature pine, the distribution of C. pini was entirely different. The aphids formed very large clusters on the stem and branches, and all a returning ant would have had to have done was climb the stem in order to find aphids. The success of finding C. pini in saplings was undoubtedly much higher than on mature pines. No comparable data was, however, collected. There was some evidence from casual observation that the fidelity to pine saplings was as high as that towards birch saplings. Indeed one marked ant which moved from the 1977 birch to an adjacent pine sapling was still being seen on that pine up to 28 days later.

In general, individual transport of honeydew was used by wood ants. A chain transport system was witnessed during July 1977 on the birch saplings but this appeared to be a transient effect. Some interactions and food exchange did occur on other trees, but generally, the majority of the crop-load of honeydew of any ant was collected directly from the aphids. In 1978, the output of honeydew from aphids on birch B became so high that many aphids could not get rid of their honeydew, except by letting it fall from their abdomens. Between 24th July and 28th July, some ants were seen drinking these discarded drops from the leaves of birch B. However, as with food exchange, such honeydew accounted for only a small proportion of a normal load. Indeed Douglas and Sudd (1980) have shown that 84% of drops produced by aphids are collected by wood ants. The spilt honeydew, therefore, represented only a very small proportion of honeydew available in the tree, especially since only a proportion of uncollected drops fell onto leaves below the aphids; the rest fell on the ground and were lost.

CHAPTER 5

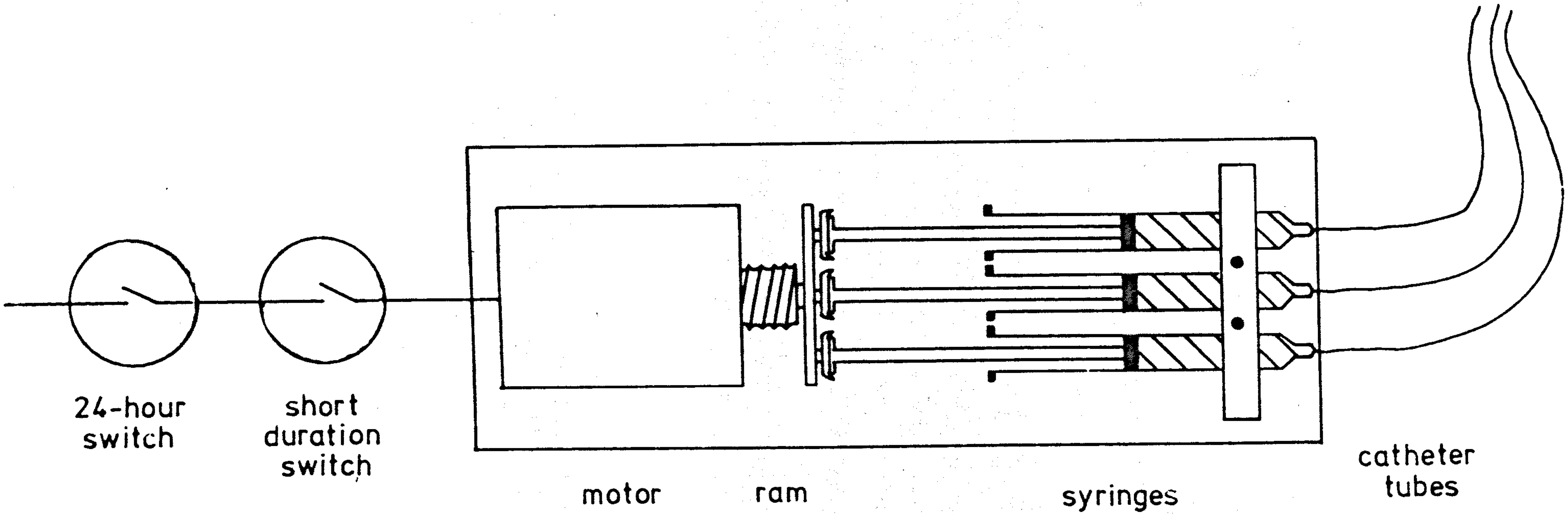
HONEYDEW COLLECTION : LABORATORY STUDIES

a). Methods

Although the fieldwork demonstrated some strategies used by wood ants, it did not provide many clues as to why individual transport was the normal collection strategy and why chain transport only occurred on rare occasions. A controllable simulation of honeydew output was therefore used in the laboratory, in an attempt to discover the important factors which affected honeydew collection. All the laboratory methods for simulating honeydew output which were described in Chapter 2 had failed to closely imitate the output of honeydew from an aphid group, since they allowed an ant to obtain a full crop of sugar solution simply by gaining access to a drinking-tube or dish. A pulsed flow was necessary, whereby an ant had to not only gain access to the source, but also had to wait for the source to provide the sugar solution. Each drop produced by the source had to be sufficiently small so that a number had to be collected before a full crop was obtained. The apparatus which was designed to perform this difficult task is shown diagrammatically in Figure 7, and plate 1 shows the actual apparatus in the laboratory.

A 24 hour switch was used to stop and start the

Figure 7 : Diagram of the apparatus used to simulate honeydew production.



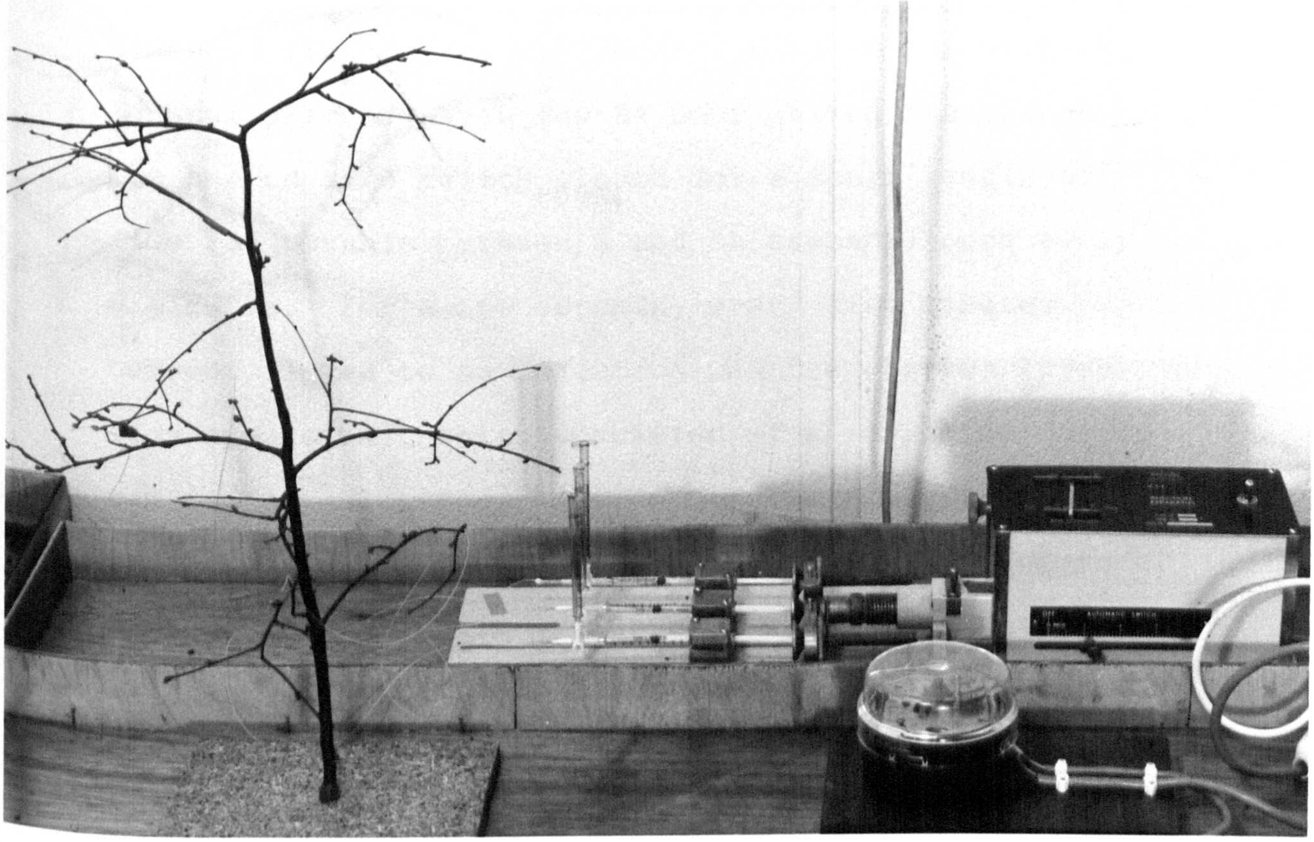
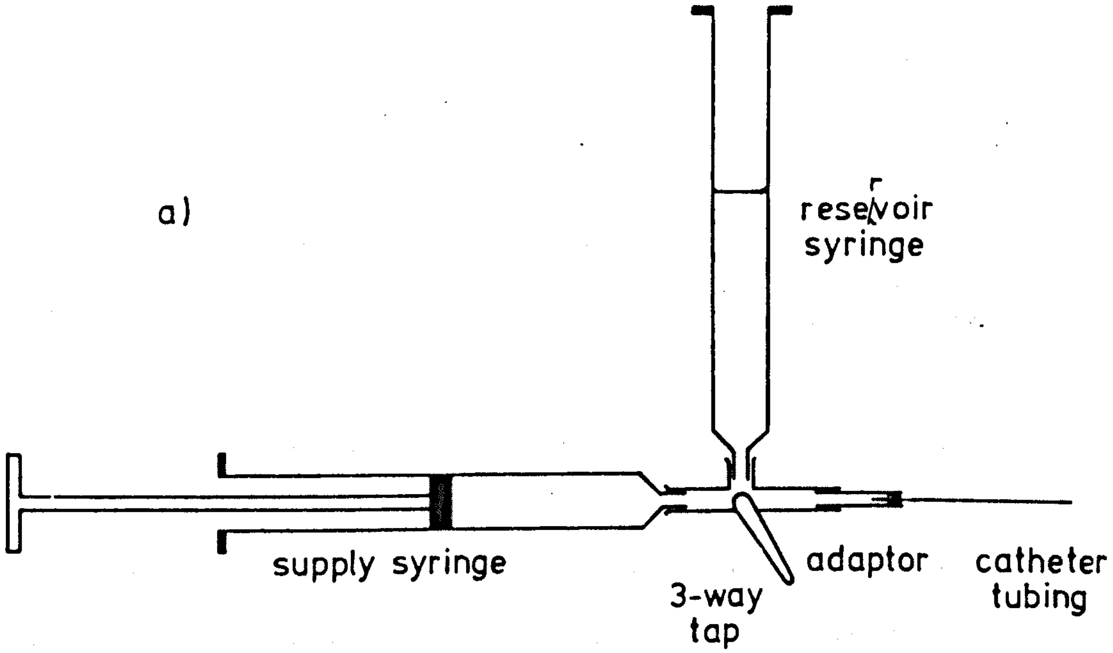


Plate 1 : The apparatus used to simulate honeydew production in the laboratory. Note that this photograph shows a real birch sapling, and not the balsa model described in the text.

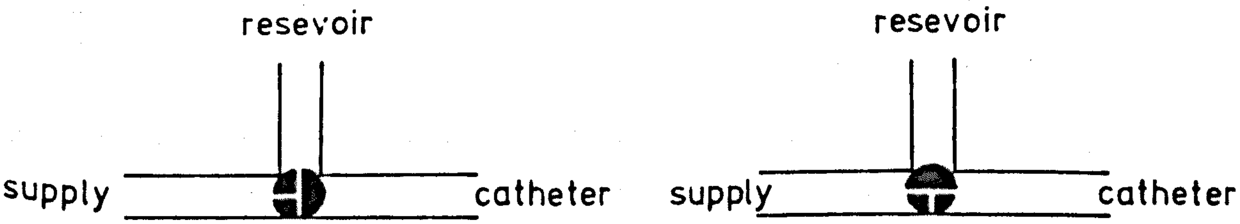
apparatus simultaneously with the laboratory lighting. This was done to simulate a cessation or reduction in honeydew output at night when sap-flow was reduced. A second time switch was connected in series with the 24 hour switch. When the 24 hour switch was closed, the second time switch closed for a short length of time (adjustable between 2 and 25 seconds) once every 5 minutes. For a few seconds, every five minutes current flowed to an injection machine (Parker Injection Apparatus), which consisted of a very slow moving ram (adjustable speed of 1 inch forward movement between 10 and 320 minutes), which pushed the plungers of three 1 ml plastic syringes to which were connected lengths of very fine catheter tubing (0.28 mm bore). These were then attached to a small balsa-wood model 'tree'.

Each syringe was attached to the catheter tubing via a three way tap and adaptor. The taps allowed the syringes to be refilled with sugar solution from a reservoir syringe, without having to disconnect the catheter tubing. This prevented air bubbles entering the catheter tubing, and minimised disturbance to the ants feeding at the ends of the catheter tubes. Figures 8 b and c show the connections made by the 3-way switch. The tubing was connected to the taps by a short adaptor tube. This consisted of a piece of polythene tubing whose external diameter was just

Figure 8:



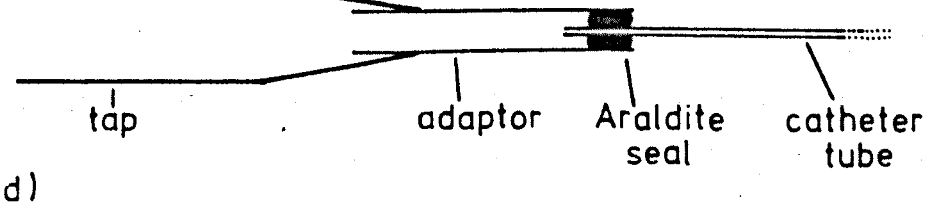
Syringes and attachments used in the artificial aphid



b) tap set for filling supply syringe

c) tap set for droplet production

Diagram of 3-way tap settings



Connection between 3-way tap and catheter tubing small enough to fit into the bore of the 3-way tap. The end of the catheter tubing was inserted into the other end of the adaptor tube and sealed in place with Araldite adhesive (Figure 8d).

With the apparatus switched on and the injection machine set to 1 inch movement in 160 minutes (i.e., 160 minutes continuous movement), a 10 second firing (controlled by the short-duration time switch) would move the ram, and hence the plungers of the syringes, 0.001 inches = 0.003 cm. This released 0.45 µl of solution, on average, from each syringe, forming as a very small droplet at the end of each catheter tube. Because the syringe plungers did not run completely smoothly along the syringe walls, the drops varied in size to a certain degree . The mean droplet volume of 0.45 µl compared favourably with the known figures for honeydew production. Tuberolachnus salignus, a large aphid which feeds on willow stems, is about the same size as Cinara kochiana. The mean honeydew droplet volume for an apterous adult is 0.78 µl, produced at a rate of about 2 drops per hour. The larval instars produce smaller but more frequent drops. For example, a second instar T. salignus produces just over 5 drops per hour, each containing 0.135 µl of honeydew (Auclair, 1963). With 3 tubes, each producing 0.45 µl drops, 12 times per hour, the laboratory apparatus therefore simulated a colony of

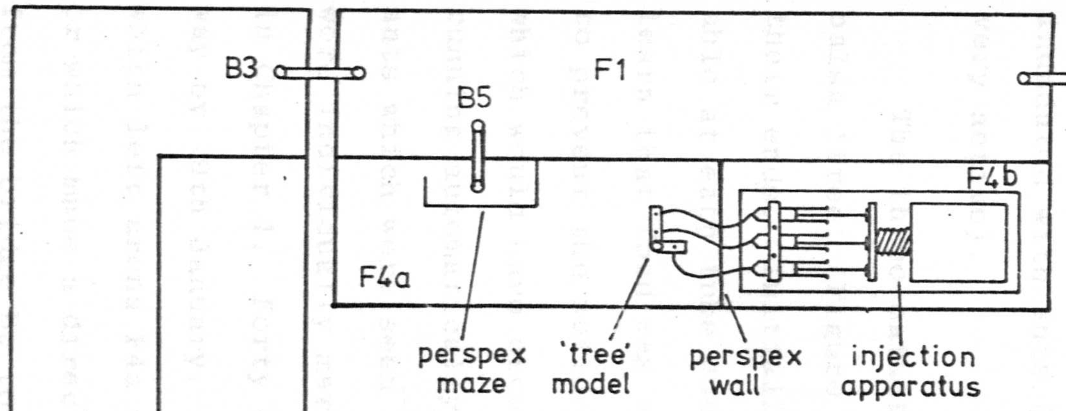
15 - 20 individuals of a large species of aphid. Horstmann (1973) has estimated that a fully-laden wood ant can hold, on average, 1.5 mm^3 of liquid in its crop. Hence, an ant would have had to collect 3 - 4 drops from a tube to obtain a full crop - in practice between 4 and 5 drops were usually collected before a full crop was achieved. Although wood ants attending small aphid species such as Symydobius oblongus or Cinara piceae must collect many more droplets at each visit before obtaining a full crop, the laboratory simulation was thought to give a useful compromise between restricting the food supply and minimising the time needed to observe a complete feeding sequence from an ant's leaving the nest on the way to the food source until its return with a full crop.

The apparatus was very promising and did allow some useful observations to be made. However, great difficulties arose with the thermostatic control of air temperature in the experimental room. In order to obtain repeatable observations, a constant temperature was critical, since a rise in temperature caused all the ants to become more active. More ants would leave the nest and run onto the arenas. If the temperature dropped, ant activity declined and few results could be obtained. Under low temperature conditions, ants which had been regular collectors of honeydew would either fail to leave the nest or would take much longer to collect a full crop of sugar solution. The results which were obtained must therefore be viewed with care, and should not be taken as strong evidence for any particular hypothesis.

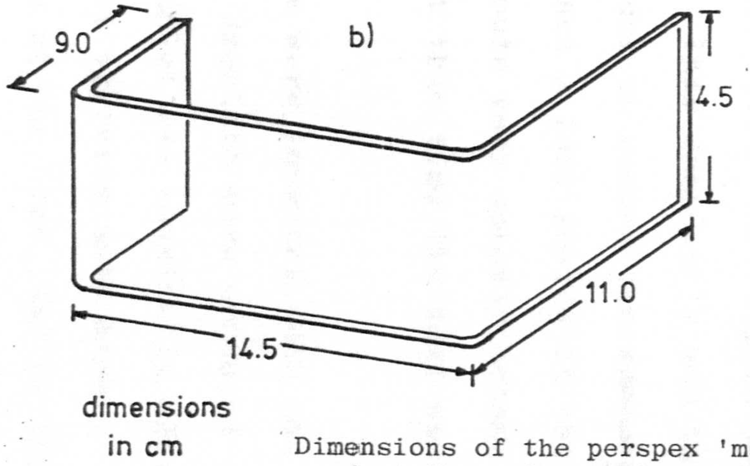
The only worthwhile results provided by the laboratory simulation were obtained between January and March 1978. At this time, the apparatus was being test-run. Although the lighting and humidity conditions were constant, and the air temperature was held as constant as possible, other variables such as the daily ration of protein food and the amount and concentration of sugar solution (not including that in the artificial syringes) available to the nest were not controlled. When experimental runs were attempted (winter 1978-79), with food supply controlled, not only was the temperature in the room fluctuating excessively, but the worker population of the laboratory nest had greatly diminished. However, in the meantime, many of the design faults in the apparatus had been rectified, and the importance of a number of environmental variables had been assessed. These results will be discussed later.

On 11th January 1978, the arenas, shown in Figure 1 were rearranged as in Figure 9a, so that the route necessary to reach the ends of the catheter tubes was entirely new. Rather than an ants having to make a complete round trip of the four arenas, it crossed a new bridge B5, three quarters of the distance along

Figure 9:



a) The foraging arenas in the laboratory as arranged during experiments with the artificial aphid.



Dimensions of the perspex 'maze' used at the entrance to arena F4a.

arena F1. A simple maze, produced by placing a C-shaped piece of perspex around B5 (Figure 9b), had to be negotiated, and then the 'tree' (see Figure 10) had to be found and climbed. This complexity was introduced into the journey in order to reduce the numbers of ants finding the tree, since a food source at the end of a simple, easily learnt route very quickly became inundated with ants (Note: at this time the nest was very active).

The three catheter tubes were inserted into the balsa 'tree' (Figure 10) and droplets were produced at their ends. Initially, a droplet was constantly available at each tube end, so that arriving ants might learn that food was available at the tree, and in order to prevent the build-up of uncollected, spilt drops which would have occurred if the apparatus had been running automatically. For the first few days, all the ants which were seen to obtain food from the tubes were individually marked using the technique described in Chapter 4. Forty seven ants had been marked in this way by 19th January. Thereafter, only un-marked ants which left arena F4a with a full crop of sugar solution, or which made a direct journey without incorrect turns from the bridge B5 to the 'tree' model were given a mark. The arrivals and departures of marked ants to and from arena F4a were recorded daily, along with the occurrences of food exchange whilst on the 'tree' or in arena F4a. Between 11th and 22nd January, the short

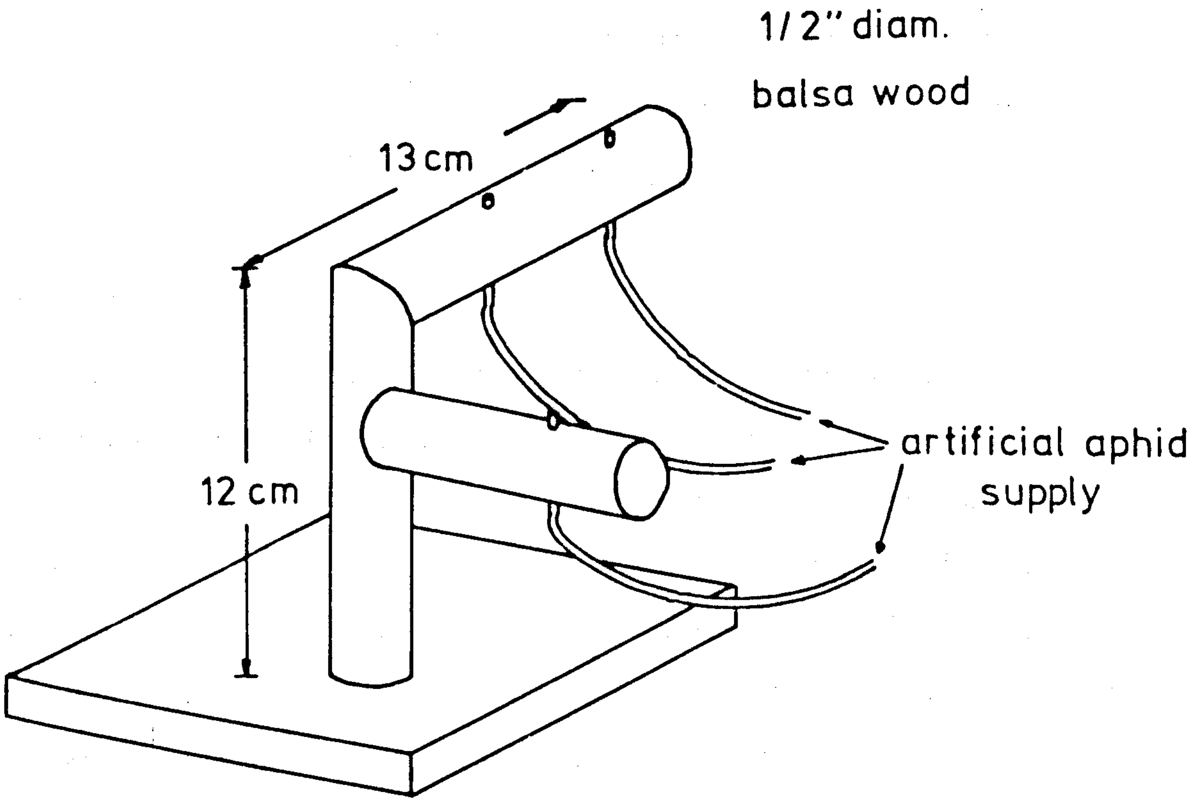


Figure 10 : Diagram of the balsa-wood model 'tree' used in the experiments with the artificial aphid.

duration time switch was not connected, so that there was a very slow but constant flow of sugar solution being produced from the tubes. On January 23rd, the short-duration time switch was connected, and a pulsed flow of sugar solution produced at the catheter tubing tips. Between 27th and 29th January the tubes became blocked and no sugar solution was available until 30th January.

b). Results

Figure 11 shows diagramatically all the arrivals and departures of marked ants in the first 7 days. Most ants became lost in the arena for long periods of time, and few returned to the arena once they found their way out over bridge B5. The maze created by the perspex wall around bridge B5 created severe problems for ants attempting to leave arena F4a and, as shown by Schneirla (1943), the return journey out of the arena had to be learnt as a separate entity from the journey into the arena. Out of 47 ants which fed from the tubes, only 2 were known to become regular foragers - ants 1 and 15. Their typical foraging behaviour is characterised in Figure 11 as very short but repeated solid bars, joined by thin short lines, showing that their stays in arena F4a were very short and that, on leaving arena F4a, they were seen returning directly to the nest. An interesting feature of Figure 11 is that although these two ants were foraging regularly

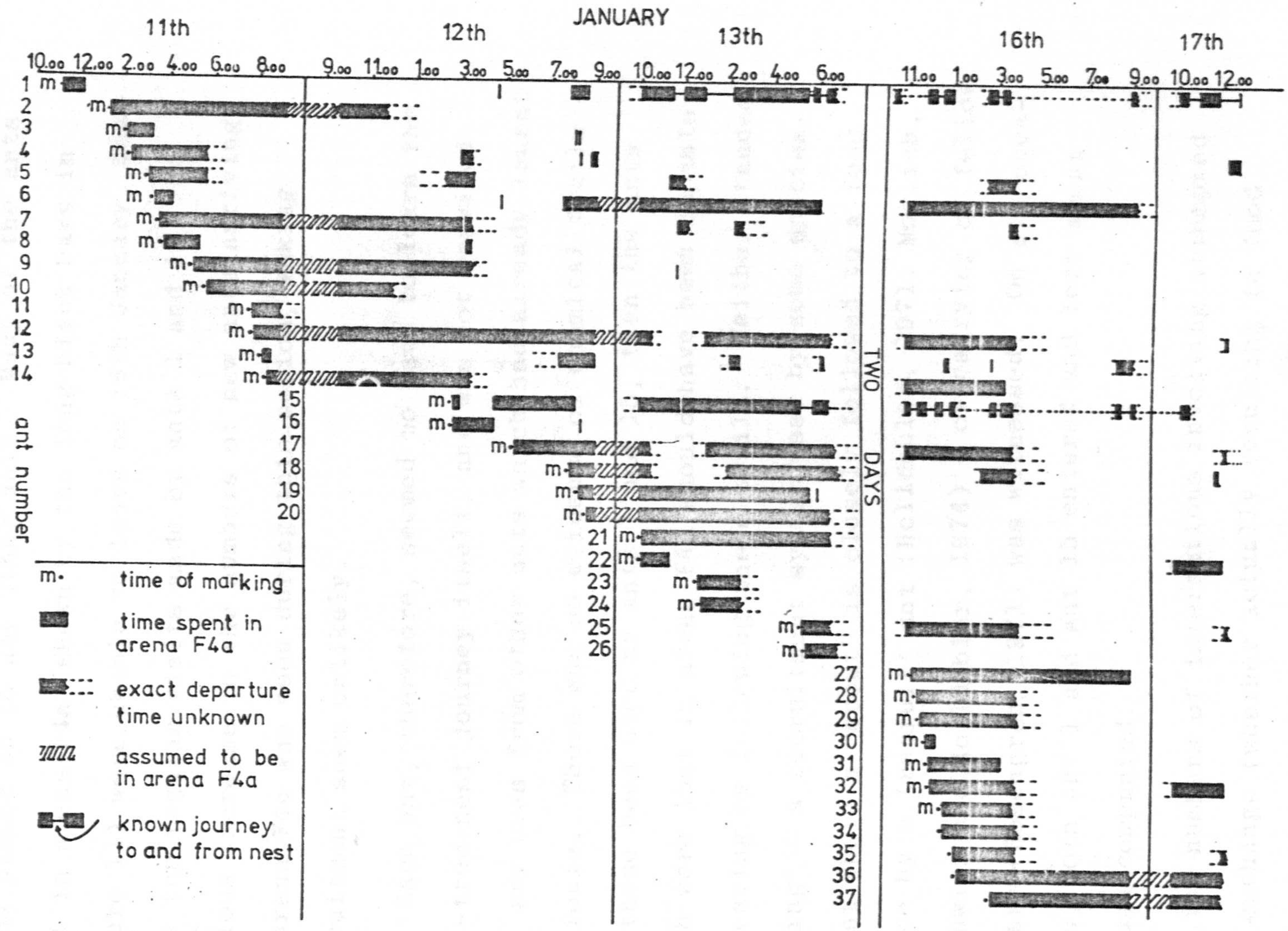


Figure 11 : Arrivals and departures of marked ants during the first seven days of the artificial aphid experiments.

on 13th and 16th January, no information regarding the journey from nest to tree or from tree to nest appeared to be passed on to any other ants. Many of the ants lost in arena F4a (shown by the long black bars in Figure 11) were unable to leave on 16th January, despite the regular visits made by ants 1 and 15. No obvious increase in the numbers of new ants arriving at arena F4a was seen during this period, making recruitment seem unlikely.

Each ant, therefore, seemed to have to learn the nest-tree-nest journey itself, and was not provided with any cues from other ants which had already learnt the route. There was no evidence of chemical trails - had these been used by ants 1 and 15, then the ants which were lost in arena F4a should have been capable of leaving by following these trails. Neither 'tandem running' - a recruitment system used by some species of ant where a "scout" is closely followed to a food source by a 'recruit' ant (Holldobler, 1971; Moglich, Maschwitz and Holldobler, 1974) - or carrying of fellow workers (Rosengren, 1971) was witnessed. On all occasions, both ant 1 and ant 15 entered and left arena F4a unaccompanied.

The numbers of interactions involving attempted food exchange (whether actually resulting in food exchange or not) and successful food exchange (resulting only in actual food exchange) were recorded between

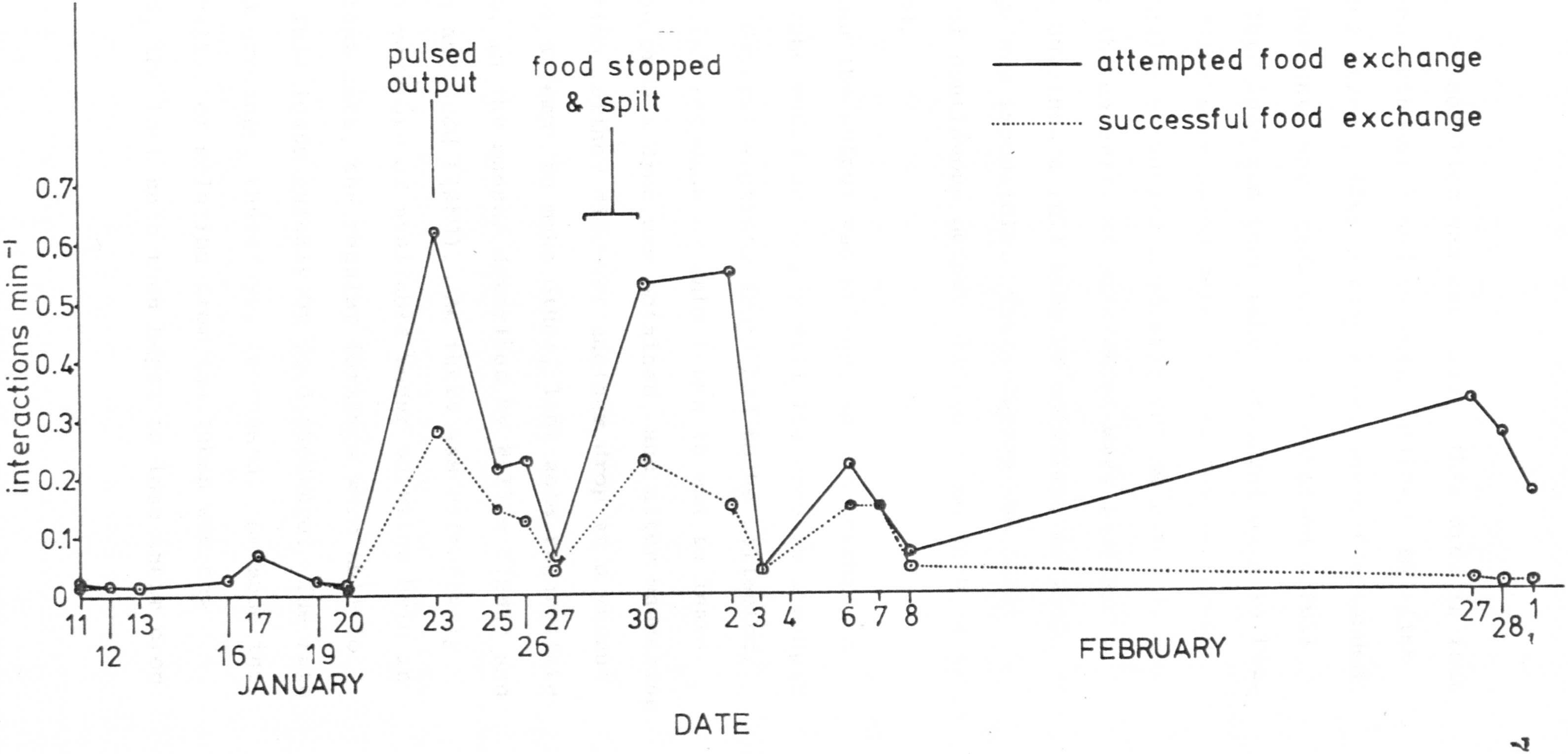
11th January and 1st March, 1978, and are displayed in Table V. The mean rates of interactions and food exchanges were also calculated and are plotted in Figure 12. Between 11th and 22nd January, during which time the artificial aphid was producing a very slow but continuous flow, very few successful or attempted food exchanges were observed. As soon as the output was pulsed, on 23rd January, the numbers of food exchanges increased dramatically, then fell gradually until 27th January. Over the weekend of 28th and 29th January, the food supply stopped, and no foraging occurred on the morning of 30th January. When the food supply was restarted, a considerable amount of solution was spilt on the tree because the droplets were not collected. This was followed by a sudden rise in the rate of food exchange which lasted several days before dropping again. After 35 days of steady pulsed output by the artificial aphid, the rate of attempted food exchanges was higher than when a continuous output was supplied, but the rate of successful food exchanges was as low as when solution was continuously supplied.

To explain these results, the availability of food, both at the tubes and in the crop contents of other ants, must be considered. When the solution was produced continuously, and with only a small number of regular foragers, an ant had only to gain access to a tube and proceed to drink at the same

Date	Total Observation Time (Mins)	Number of attempted Food exchanges observed	Number of successful Food exchanges observed	Mean attempted exchange rate (Min^{-1})	Mean successful exchange rate (Min^{-1})
11/1	445	10	7	0.022	0.016
12/1	347	7	7	0.020	0.020
13/1	289	5	4	0.017	0.014
16/1	250	7	6	0.028	0.024
17/1	123	8	8	0.065	0.065
19/1	163	4	4	0.025	0.025
20/1	111	2	1	0.018	0.009
ARTIFICIAL APHID BEGINS PRODUCING PULSED OUTPUT					
23/1	21	13	6	0.619	0.286
25/1	28	6	4	0.214	0.143
26/1	65	15	8	0.231	0.123
27/1	125	8	5	0.064	0.040
FOOD STOPPED. FOOD SPILLAGE WHEN RESTARTED					
30/1	100	53	23	0.530	0.230
2/2	60	33	9	0.550	0.150
3/2	100	4	4	0.040	0.040
6/2	188	41	28	0.218	0.149
7/2	27	4	4	0.148	0.148
8/2	133	9	6	0.068	0.045
27/2	256	84	5	0.328	0.020
28/2	131	35	2	0.267	0.015
1/3	120	20	2	0.167	0.017

Table V Food exchange around artificial aphid in laboratory - January-March 1978.

Fig. 12 Mean rates of attempted and successful food exchanges observed in the laboratory : 1978.



rate as the solution was supplied. This did, in fact, occur and both ant 1 and 15 learnt quickly to climb the model 'tree', find a tube which was not attended by another ant, and drink until it obtained a full crop. This load was then taken straight back to the nest. Other ants which were lost in the F4a arena occasionally exchanged food with fellow ants, but in general the majority of ants which were lost had already obtained a full crop of solution, so food exchange was impossible. Thus, during the first period of continuous output, little or no food exchange occurred.

When the output was pulsed, an ant reaching a vacant tube could no longer fill its crop in a single visit. Several separate drops had to be collected. The initial response of ants 1 and 15 was to leave the tube once a drop was obtained, and after wandering for a time, either discover another drop at a vacant tube, or attempt to make other, lost ants regurgitate to them, in the manner described by Wallis (1961) and Douglas and Sudd (1980). As there was effectively a large reservoir of available sugar solution held in these lost ants, the regular foragers were able to obtain full loads quickly by food exchange. The rate of food exchange, therefore, increased. Because the availability of solution from the tubes was now reduced, the lost ants then began to lose their crop loads to other soliciting ants so this ant-held reservoir of solution began to diminish. With fewer attempted food exchanges leading to successful regurgitation by the solicited ants, regular foragers had to resort to waiting at the tubes and collecting each drop as it was produced. The last three data points in Figure 12 suggest that after a long period of pulsed output of solution, a steady state of foraging was reached in which attempted food exchange was quite common, but few of these attempts ended in actual regurgitation. In the period between droplet production, the regular foragers usually attempted to obtain food from nearby ants. However, since the regular foragers became very efficient at collecting any available droplets as they were produced, most lost ants had little surplus in their crops, so refused to give up any food. Regular foragers also refused to give up any of their crop contents, and appeared, instead, to be more interested in obtaining their own crop-load of solution than in giving any away. Attempted food exchanges during this period were, therefore, generally unsuccessful. It is perhaps surprising that any attempts should even have been made, bearing in mind the low probability of success. With food otherwise unavailable between firings of the artificial aphid, even a low probability of success might have made attempts worthwhile.

A particularly interesting feature of Figure 12 is the sudden rise in regurgitation rate when surplus spilt food was available on 30th January. Access to food then became much easier and any ant could obtain a full crop of sugar solution as quickly as it could drink it. On obtaining a full load, both regular foragers and ants which were lost tried to regurgitate again. Rather than trying to return to the nest, the full ants would approach others whilst holding their mandibles open, trying to get other ants to accept their crop contents. With unlimited food, ants did not have to be solicited to give up their crop contents - rather the roles were reversed and the donors solicited the acceptors. Although no numerical data could be obtained on this behaviour, it appeared that it was induced by a sudden increase in the availability of food. Similar behaviour was observed around a newly produced petri-dish of sugar solution (see Chapter 2).

c). Conclusions

The laboratory data suggest that two factors may be important in the initiation of food exchange: the amount of food held in the crops of ants which are unable to return to the nest, and the ease of access to food sources. However, it is unlikely that a reservoir of food in the crops of lost ants can account for the chain transport seen in July 1977. Many of the collector ants (the donors) were known to have returned to the nest at least once, so were clearly not lost. In addition, novice ants probably reach most trees all year round (as suggested by the high turnover of marked ants in field experiments), and it is, therefore, difficult to see why the lost novice ants on a single birch during a particular short period should induce chain transport whilst individual transport occurred on all other trees and at all other times of the year. Access to food is possibly more important to wood ants. In the laboratory, access depended on the relative number of ants per tube and the number of drops required to obtain a full crop. In the wild, access would depend on the ratio of ants to aphids at an aphid group, the size and rate of droplet production and the dispersal of aphids within a tree (e.g., an aphid species with small widely dispersed colonies of individuals which produced a few small droplets would be more difficult to exploit than an aphid species with large, closely distributed colonies of large individuals, which produced very frequent large honeydew droplets). With an increase in the availability of food, and hence a reduction in the competition for that food, an ants reluctance to give up its crop contents appears to decrease to the extent that a sudden change to unlimited food induces ants with full crops to actively seek others to whom to regurgitate. In fact this technique was used when photographs of trophallaxis in wood ants were required. Although such an extreme change in food availability is unlikely in the wild, an unusually rapid increase in aphid numbers, the size of aphids and honeydew output by each aphid could at least cause collecting ants to give up their crop contents more freely with little solicitation by other ants. If this had occurred for some environmental reasons, unique to the birch studied in 1977, then it is possible that a number of ants could have learnt to collect honeydew from these freely-donating collectors, and therefore initiate a 'transporter - collector' chain transport system. This hypothetical system would have a certain degree of stability. If too many of the foragers on the tree became 'transporters' then fewer ants would be left as collectors, and loads collected from other ants would be more difficult to obtain compared with droplets collected directly from aphids. "Transporters" would therefore revert to collecting aphid-produced honeydew, so tending to result in a stable ratio of 'collectors' and 'transporters'. There is some evidence that the chain transport observed in 1977 depended on the relative ease of collection from ants versus aphids: during 42 minutes of continuous observation of a known transporter ant, 38 aphids were solicited and only 1 droplet was obtained - a 3% success rate. 27 ants were also solicited and 8 regurgitated - a 30% success rate. As far as this ant was concerned, collecting second-hand loads was clearly more worthwhile than collecting from aphids.

The stability of the chain transport system, as proposed above, depends on the total foraging population within a tree remaining constant. If there is a turnover of foraging ants on each tree, as appears to be the case, then chain transport would be expected to be a transitory phenomenon. During 1977, the average half-life of a marked forager was 10 days, and not all losses could be ascribed to loss of the paint marks. Yet there were always large numbers of ants on each aphid-infested tree. This implies that there is a constant eflux of new foragers from the nest arriving on a tree. Should chain transport occur on a tree, it would be expected to subside gradually, since newly arriving ants would add to the total number of foragers on that tree, and make the task of collecting drops of honeydew from aphids more difficult, even if the output was still higher than normal. With aphid-collected loads more difficult to obtain, 'collectors' would become more reluctant to regurgitate their crop-contents, and so 'transporters' would revert to collecting from aphids.

To summarise, chain transport, once initiated, would be more or less stable while the forager population, the aphid numbers and honeydew output remained stable. A turnover of the forager population, or a decrease in the availability of honeydew (e.g., due to weather conditions) would make it disappear.

This model of chain transport requires further evaluation both in the field and the laboratory before its applicability can be evaluated. True chain transport could not be demonstrated in laboratory experiments. However, there was some evidence of a grouping into at least two populations - one which collected from the tubes and other ants, and a second population which was solicited by other ants.

Twenty ants were watched in arena F4a for 30 minutes each, and the numbers of times the various behaviours were performed were recorded. The results are shown in Table VI. These results were obtained between 28th February and 6th March, 1978. Using a technique called Reciprocal Averaging (Hill, 1973), an ordinating technique similar to Principal Components Analysis (Nichols, 1977; Noy-Meir and Whittaker, 1977), the individual ants were ranked on two axes, according to their relative frequencies of the six behaviour categories. From the relative frequencies of the behaviour types, each ant can be given an ordination value, calculated using initial ordination values (which are simply guesses) given to the six behaviour types. These ant ordination values are then used to recalculate more accurate ordinations for the behaviour types, and these values, in turn, used to recalculate the ant ordination values. This reciprocal use of ant and behaviour ordinations is continued until stable

Ant Number	Number of regurgitations	Number of failed solicitations by other ants	Number of failed attempts to make other ants regurgitate	Number of failed attempts to obtain food from tube	Number of successful acceptances	Number of successful tube feeds
			GROUP B			
10B	0	1	0	0	0	0
23B	1	5	1	0	0	0
40B	0	5	0	1	0	0
33B	0	2	1	0	0	0
42	0	4	1	1	0	0
27B	1	4	3	1	0	0
			GROUP A			
41B	0	4	0	7	0	0
28B	0	1	5	0	0	0
18B	0	1	0	2	0	0
38B	2	4	5	12	0	2
45B	1	2	3	9	0	0
29A	0	6	8	12	0	3
30B	0	0	1	0	0	0
12B	0	2	4	12	0	0
26B	0	1	2	6	0	0
25B	0	3	12	17	2	1
7B	0	5	19	39	1	4
29B	0	2	10	19	2	3
13B	0	0	0	9	0	4
39B	0	0	0	11	1	4

Table VI Frequency of feeding behaviours recorded for 20 ants in the laboratory (1978). Each ant was observed for 30 minutes. The table has been ordinated using reciprocal averaging and is laid out so that ants at the top of the table and behaviours at the left of the table have the highest ordination scores.

values are obtained (these values can be shown to be independent of the initial guessed values - the guesses simply initiate the calculation). Because the ants are used to calculate the behaviour ordinations and vice versa, the two ordinations are interdependent. If behaviour B had a high ordination value, then an ant which performed behaviour B with a high frequency would itself tend to have a high ordination value. As with Principal Components Analysis, ordinations can be made on several axes: the second axis ordinates the subjects after the effect of the primary axis has been removed.

Table VI has been set out in the ranking given by the first axis of ordination. On this axis, regurgitations have a high score, whilst successful tube feeds and acceptances a low score. Similarly the ants at the top of the table have a high score - in other words, they show proportionally high frequencies of regurgitations and failed solicitations by other ants. Since accepting and feeding behaviours have a low score, the ants at the bottom of the table are more likely to accept or feed from the tubes. Interestingly, this is the type of ordination of behaviour types which might be expected if there was a population of 'collectors' and a population of 'transporters'. 'Collectors' would appear at the top of the table as regurgitation is their main behavioural characteristic, whilst 'transporters' should appear at the bottom, as they are characterised by high frequencies of acceptances. However, although the first axis gives a clear division of ants into two groups (see Figure 13a), none of the regurgitating and solicited group (Group B) fed from the tubes. Had these been true collectors, then they would have been expected to score highly on both regurgitations and tube feeds, and the behaviour 'successful tube feeds' would have a high ordination value instead of its very low value on the first axis. In fact, all the group B ants were known to be lost in arena F4a, and acted as a resevoir of sugar solution for the experienced foragers.

Figure 13b is a plot of the ants on the first and second axes. All the ants which were known to be regular foragers fall within the central group (A1). An analysis of the behaviours which characterise this group is shown in Table VII. This demonstrates that they all attempted to obtain food from other ants and from the tubes with a high frequency. This is what would be expected from 'transporter' ants. However, the frequency of successful acceptances and tube feeds is very low for all these ants.

Since casual observation suggested that a true chain transport system of the type witnessed in the field in 1977 was not occurring in the laboratory,

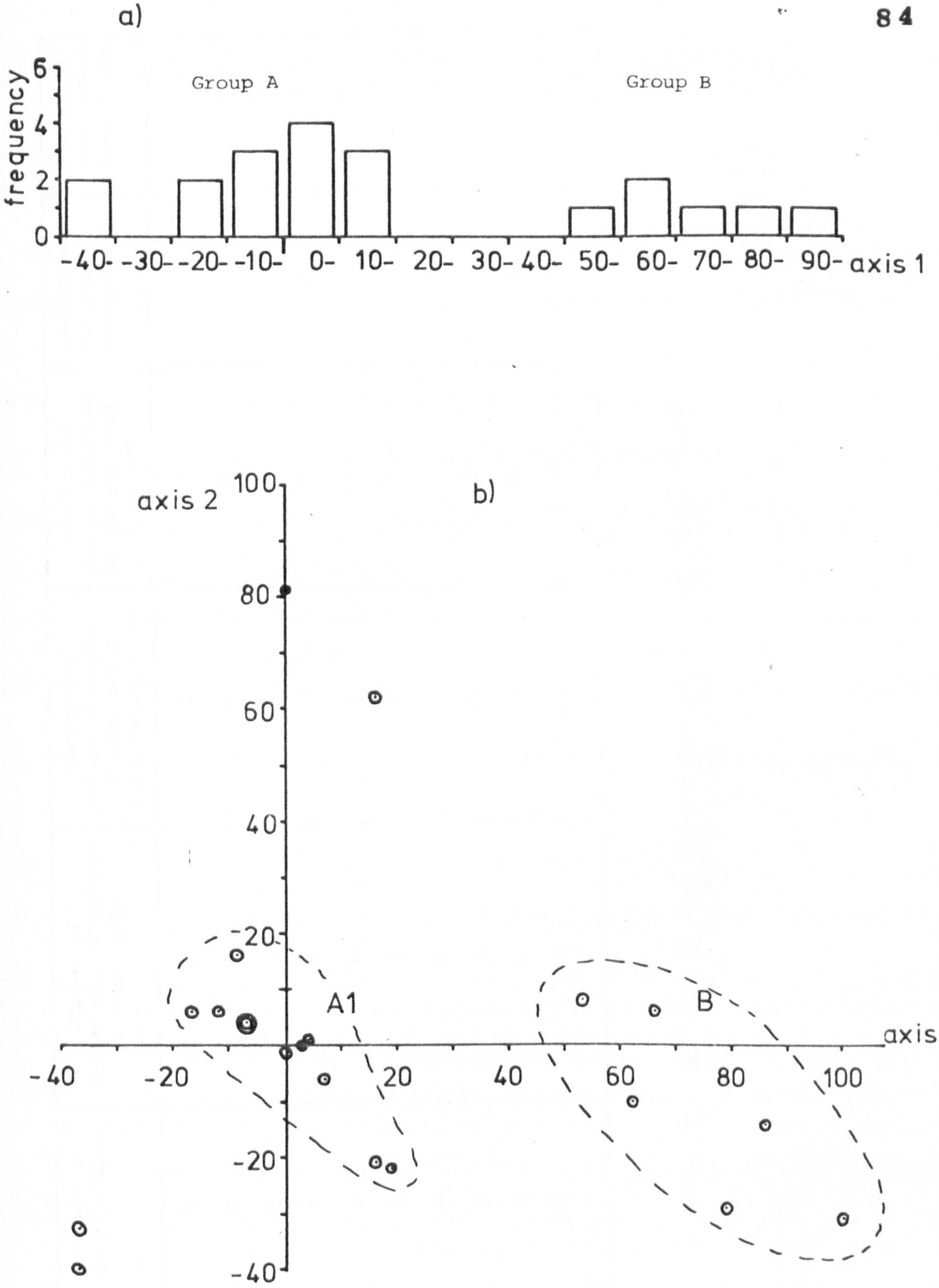


Fig. 13 a) Frequency distribution of laboratory ants as ordinated on the first axis using Reciprocal Averaging.

b) Ordinations of laboratory ants on the first and second axes using Reciprocal Averaging.

Ant Number	Number of regurgitations	Number of failed solicitations by other ants	Number of failed attempts to make other ants regurgitate	Number of failed attempts to obtain food from tube	Number of successful acceptances	Number of successful tube feeds
41B	0	4	0	7	0	0
18B	0	1	0	2	0	0
38B	2	4	5	12	0	2
45B	1	2	3	9	0	0
29A	0	6	8	12	0	3
12B	0	2	4	12	0	0
26B	0	1	2	6	0	0
25B	0	3	12	17	2	1
7B	0	5	19	39	1	4
29B	0	2	10	19	2	3

Table VII As Table VI, but showing the frequencies of behaviours of only those ants belonging to group A1 (see fig 13b).

it was unlikely that Reciprocal Averaging would have detected 'transporter' and 'collector' populations. The analysis was, however, quite powerful at demonstrating a split into 'lost' and 'experienced forager' ants. If chain transport could be induced in the laboratory, Reciprocal Averaging might prove to be a useful method of describing its features more mathematically. Indeed, there seems little reason why it could not be used in the field. By obtaining the relative frequencies of the feeding behaviours of ants (successful and unsuccessful regurgitations, solicitations and aphid attendances) on trees where chain transport is known to occur, the phenomenon could be described more precisely than the rather anecdotal treatment given in Chapter 4. Unfortunately, such data was unavailable in 1977, and chain transport was not observed during the 1978 fieldwork.

d). Comments on the laboratory experiments

The purpose of the laboratory experiments was to discover the environmental variables important to the honeydew-collecting strategies of wood ants. The variables - size of honeydew droplet, rate of honeydew production, number and distribution of honeydew sources - all had an effect on the feeding behaviours of ants close to the sources. For the study to have achieved its goal, three of these variables should have been held constant at any one time, so that the effects of the fourth variable could be assessed. Of course, to study any combined effects of two or more variables, further permutations would be necessary, but such a task would represent a complete study in its own right. The laboratory experiments in this study can act only as a pointer to future experiments. The equipment which was used in the study was the end product of a large number of trials with a wide variety of materials and equipment. The experiences gained over these long trial periods are worthwhile discussing, since the final equipment proved reliable and would be a worthwhile tool for a more complete study of wood ant foraging.

<u>i). Contamination of the sugar solution</u>: Because the equipment was used at temperatures close to 20°C the sugar solution was prone to bacterial and fungal infection. If contaminated, it had to be replaced, after only one or two days. Gases produced by the contaminants forced the sugar solution out of the tubes, thereby increasing the effective rate of droplet production. Since one of the features of any automatic feeding device should be that it is able to run unattended for long periods (the equipment could run potentially for up to a week without refilling), the sugar solution, syringes, taps and catheter tubes had to be sterile. Ideally the sugar solution should be boiled and filtered to remove any micro-organisms.

ii). Sugar solution concentration: The attractiveness of a sucrose solution given to wood ants depends greatly on its concentration. The solution in the artificial aphid, however, had to be as dilute as possible, since the higher the viscosity, the more problems there would be in passing the solution through the very narrow catheter tubing. In order to assess the optimum concentration (i.e., the weakest sucrose solution which was highly attractive to wood ants), the time taken for a fixed volume of sucrose solution to be drunk by ants on the nest was measured. The temperature and humidity were constant throughout the experiment, and the experiments were performed only on afternoons, to ensure that diurnal factors could not affect the results. The nest was watered every morning at the same time with the same volume of water (to decrease dehydration of ants within the nest), and 10 chopped mealworms were placed on the nest at the same time, each day. A large petri-dish, placed in the adjacent feeding box, was kept constantly full of sucrose and honey solution. The nest, therefore, had available an unlimited supply of sugar solution. The attractiveness of the additional drops, placed on a glass slide was measured by the time taken for the drop to be drunk by the ants. The glass slide was placed on the nest surface, and remained in position throughout the experiment to prevent disturbance. The 0.2 ml drops were accurately dispensed using a

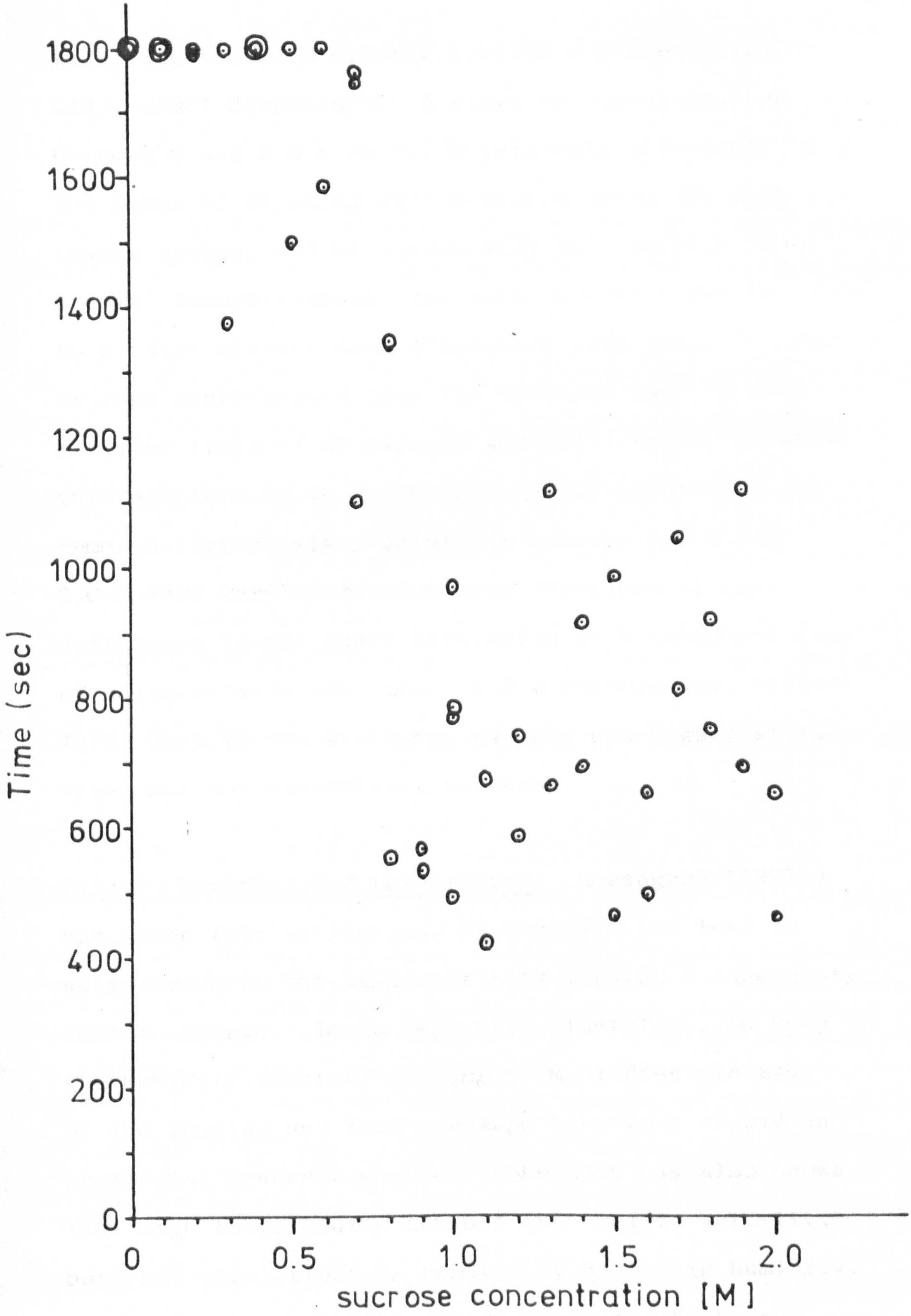


Fig. 14 Times taken for 0.2ml drops of sucrose solution to be consumed by ants at the nest : laboratory results (1979).

Micro-Repette Mk 2 syringe (Jencon's (Scientific) Ltd., Hemel Hempstead). A range of concentrations between 0 and 2.0 M at 0.1 M intervals were used. The times of drinking were measured twice for each concentration, and by randomising the sequence of droplet concentrations, the wood ants were unable to predict whether each successive drop would be more or less concentrated than the previous one. A maximum time limit of 30 minutes was set. Figure 14 shows that droplets up to 0.6 M were either ignored or removed very slowly. Solutions between 0.9 M and 2.0 M were very attractive, but there was little difference in the speed with which such concentrations of solution were consumed. 1.0 M sucrose was, therefore, used in the syringes, as this was highly attractive, but not excessively viscous.

iii). Humidity and temperature: Rosengren (1977b) has shown that an increase in humidity can lead to an increase in the number of ants leaving a laboratory nest to forage. It is important, therefore, to keep the humidity constant if long term studies are made of the feeding and food-exchange behaviour around an artificial honeydew source. Rosengren has also shown that high temperatures inhibit the traffic activity, but that this effect is removed by a rise in humidity. Citing Horstmann (1970) and de Bruyn and Kruk-de Bruin (1972), he considers that 22.5°C is the optimum foraging temperature. As such a complex interaction exists between temperature and humidity, tight control of both variables is especially important in a laboratory study of the foraging and feeding behaviour of wood ants.

CHAPTER 6

OVER-WINTER TREE FIDELITY

Part 1 : INTRODUCTION

It has been shown that wood ants, during their active period, show a high degree of fidelity to particular trees. By the first week of November, the activity of wood ants finally ceases. In October, all the aphid species concerned produce sexual forms which mate, lay eggs and die. The honeydew output, therefore, ceases by late October, and when the aphids finally die, the ants leave the trees (c.f. Horstmann and Geisweid, 1978), return to the nest and are not seen again above ground until the following Spring. When the aphids hatch in late April to May, the wood ants once again begin collecting honeydew (see later). Rosengren (1971) showed that ants, marked in Autumn on the trails, tended to appear again on the same trails in the following Spring. In other words, the trail fidelity, at least, persists over the winter. Rosengren had not, however, determined the extent of over-winter tree fidelity. The trail from nest 2 which accessed the long line of pine and birch saplings provided an excellent opportunity to assess the extent of this over-winter tree fidelity.

Part 2 : 1977-78 OVER-WINTER FIDELITY

In 1977, a trial experiment was run, using solely ants from the birch 4.1 m from nest 2. 54 ants were mass marked, using the technique described in an earlier chapter: 35 were marked with red paint on 14th October; 19 were marked with silver paint on 20th October. During this period, there was a very high turnover of ants at this birch. By 20th October, after only 6 days, only 7 red ants were left on the tree. By 3rd November, only 2 red ants and no silver ants were left. All activity ceased by 20th November.

The following Spring the saplings in the near vicinity of the birch (within a radius of about 3m) were regularly searched for marked ants. Although it was difficult to confidently identify individual ants from day to day (since mass marking inevitably results in many ants having similar marks), approximately 13 individuals were resighted between 25th April and 11th May, all either on the original birch or on saplings within 3 m of it.

The ants on most of the saplings along the forage trail up to a distance of 53 m from the nest were also regularly counted over this period as part of another experiment (see later), but no red or silver ants were seen on any of these saplings. The ants on this birch sapling therefore appeared to show a considerable degree of over-winter fidelity to at least a radius of 3 m around the trees.

No marked ants were seen at the original birch after 11th May 1978. However, one silver ant was seen on the trail, 35 m from the nest on 6th June 1978, and one red ant, which initially had been a regular visitor to the original birch until 11th May, was seen attending aphids on 20th June 1978 on a tree 35 m from the nest. It was last seen on the trail on 21st June. Rosengren (1971) has provided evidence that the ants which appear in the early Spring are the older ants from the previous year. They die out quite quickly in the Spring - he did not see any later than June - by which time the younger workers (probably those which emerged from pupae at the end of the previous season) have started foraging regularly.

The results of the trial experiment are insufficient proof of tree fidelity. It could be argued that the marked ants returned to the original birch simply because it was one of the closest trees to the nest along that particular forage trail. Indeed, as marked ants were found on other adjacent trees as well, the ants, in Spring, may have spread outwards from the nest along each trail. The first departing ants may exploit aphids on the closest trees, and ants which depart later may have to move further along the trail until the first aphid infested tree is found which has sufficiently low numbers of already attendant ants to make honeydew collection worthwhile. Zakharov (1978) has proposed a similar theory of wood ant foraging. He suggested that younger ants are forced to forage to distant trees because the older ones have already started foraging on trees closer to the nest, having established what he termed an 'Elementary Search Range'. He argued that as wood ants age, they move to trees nearer the nest. If, as Rosengren shows, the older ants emerge first in the Spring, then these, according to Zakharov, should indeed go to the first trees along the trail.

A larger scale marking experiment was therefore necessary to decide whether tree fidelity was actually retained over the winter.

Part 3 : 1978-79 OVER-WINTER FIDELITY

In Autumn 1978, five saplings were chosen on the nest 2 trail at various distances from the nest. The first birch sapling was the same tree used in 1977-78. Ants were again mass marked on each tree, on 6 occasions between 21st September and 27th October. As many ants as possible were marked on each tree at each marking session. The ants were marked with a colour unique to each tree. Table VIII shows the numbers of ants marked on each tree. Between 21st September and 3rd November, only 6 of these marked ants were observed to have moved to other trees. Of these, 2 were on trees adjacent to those on which they

			DATE (1978)						
TREE	Distance from nest (m)	Colour of Mark	21/9	26/9	5/10	12/10	18/10	27/10	TOTAL
Birch	4.1	Red	75	25	22	9	5	3	139
Pine	19.8	Silver	36	30	17	27	25	8	143
Birch	22.1	Green	7	4	0	0	0	0	11
Pine	32.4	Orange	30	9	14	10	4	2	69
Birch	46.9	Turquoise	19	0	0	0	0	0	22
		TOTAL	167	71	53	46	34	13	384

Table VIII Numbers of ants marked on pine and birch saplings along the nest 2 sapling trail.

had been originally marked, whilst 4 had changed to trees more than 10 m from their original tree.

In April 1979, nest 2 and its sapling trail were checked once a week to ensure that the Spring activity was seen from the very beginning of honeydew collection. Although the first aphids did not hatch until 27th April, there was some activity on the surface of the nest as early as 5th April. An orange-marked ant was seen on the nest surface on 11th April, and a silver-marked ant was seen on 20th April. Between 25th April and 23rd May, every tree up to a distance of 53.1 m from the nest along the nest 2 sapling trail was checked every other day. Records were kept of any marked ants which appeared on these trees. Three-dimensional graphs were plotted by computer (using the GINOSURF package), showing the frequency of occurrence of ants of each colour, for each tree over the 15 observation days (Figures 15 to 17). No green or turquoise marked ants were seen, and indeed the returns of marked ants of any colour were surprisingly low. Nevertheless, the results were very interesting. Figure 15 shows that over the 15 observation days, red marked ants were only found on the original birch and on one adjacent pine, also 4.1 m from the nest. Figure 16 shows the equivalent data for the silver-marked ants. Most silver ants were found on the original tree. However, from 3rd May, one or two were found on a pine, 3.7 m further along the trail, and on 15th May, one was

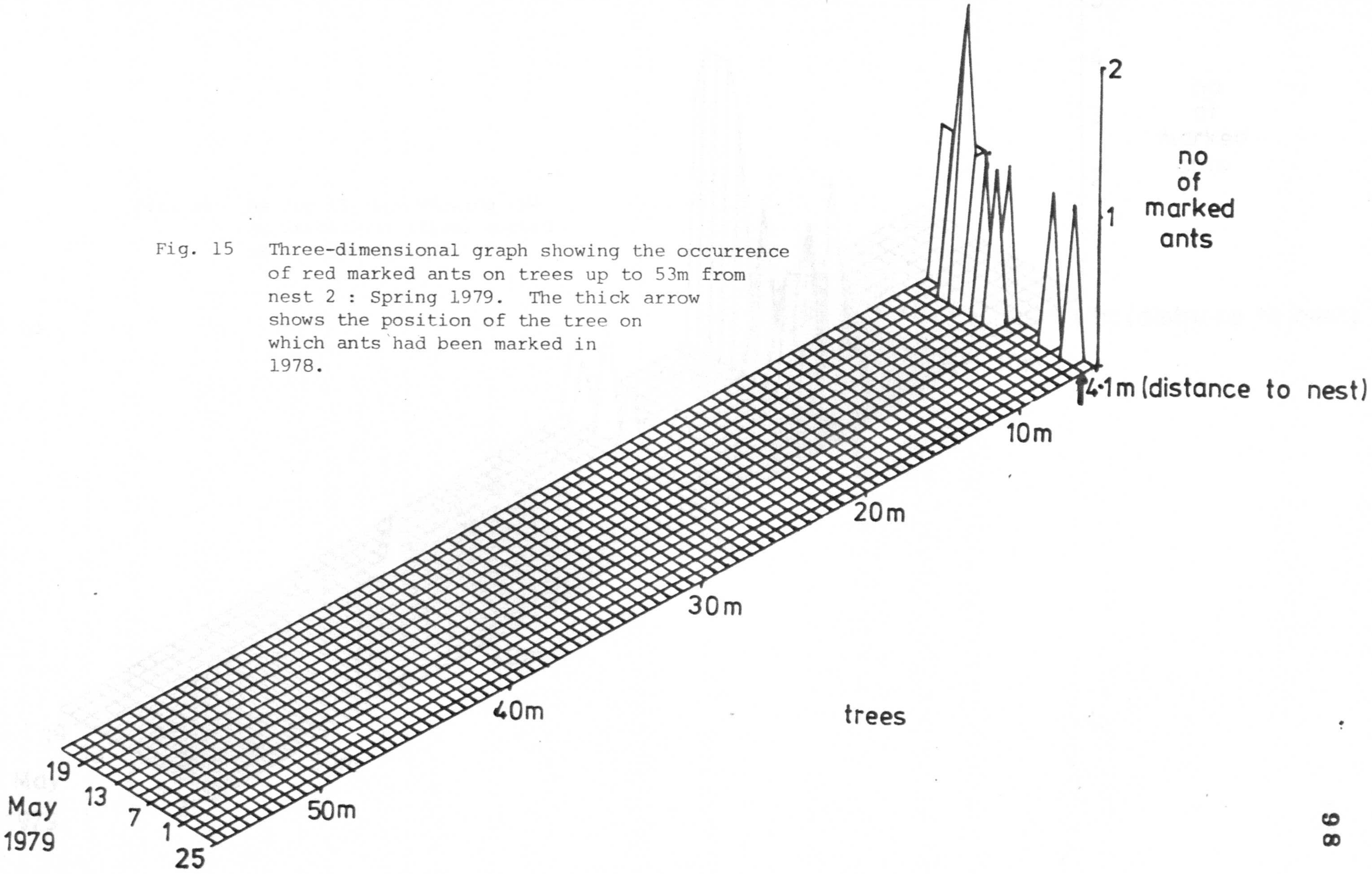


Fig. 15 Three-dimensional graph showing the occurrence of red marked ants on trees up to 53m from nest 2 : Spring 1979. The thick arrow shows the position of the tree on which ants had been marked in 1978.

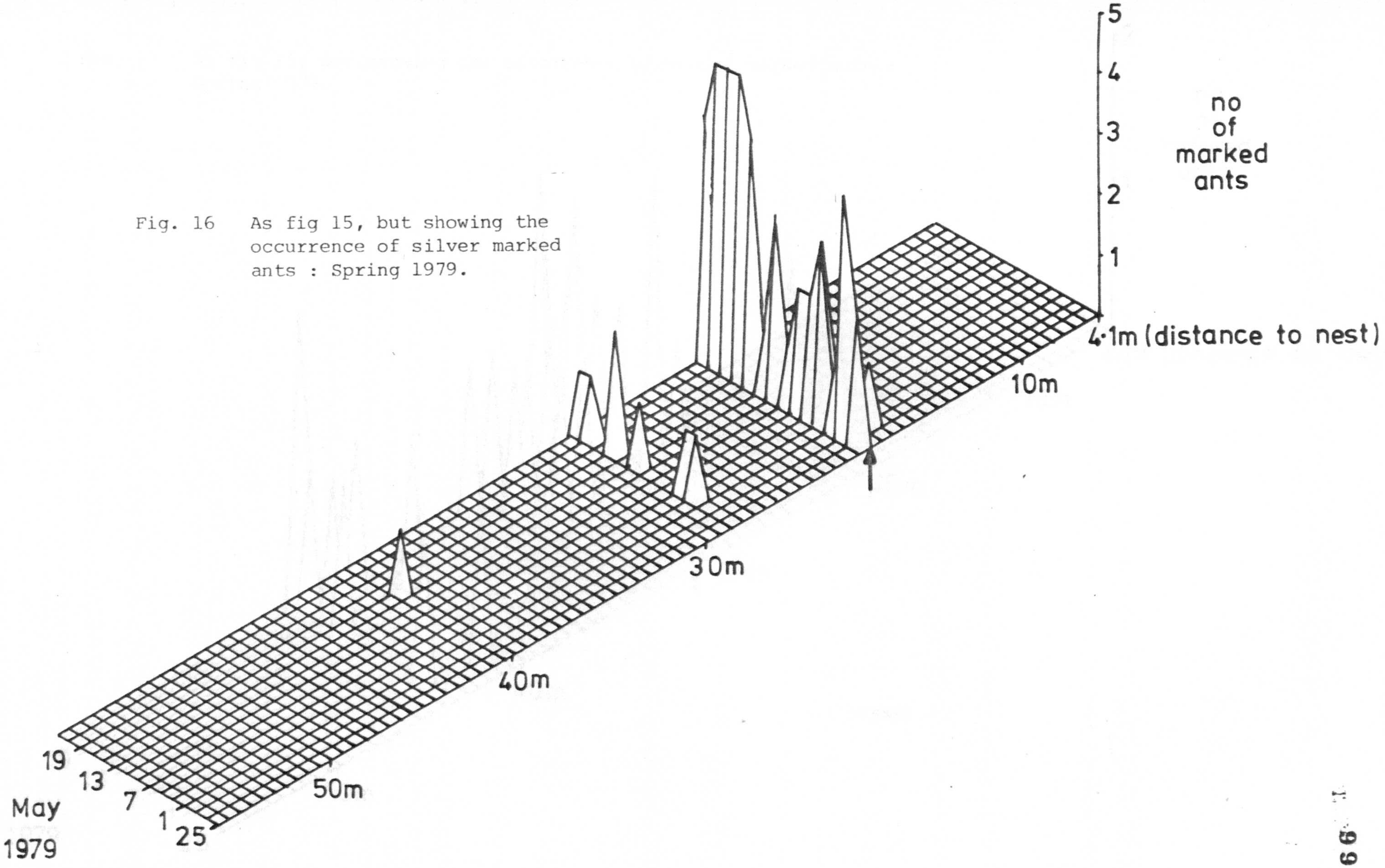
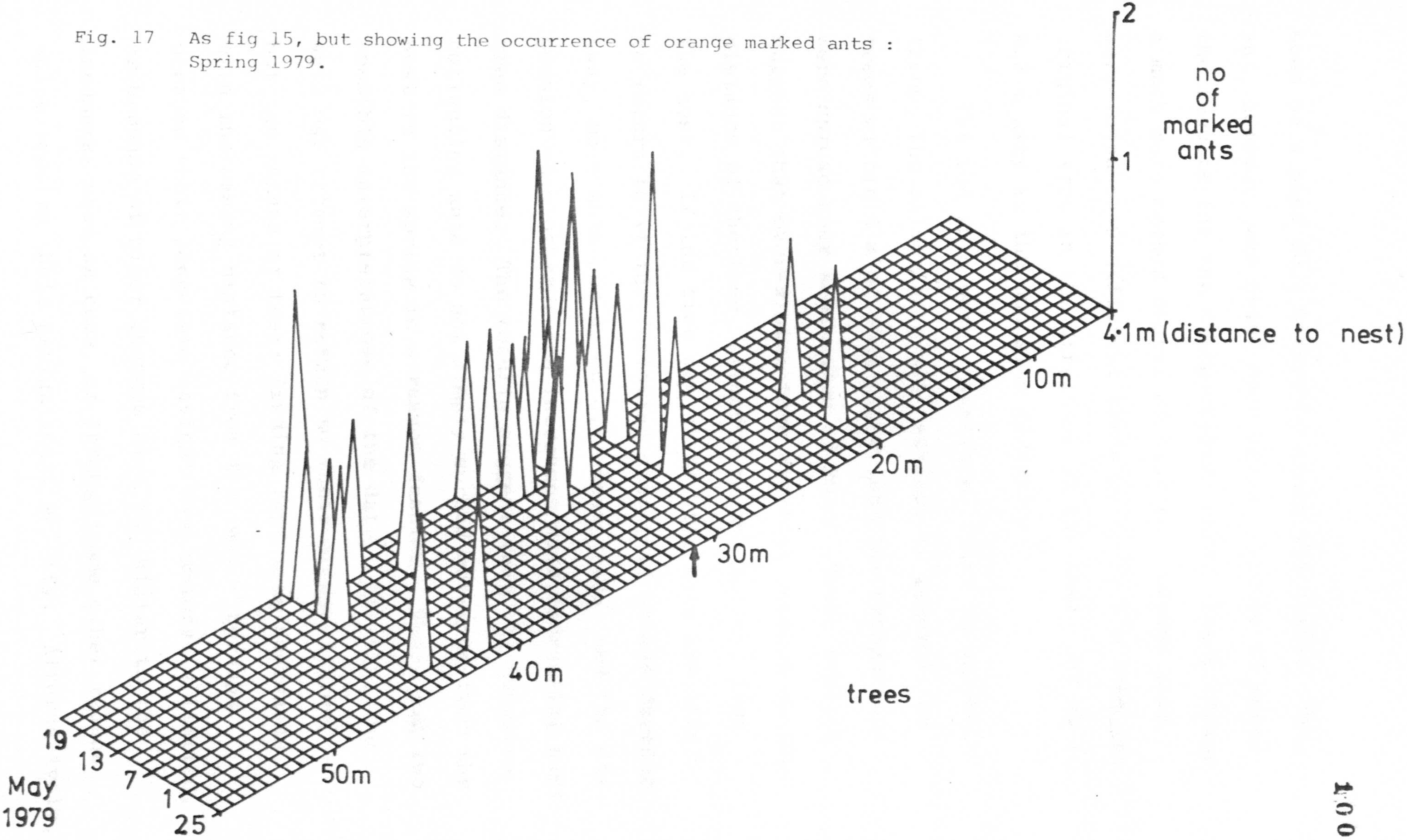


Fig. 16 As fig 15, but showing the occurrence of silver marked ants : Spring 1979.

Fig. 17 As fig 15, but showing the occurrence of orange marked ants : Spring 1979.



seen on a pine 20.1 m further along the trail. This ant, however, was never seen again. Figure 17 shows the results for the orange-marked ants. These showed a much more marked degree of scatter. Orange ants were found on 9 different trees up to 10.5 m from the original tree in the direction of the nest, and up to 9.3 m away in the opposite direction.

The red ants were, therefore, found on adjacent trees, the silver ants were spread, in general, on trees within 4 m of each other, and the orange ants were spread over a distance of 20 m. These results suggest that over-winter tree fidelity depends on the distance of the tree, attended in the Autumn, from the nest. If the tree was close, the ants are likely to return to it the following year. If it was further away, more ants end up on different trees, and the dispersion onto other trees increases with increasing nest-tree distance. The results suggest that the honeydew collecting ants do not simply spread outwards from the nest in the spring in a random fashion. There are two possible interpretations of the data. Firstly, the ants may attempt to return to their original tree, but the chance of their finding that tree decreases with increasing distance from the nest - perhaps because their long-term navigational memory is limited, or because of minor changes over the Winter to the landmarks used as cues, or through some other reason which impairs their navigational ability. Alternatively, they could be conforming to Zakharov's theory: the red ants marked in Autumn would have been older than the orange and silver ants, since they were closer to the nest. The following Spring, these red ants would establish their 'Elementary Search Range' close to the nest again. The orange and silver ants would be forced to find trees further from the nest. The orange ants, which Zakharov would view as the youngest of all the marked ants, would be forced to forage at the extreme end of the trail. Therefore, what could appear to be reduced fidelity over distance would be explained by Zakharov's theory in terms of the age structure of the worker population on the trail. It is difficult to prove which interpretation is correct. Of course, the red and silver ants which were marked close to the nest in 1977 and which were seen in June 1978 35 m from the nest do not fit with Zakharov's predictions. However, it would be dangerous to refute his theory on such scanty evidence. It was unfortunate that there were so few actual re-sightings of marked ants in 1979, despite the very thorough regular searching. A further replication of this experiment, perhaps on an even larger scale, involving many more trees, might provide more successful results to show whether age structure or navigational memory is the important factor for honeydew-collectors in the early Spring.

The very low recovery of marked ants in the Spring may have been a consequence of several factors. A large proportion of older foragers probably die in most winters, and the very severe winter of 1978-79 (snow was still falling in early May, 1979) may have increased their mortality. Nest 2 had also been badly damaged by either a fox or a badger in the late Autumn of 1978. Many workers could have been killed as a result, since foxes are known to devour wood ants (Rosengren, 1969). Ants with conspicuous paint marks may also have been vulnerable to predation from birds, particularly woodpeckers, which are the main predators of wood ants in late Autumn and Winter (Rosengren, 1969; De Bruyn, Goosen de Roo, Hubregtse-van den Berg and Fegen, 1972). Of course, although unlikely from the evidence of Rosengren (1971), some marked ants may have left the nest using different trails. It was impossible to check whether this had occurred, since other trails from this nest were inconspicuous in Spring, and connected the nest to the very large trees in the plantation.

CHAPTER 7

EARLY SPRING HONEYDEW COLLECTION

Part 1 : INTRODUCTION

The beginning of the season creates a number of problems for wood ants. When the aphids first begin to hatch, there is generally little protein food available in the form of other insects, and few carbohydrate sources, except perhaps, for some nectar in early flowering plants. Aphid predators such as ladybirds are quite abundant around late April and early May, so any aphids which hatch but are not found soon by wood ants are liable to be killed. The unhatched eggs of aphids were not attended by F. lugubris, although egg attendance near the nest has been reported in F. polyctena (Hortsmann and Geisweid, 1978). Once attended by wood ants, the aphids are defended vigourously. Ideally, then, wood ants should be ready to go to trees which support aphids as soon as the aphids begin to hatch. In other words, the environmental cues which stimulate the hatching of aphids should also initiate the onset of honeydew foraging in wood ants.

Each ant does have a certain amount of energy reserves in the Spring in the form of fat deposits built up over the previous Summer, but these must last the non-collecting ants (i.e., the consumers) until honeydew begins to reach the nest. During the first few weeks after hatching, the aphid nymphs appear to produce so little honeydew that few attending ants return to the nest with full crops. In 1978, for example, no attendant ants were seen with full crops in the four weeks between 21st April, when the aphids hatched, and 23rd May. The output of honeydew from the aphids in this period may even have been less than the rate at which it passed through the proventriculus of the ants collecting it.

Part 2 : FIELD OBSERVATIONS

The initial exploitation of the aphids along the nest 2 sapling trail in early Spring was investigated in 1978 and 1979 by counting the numbers of ants on saplings up to 53 m from the nest. In 1978, the very beginning of the season was missed and there were already large numbers of ants on some of the pine saplings. The first birch aphids were beginning to hatch at the start of the observations. The pine aphids did not hatch until 27th April in 1979, and birch aphids began to hatch on 7th May. The 1979 honeydew season therefore began about 2 weeks later than in 1978, and it was possible to observe the first 30 days of the season in full.

In 1978, 49 saplings were selected. Very small saplings were not used. On each observation day, the numbers of ants (up to a maximum of 50) on each sapling was recorded, and each sapling was checked for aphid eggs and whether or not the eggs had hatched. Observations were made rather irregularly in 1978, on 21 occasions over the 59 days between 25th April and 22nd June. 11 observations were made during the first 18 days, so any changes in the early part of the season were recorded with reasonable accuracy. Between 22nd May and 22nd June, at least one count was made each week, so the latter part of the results showed general trends.

In 1979, a weekly check was kept during April for the first signs of honeydew collection - trees were checked for hatched aphids or patrolling ants. The first hatched aphids were seen on 20th April, so between then and 23rd May, much more frequent observations were made. Over these 30 days, the numbers of ants were counted on 76 saplings up to 53 m from the nest, every second day. Unlike the previous season, every reasonably large sapling was included in the study, along with any saplings with aphid eggs, no matter how small the sapling. Some of these were as little as 15 cm high. Most of the trees investigated in 1978, by comparison, were over 30 cm high. Once again, records were kept on whether or not each tree had aphid eggs and the date the eggs began to hatch. The maximum number of ants counted on any tree was increased to 60. It was impossible to make accurate counts if there were any more than this number on a tree.

The results for each year were plotted as 3-dimensional graphs (using the SYMVU computer package), showing the numbers of ants on each tree over the periods of observation. Additionally, the maximum daily temperature for Langdale Forest (provided by the Forestry Commission), was plotted and the two graphs are given in Figures 18 and 19.

Figure 18 shows the results for 1978. Each line represents the numbers of ants on a particular tree. The trees are arranged in order of distance from the nest, but the position on the abcissa is not proportional to this distance. The lines at the left hand side of the graph represent the trees at the nest end of the sapling trail, and those at the right hand side represent the trees furthest from the nest. The line at the extreme right hand end is the maximum temperature plot for the observation period. The base line for both the trees and the temperature represents zero, and the maximum height represents 50 ants.

On day 1 of the 1978 observation period (25th April), 2 pine saplings were already attended by more than 50 ants, and in general, high numbers of ants were soon achieved by many of the trees along the first 25 m. of the trail. Trees between 30 and 40 m did not achieve large numbers of ants until 8th - 12th May, but

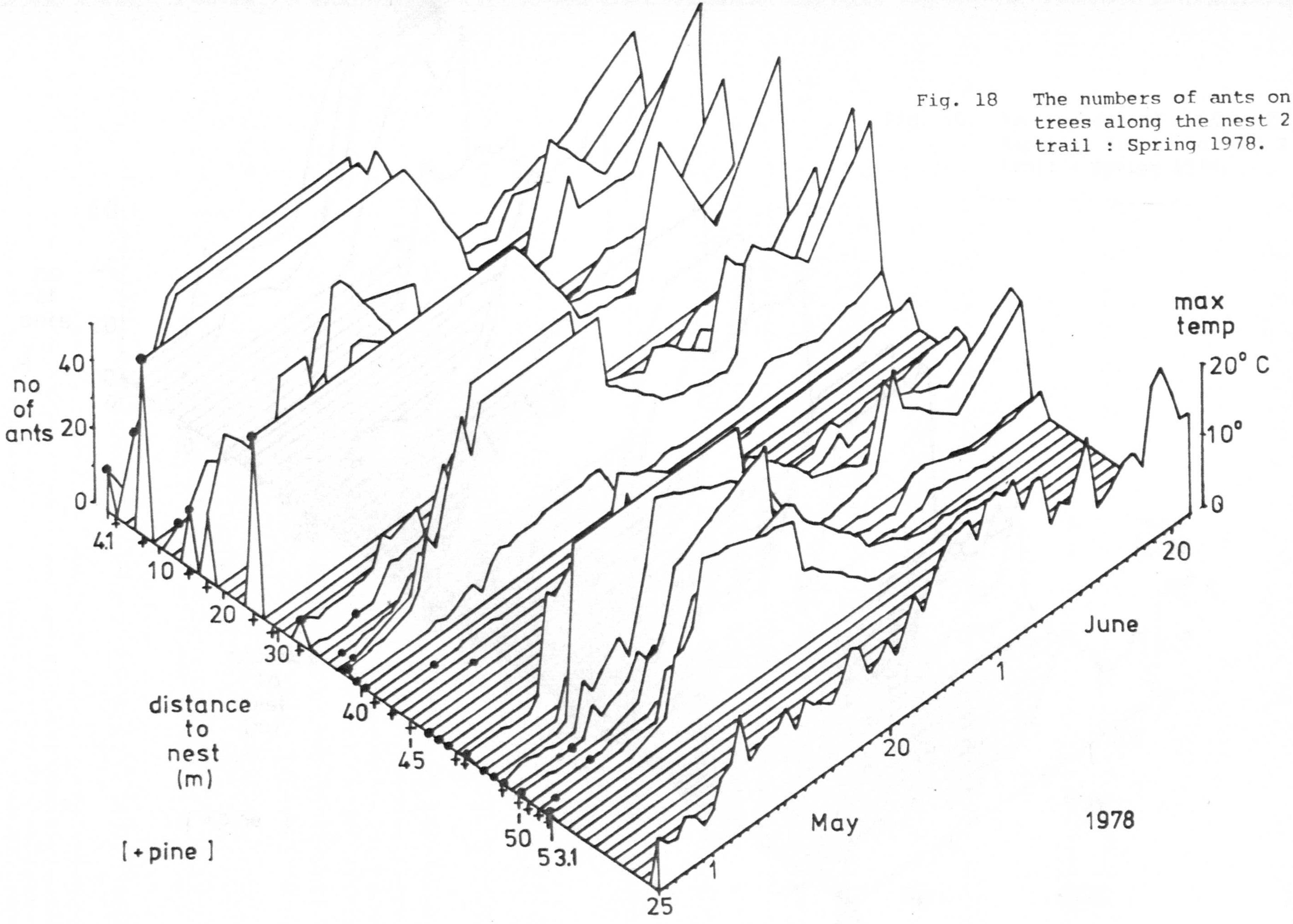
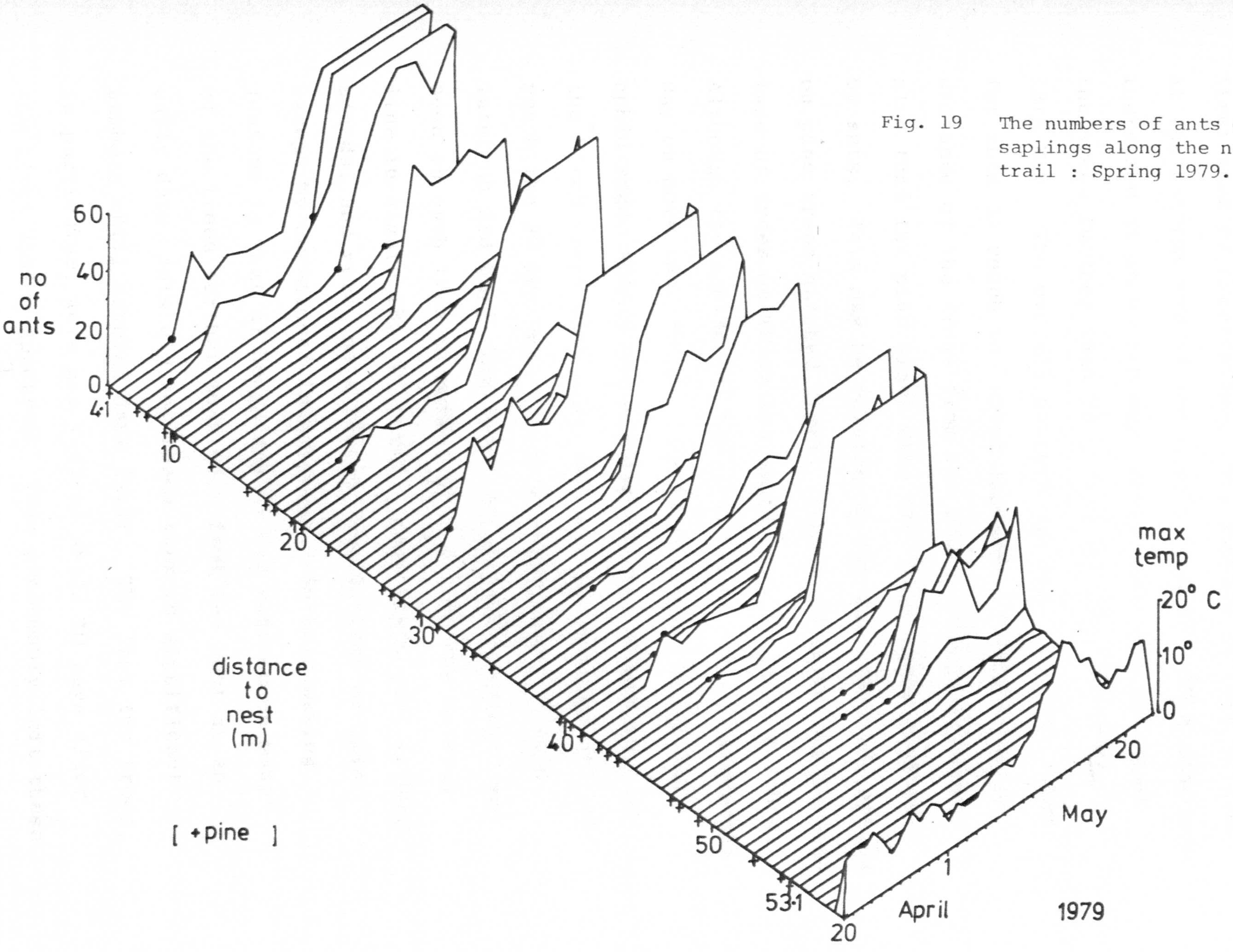


Fig. 18 The numbers of ants on 49 trees along the nest 2 forage trail : Spring 1978.

Fig. 19 The numbers of ants on 76 saplings along the nest 2 forage trail : Spring 1979.



tended to have a small number in attendance in the first week of observation. The numbers of ants on trees at the extreme end of the trail, from 47 - 50 m suddenly increased at about 4th May, whilst ants did not reach the trees further than 50 m from the nest until 9th - 12th May. The overall pattern was that the time taken for ants to reach the trees appeared to depend on the distance of the trees from the nest. Figure 18 shows also that the pine trees were the first trees visited by ants. This may be related to the fact that the aphids on pine trees hatched first. Figure 20 shows the percentage of trees on which the aphids had actually hatched. Although the aphids had hatched on the first observation day on more than 90 per cent of the trees which had aphid eggs, aphids had hatched on only 39 per cent of the birch trees with eggs, and the birch trees did not reach the 90 per cent hatching figure until 8 days later on 3rd May. The first day on which aphids were seen on each tree is marked by a dot on the relevant line in Figure 18. Of course, some trees were without aphids, and were, as a result, not visited by ants, except by occasional individuals. An interesting feature is that although aphids had hatched on many of the trees further than 45 m from the nest at an early date, ants did not reach them in significant numbers until several days later. The last two trees, in particular, were not visited until 10 days after the first aphids appeared. This presumably left these

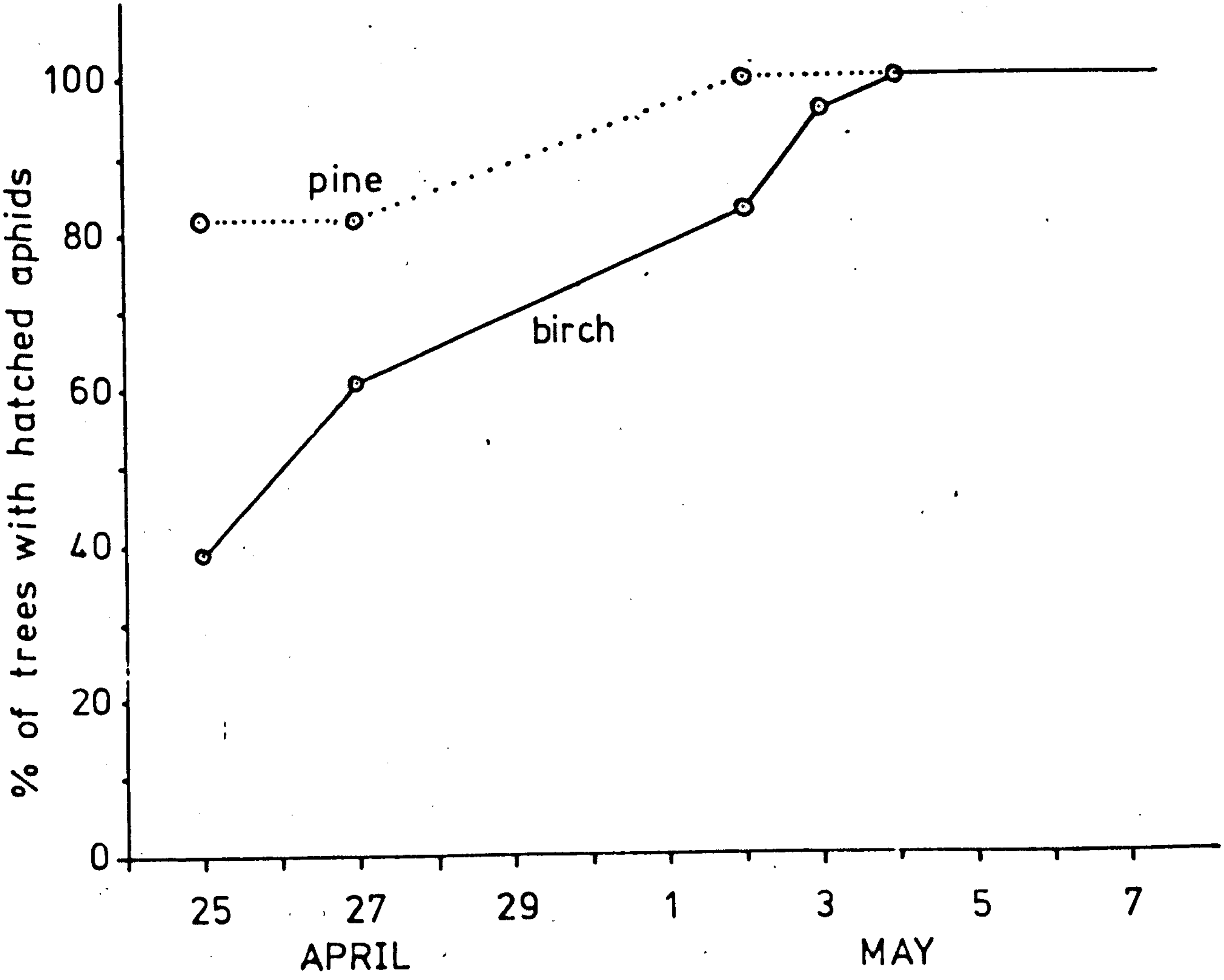


Fig. 20 The percentage of birch and pine trees on which aphid eggs had hatched : Spring 1978. Only trees with aphid eggs are considered here.

aphids open to predation. One pine, at 49.4 m from the nest and on which aphids had hatched by the first observation day, was not reached by ants until 4th May. On 2nd and 3rd May, an adult ladybird was seen on this tree, and 2 more ladybirds were seen on another pine at 51.3 m from the nest on 3rd May. Again, although aphids had already hatched on this latter tree by the first observation day, it was not reached by wood ants until 6th May. No ladybirds were seen on any tree with more than 4 attendant wood ants. An interesting discovery was that of an ant of the genus *Myrmica*, which was found attending aphids on the pine 51.3 m from the nest. This was seen on 2nd and 5th May before wood ants had reached the tree, but was notseen thereafter.

On the basis of the results for 1978, the initial appearance of wood ants on the trees seemed to depend on the distance between the nest and the trees. The further away the tree, the longer it took for ants to reach it. The trees over 50 m from the nest were not reached until at least 10 days after the aphids had hatched. This finding seems to imply that there is a gradual outward spread of ants from the nest in Spring, but, as has been shown earlier, ants appeared to return to the section of trail in which they had collected honeydew the previous season. Since, even in cold weather, a 35 m journey takes an experienced forager only 2 hours, the results of 1978 imply that the ants which attended trees far from the nest either fail to complete the outward journey in the early days of Spring, or leave the nest later than ants which had attended trees close to the nest, with the ants attending trees 50 m away leaving at least 10 days later than ants from trees up to 20 m from the nest.

The experiment was repeated in more detail in 1979 in order to check the validity of the 1978 results. Figure 19 shows the numbers of ants on 76 saplings between April and May 1979. The graph is orientated in the same way as in Figure 18, with trees close to the nest at the left hand side of the graph, and with the maximum daily temperature at the extreme right hand end. The first thing which is apparent is that it took much longer before the numbers of ants increased to high levels in 1979 than in 1978. However, as in 1978, the pine trees were the first to be visited again because the pine aphids (C. pini) hatched before the birch aphids (Symydobius oblongus). The very first birch aphids appeared on 7th May, but most did not hatch until 13th May. Once again, trees close to the nest were reached almost as soon as the aphids appeared, but trees 50 m or more from the nest were not reached until several days after the first appearance of aphids. However, the 1979 graph shows clearly a very sudden increase in numbers on 13th May. This occurred on both pine and birch trees, so the sudden appearance of birch aphids at this time cannot be the reason. The 13th May was the first warm day of the Spring, representing a sudden change in the weather. Indeed, snow had been falling two weeks earlier, between 1st and 3rd May and was still lying until 5th May. This rapid change in the weather can be seen in the maximum temperature plot and provides an explanation of the initial honeydew foraging in the Spring. Temperature, more than any other factor, seems to have a very great effect on the behaviour of wood ants. This effect can be best shown by rotating Figures 18 and 19 anti-clockwise through 45^{o} and viewing directly across the lines (Figures 21 and 22). Figure 21 shows the graph for 1978. Most of the lines can be seen to have similar undulations. Because a maximum of 50 ants was counted on each tree, undulations which occurred on trees with more than 50 ants are not visible. The first increase in temperature, which occurred as a sudden peak (arrow 1), coincides with a sudden increase in ant numbers on many of the trees, especially on those a long distance from the nest. Later, during a long hot period (the area marked '2') the numbers of ants fell on all trees, but increased again at the end of this hot weather. Another hot period (area '3') caused a drop in numbers, with a subsequent increase at the onset of cooler weather (arrow 4). It must be remembered that the last 6 weeks of this graph only shows overall trends, since the numbers of ants were counted on only 6 occasions over

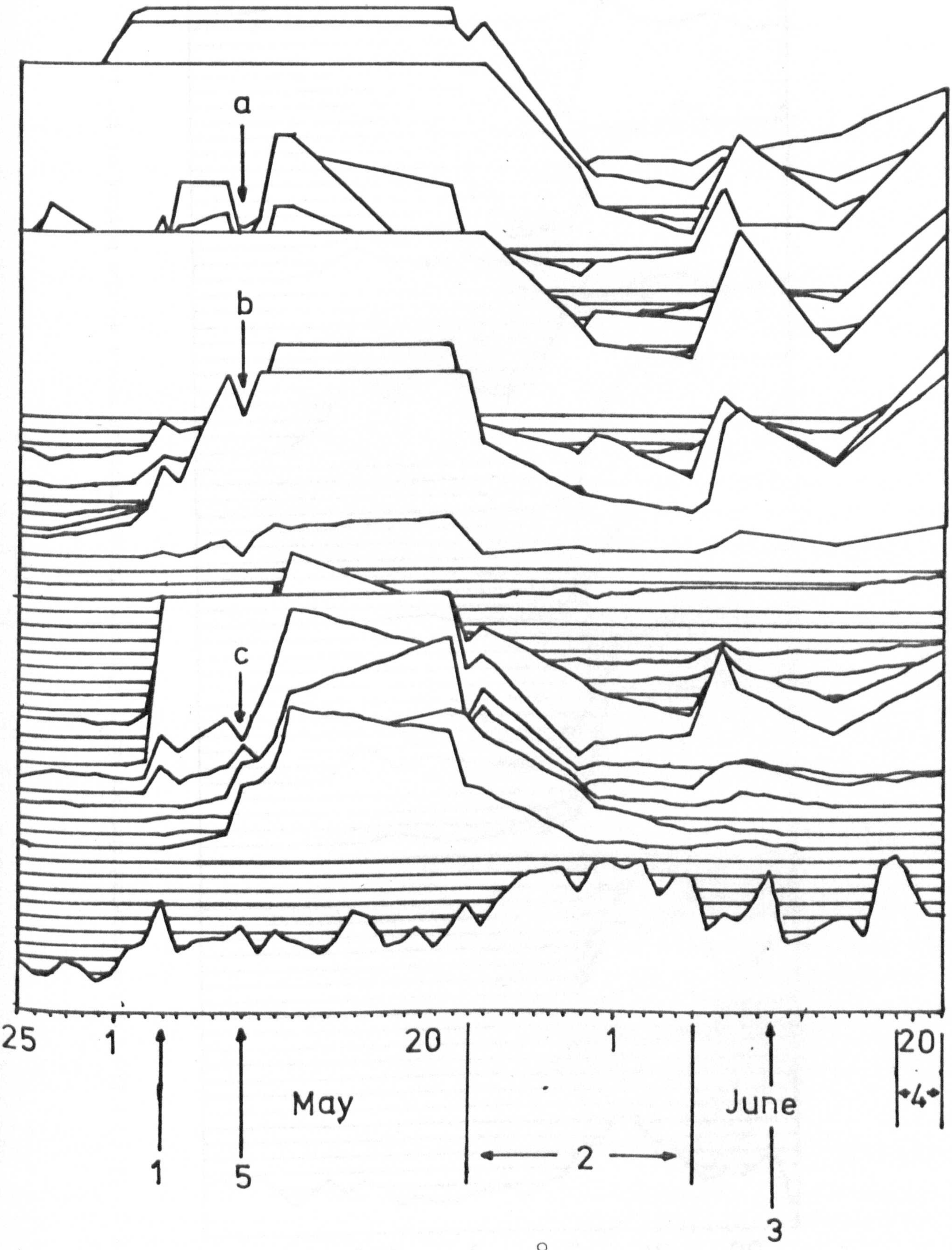


Fig. 21 As fig 18, but rotated through 45°. The meaning of the arrows is described in the text.

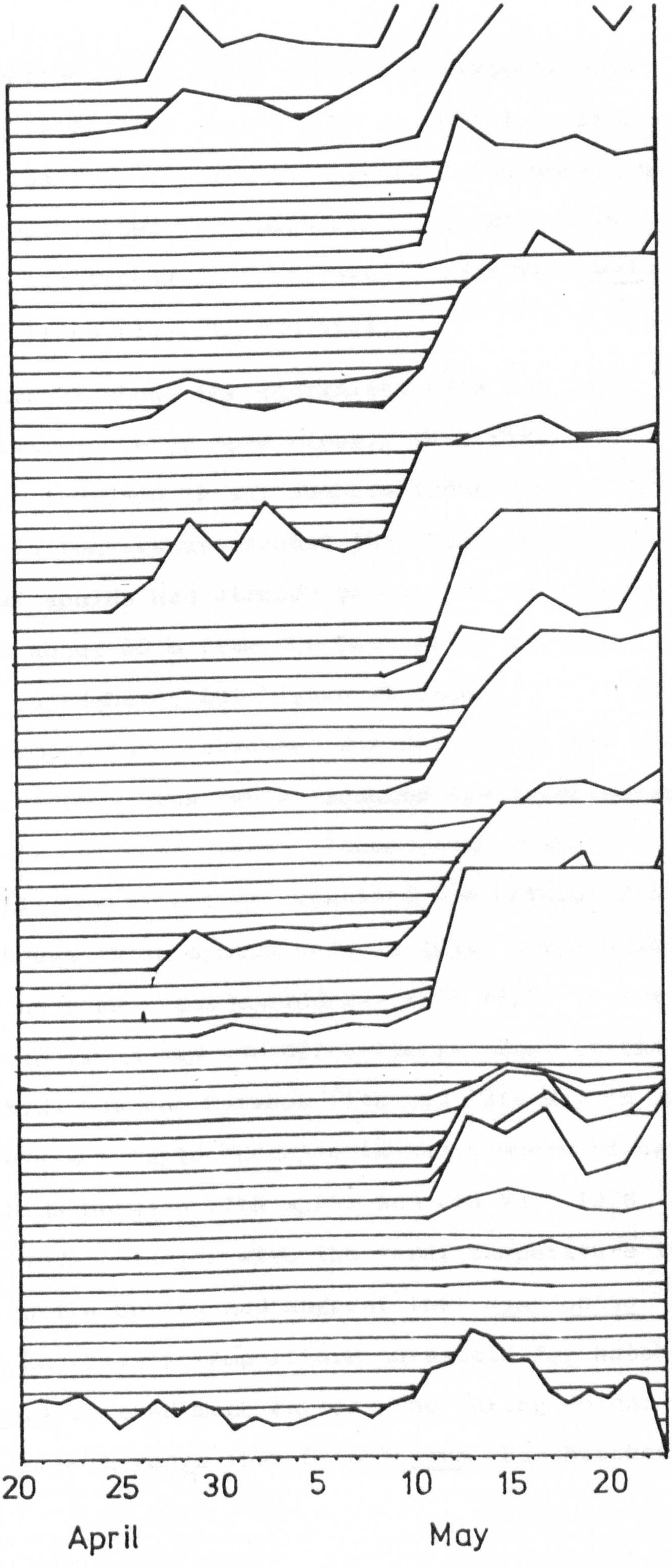


Fig. 22 As fig 19, but rotated through 45°. The max. temperature is shown at the bottom of the page.

the hot period (area '2'), and the subsequent data is interpolated from counts made on only 4 occasions. The early part of the graph, however, is almost completely represented and demonstrates clearly that until the first peak in temperature, ants were only attending trees close to the nest.

Figure 22 shows the equivalent data for 1979, and demonstrates even more clearly than Figure 19 the sudden increase in ant numbers induced by a rapid increase in temperature around 13th May. Figure 19 shows that aphids had already hatched on several of the trees about 50 m from the nest prior to this increase in numbers, but Figure 22 demonstrates that it was the temperature increase, and not simply the presence of birch aphids, which induced the increase in ant numbers on these trees. Indeed, the numbers of ants on all the pine trees remained low before 13th May, although these aphids were in quite large numbers, but all the pine trees showed the same rapid increase in ant numbers as did the birch trees. Most of the birch aphids hatched between 11th and 13th May in 1979, and there was a rapid increase in the numbers of hatched birch aphids between 27th April and 3rd May, 1978. Both these periods coincide with the first temperature increases in the Spring and suggest that *Symydobius oblongus* may have a temperature threshold for hatching. *Cinara pini* hatched much earlier and during colder weather in both years than *S. oblongus*, but hatched later in 1979 than in 1978. A day-length response is, therefore, unlikely to be the effective causal agent in the hatching of C. pini. It may, like S. oblongus, have a temperature threshold, but this would be lower than for S. oblongus. However, the late April temperatures were similar in both 1978 and 1979. In other words, a response to air-temperature cannot adequately explain the difference in the hatching dates of C. pini between the two years. A big difference between 1978 and 1979 was, however, manifested in the hours of sunlight. Figures 23 and 24 show the maximum and minimum air temperatures and the hours of sunlight for April in 1978 and 1979. The occurrence of C. pini nymphs coincides approximately with peaks in the hours of sunlight. Since the temperature of an aphid egg will depend on both the air temperature and incident sunlight, a temperature threshold could be reached on a day in which the sun was not obscured by cloud even if the air temperature was quite low. The later date of hatching of S. oblongus suggests that its eggs must reach a threshold temperature and that that threshold must be sustained for a longer period. In that case, just one day of sun would not be sufficient. It is interesting to note that eggs of C. pini are invariably laid along the top surface of the needles of pine, and therefore exposed to the sun in Spring. S. oblongus eggs, on the other hand, are laid in the base of the birch buds, and therefore

Fig. 23 Maximum and minimum daily temperatures and hours of sunlight recorded in Langdale Forest : Spring 1978. The arrows show peaks of sunlight which correspond with increases of aphids on trees.

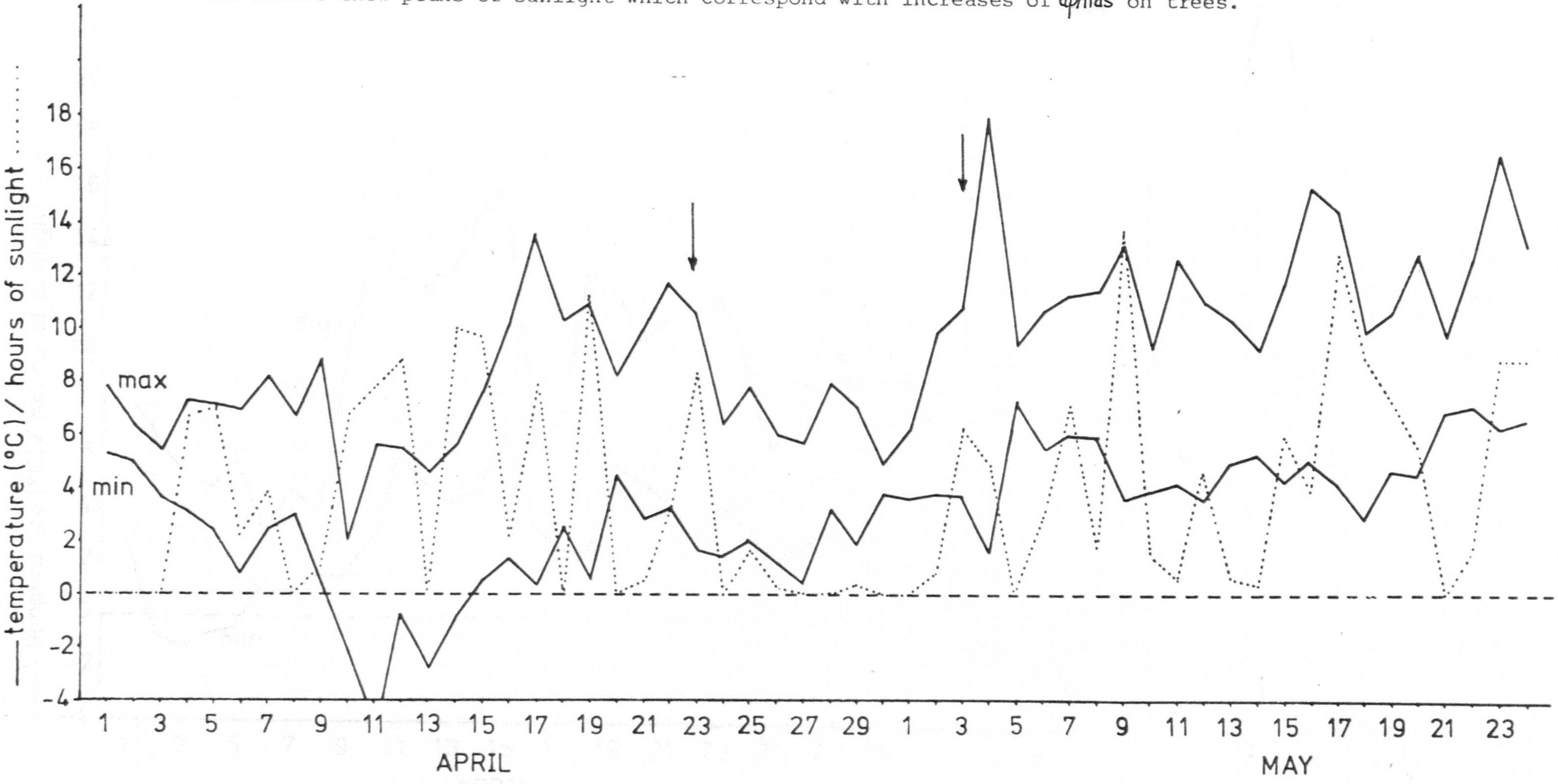
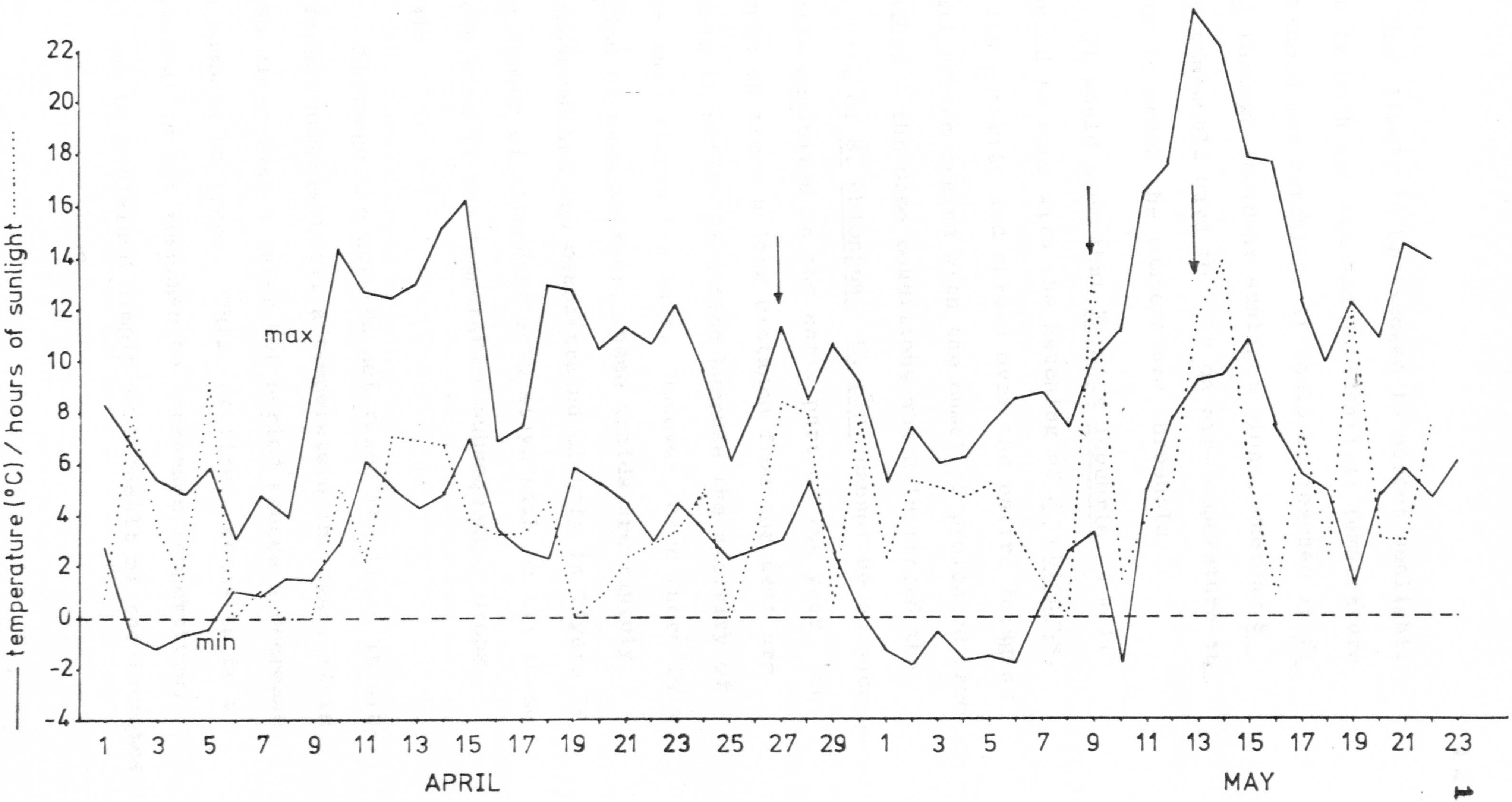


Fig. 24 As fig 23, but showing the equivalent data for Spring 1979.



are less likely to be exposed to direct sunlight. Even if both species had an identical temperature threshold for hatching, it could be reached in C. pini through incident sunlight alone, whereas S. oblongus would have to rely on air-temperature in order to reach the temperature threshold.

It would seem that Formica lugubris is well adapted to cope with the hatching of S. oblongus, as its activity and spread over the entire foraging trail system begins with the onset of prolonged warm weather - the same conditions which initiated the hatching of S. oblongus. C. pini cannot be as successfully exploited in the early part of the year, and nymphs on trees a long distance from the nest are liable to suffer predation because the activity of wood ants starts too late. However, once there is a period of warm weather, these aphids are rapidly discovered and, as demonstrated clearly in Figure 19, the number of attendant ants stays high on all these trees even if the temperature subsequently drops again.

Although the ants do not reach the trees in significant numbers until a temperature increase, it is also clear that a later hot period causes a decrease in numbers on trees. This, at first, seems to be a reversal in the response to increased temperature, but can be explained simply as a result of the increase in activity of the wood ants. When no ants are on any trees, an increase in wood ant activity will bring the ants from the nest onto the trails and many will reach the trees. Later, when ants are regularly attending aphids in the trees and when a large number of ants on the trails are going to and from foraging grounds, an increase in temperature will increase the numbers leaving the nest proportionately less than at the beginning of the season. There will be little increase on trees, then, from new ants leaving the nest. The ants already on the trees, however, by becoming active, are likely to leave the trees and run about on the trails. Indeed, on hot days, little honeydew collecting actually occurs, and ants which normally collect honeydew can be observed to become very active. Very often they will simply not remain inactive enough around aphids to collect honeydew. In other words, a count made on a hot day is likely to show fewer ants on a tree than on a cool day when most ants are back collecting honeydew. This is born out in Figure 21. For example, the small peak in maximum temperature marked by arrow 5 (which coincided with a peak of 14 hours sunlight) coincides with a drop in the numbers of ants on many of the trees (arrows 'a', 'b', and 'c'). The counts were always made between 2.00 and 4.00 p.m., by which time the temperatures had already had an effect on ant activity. The next day was cooler (with only

1.5 hours of sunlight), and the numbers of ants increased on most of the trees (note that data was obtained for these two days and that the graph is not merely interpolated in this region).

CHAPTER 8

THE TRAIL SYSTEM OF FORMICA LUGUBRIS

Part 1 : INTRODUCTION

The trail which connected nest 2 to the saplings which has been described earlier was just one of a whole network of trails in the study area. The trail system on the West side of the forest road in particular appeared interesting, and plotting the trails seemed to be a valuable exercise for a number of reasons. Although many workers in the past have produced maps of ant colonies along with their trail systems, none have described their plotting technique (e.g., Stammer, 1937; Rosengren, 1971; Zakharov, 1973; Welch, 1978). Some have produced what appear to be sketch maps, whilst others have produced seemingly accurate plots (although they have not commented on their level of accuracy). Researchers, in the past, have also commented on the constancy of ant trails from year to year (Chauvin, 1962; Sudd, 1967; Rosengren, 1971), unless there is disturbance to the foraging ground through tree-felling for example (Rosengren, 1978). However, empirical evidence of this is impossible to demonstrate unless the trails are plotted over several years with a high level of accuracy.

Part 2 : METHODS

The study area was mapped in 1977 and 1978.

Unfortunately, the surveying equipment used in 1978 was unavailable in 1977. However, a prismatic compass and tape proved reasonably accurate and were employed in 1977. The road edges, the boundary of the forest, the nests and trails were all plotted using the compass and tape, each point being defined by a compass bearing and a distance from a series of 'control points'. Each 'control point' was, in turn, plotted in relation to a single 'bench mark'. This 'bench mark' was not, however, an Ordinance Survey bench mark, but was simply a metal pin, knocked firmly onto the road-side. Its position had been carefully selected so that as much of the study area as possible could be viewed from it. Using the compass and tape, the plotting accuracy was in the order of ± 1 m for a point 15 - 20 m from a control point. Since the accuracy of the prismatic compass was ± 1 degree, points were plotted only up to 20 m from any control point. To minimise errors, the bearing of a point from a control point (α) was checked by also taking the bearing of the control point from the required point (β). The mean bearing:-

$$\frac{(\alpha + (180 - \beta))}{2}$$

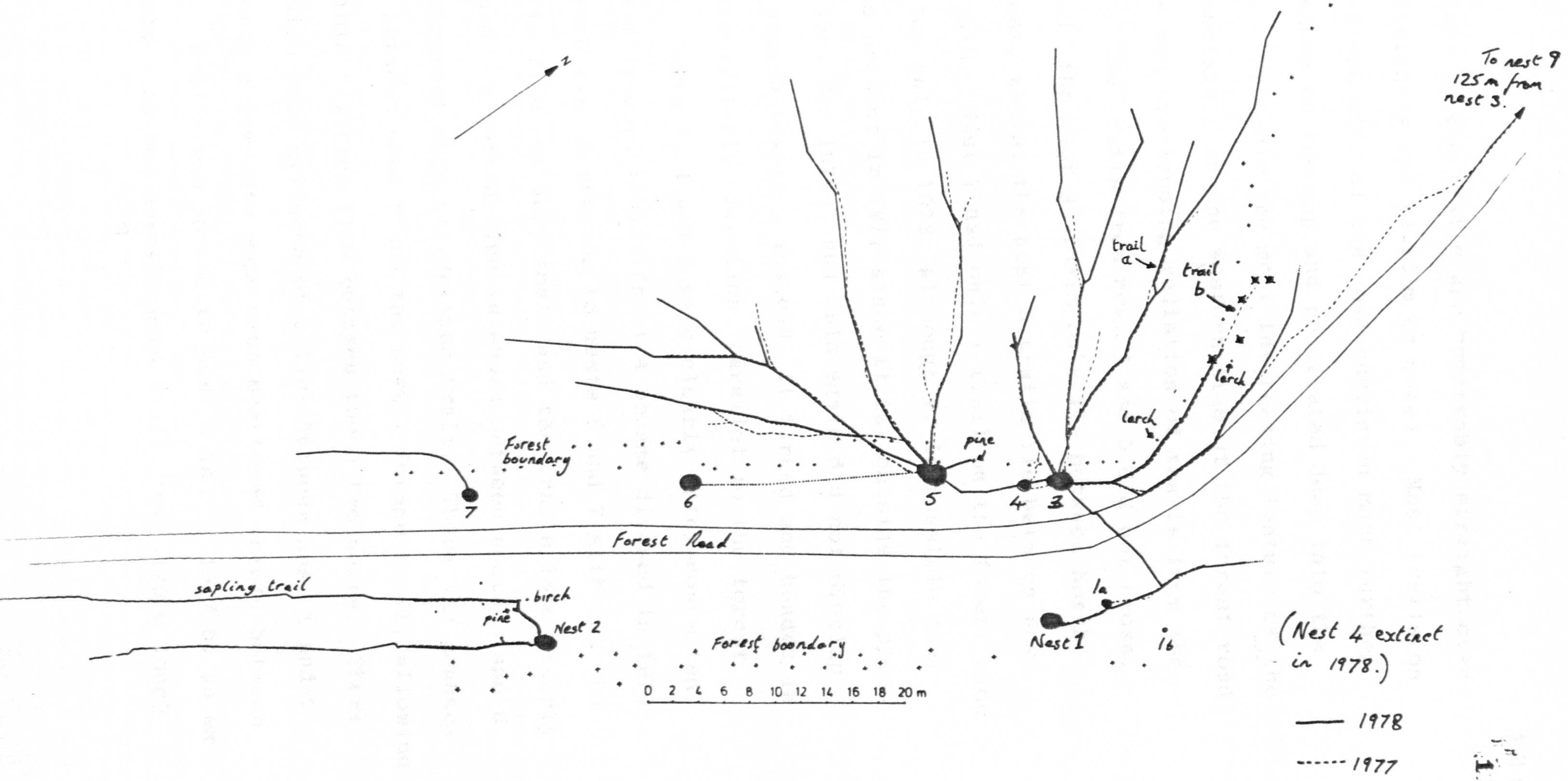
was used as the true bearing of the plotted point from a control point. Plotting the trails within the forest cover proved to be very laborious, because of the restricted visibility caused by the tree trunks, and also because the tape had to be re-threaded between the trees each time a new point was plotted.

In 1978, the entire area was re-mapped, but this time a surveyor's staff and tacheometric level were used. The distance between the level and staff could now be measured optically (for method, see Ritchie et al, 1977), allowing easy measurements to be made even under quite thick forest cover. The angle between the line joining the level and a control point and the line joining the level and the required point was measured from a dial on the level, and was accurate to at least ± 0.5 degrees. In addition, the level allowed the true horizontal distance to be measured to within 0.1 m. Each point was estimated to have been plotted with an accuracy of at least ± 0.4 m from its true position.

Part 3 : RESULTS

Figure 25 shows the study area and the trails for both 1977 and 1978. The 1977 trails are shown as dotted lines and those for 1978 are shown by solid lines. There is a remarkable similarity in the trail systems in the two years, as shown by the very close overlap of the lines. Most of the variation between years is well within the expected plotting error. This was verified by marking out the first 40 m or so of a trail (marked 'a' in Figure 25), in 1977 using small sticks. Ants in 1978 and 1979 followed the route exactly.

Fig. 25 Map of the study area showing the position of trails, nests and the forest boundary : 1977 & 1978.



Many of the trails are remarkably straight over long distances (up to 30 m or more). Most trails on the Western side of the road continued much further than shown on the map and penetrated deep into the forest. Probably the most interesting feature of the map, certainly on the Western side of the forest road, is the non-overlapping radiation of trails from the nests. The trails from nest 3 and 5 did not cross. Instead, the nest 3 trails only lie between North and West, whilst the nest 5 trails lie between West and South. Nest 7 had only 1 trail on the forest side (plotted only in 1978, although it is possible that it was present in 1977 since it lay outside the plotting area for 1977), and this again did not overlap with nest 5 trails. Instead, it turned and headed in a South-Westerly direction, parallel to the forest road. Nests 3, 4 and 5 were clearly inter-connected by heavily-used trails (nest 4 became disused in 1978), but were also connected to nests 6 and 7 although the traffic flow was very small and the trails less clearly defined. A dotted line is shown between nests 5 and 6 to represent this ill-defined trail. There was connection between nest 3 and the nest 1 forage trail, allowing possible traffice flow between these two nests. There was also some evidence of a link between nest 1 and 2 but only a few ants were seen scattered thinly between them. Nest 3 was joined to nest 9 in 1977 by an extremely long but heavily used trail (over 120 m long).

All the nests in the study area therefore appeared to be inter-connected to a certain degree.

In the Winter of 1977-78, extensive forestry work and excavation was carried out in the area surrounding nest 9. This nest was completely destroyed and several of the trees close to nest 3 (marked as a cross in a circle on trail 'b' in Figure 25) were felled. There was also considerable ground disturbance in the area shown in Figure 3. In 1978, the very long trail from nest 3 to nest 9 was no longer followed by any ants. Although the first 10 - 15m of trail at the nest 3 end was followed exactly as before, the trail changed direction as soon as it reached the disturbed ground, and ended soon afterwards. The felling of the trees also caused the 1978 trail marked 'b' to stop once it reached the new, closer forest boundary. This disturbance of the foraging trails as a result of forestry work agrees with the findings of Rosengren (1978) who concluded that tree felling in the winter reduces the ability of foragers, emerging in the spring, to locate their previous routes because of the lack of familiar visual cues.

Part 4 : DISCUSSION

There are three features of the foraging trails of *Formica lugubris* which deserve closer examination: their constancy, straightness and non-overlapping radiation. The constancy of trails between May and

November is probably a result of each honeydew-collecting ant's tree and trail fidelity, since a large proportion of the ants on the trails are honeydew collectors (75% of returning ants at the nest margin have come from trees (Horstmann, 1973)). Similarly, the constancy between years may be due to over-winter tree and trail fidelity. This, of course, raises the problem of how each individual ant repeatedly uses the same trail and returns to a particular tree. Therefore, before any discussion of forage trails is possible, the navigation of wood ants must be considered.

Wood ants are known to use a number of different cues in order to navigate between two points. Jander (1957, 1963), demonstrated that they could use the sun and moon as a light compass, and that, deprived of a direct light source, could use the polarisation of the light in the sky. Although this would enable a wood ant to make a straight journey between two distant points in a clear area of ground, it cannot easily explain the very long, straight trails within dense forest, where the sun and most of the sky can be obscured. It has been shown that the light compass is not used in Spring (Jander, 1957), which led Rosengren (1971) to believe that wood ants, emerging in the Spring, must use landmarks to follow the previous years trails. The ability to navigate using visual cues is particularly well developed in wood ants (Schneirla, 1943; Jander, 1957; Vowles, 1965;

Rosengren, 1971, 1978), and in a forest, clearly defined landmarks must abound. Of course, in order to use a route repeatedly, the visual cues and landmarks must be remembered. Jander (1957) has shown that F. rufa can remember a specific journey after at least a week's isolation, but Rosengren's (1971) evidence of route fidelity after 5 months winter hibernation, along with the evidence reported here of tree fidelity after 6 months hibernation demonstrates that wood ants must have a remarkable memory of navigational cues. However, if the over-winter fidelity results for 1979 are looked at in terms of decreased fidelity with increased nest-tree distance (i.e., disregarding the possible explanation of Zakharov (1978) in terms of 'Elementary Search Ranges') it is possible that the memory of sufficient landmarks to navigate to a distant tree is incomplete after a six month hibernation period.

Many species of ants are known to lay pheromone trails to guide others to food sources (Wilson, 1971). There is some evidence that wood ants can use chemical trails, although perhaps only when no other cues are available (Moglich and Holldobler, 1975; Horstmann, 1976; Elgert and Rosengren, 1977; Henquell, 1976), and can use pheromones for recruitment if a nest is starved (Horstmann, Bitter and Ulsamer, in press). However, observations of F. lugubris both in the field and laboratory gave no reason to believe that trail laying was used by honeydew collecting ants. Indeed, Rosengren (1971) performed experiments which showed that route fidelity in wood ants was not caused by pheromones or odorous deposits. In addition, one can consider a number of arguments against their use by wood ants.

Most ant species which are known to navigate using chemical trails feed opportunistically in the area around their nest. Their food sources tend to be patchily distributed and available for only short periods. It is, therefore, sensible that these species should mark out trails to newly found food sources, in order to attract others to the short-term food source. Many of the recruited foragers may never before have foraged in the area around the food source, and before these foragers can learn to use visual or tactile cues, the food will have been carried away. Honeydew-collecting wood ants, however, exploit a very long term and relatively static food source. It is true that individual aphid groups can move within a tree or completely die out, but these changes take place over days or weeks. A tree can support aphids for many years, so a honeydew collector in Autumn is likely to discover aphids on the same tree the following spring. Since an odour trail must be constantly relaid, a species with large foraging grounds must consume a considerable amount of metabolicallyproduced chemical. If the location of food sources is such that no other cues are possible, then this metabolic outlay is inevitable, but clearly it would be more efficient for wood ants to use the available visual cues which, like the food sources, will generally remain static. Interestingly, the Harvester Ant (Pogonomyrmex spp.), an ant whose diet of seeds is patchily distributed, relies strongly on visual cues on the main (long-term) trunk trails and in the area close to the nest, and uses chemical trails primarily along the short-term trails between the trunk trails and a source of seeds (Holldobler, 1976).

On emergence in the Spring, it would be unlikely for wood ants to be able to detect a chemical trail on their foraging routes. The forage trails within the forest, although clearly visible as cleared tracks through the forest litter during September, become covered with fallen larch needles. In addition, the winter snow and rainfall would dilute any chemicals laid along the trails. The ground on which wood ants would lay trails seems unsuitable for long-term chemical markers, as much of the forest litter is quite porous. However, if used, a fork in a trail would provide a serious problem. With chemical markers along each trail, a forager relying solely on olfactory cues would be expected to chose either one with a probability of 0.5. The observed fidelity rates of foragers in these circumstances are clearly too high to be explained by chemical trails alone.

Tactile cues are probably important to wood ant foragers, and, like visual cues, must be readily available within a forest. However, because the previous year's trails can become covered by a layer of forest litter during the winter, the tactile cues available on a trail in spring could be very different from those available the previous autumn, suggesting that visual navigation is used by the first foragers in Spring.

One last method of navigation which is undoubtedly important to wood ants is the following of topographical features such as crevices in rocks or cracks in the earth (Rosengren, 1971). The forage trail connecting the saplings to nest 2 (described earlier) is a good example of the use of topographical features, as it ran along the bottom of a drainage trench for most of its length. However, many of the trails on the other side of the road showed no such tendency. Although many of the trails running parallel to the forest road followed ploughing furrows, the trails running at right angles took routes which followed no obvious features at all.

The constancy of trails between years can, therefore, be explained by the early Spring foragers using visual cues remembered from the previous season. As it seems likely that the early spring foragers are the older workers of the nest, the foraging tradition must be passed on to the younger ants which had not left the nest before the onset of the winter. Without a foraging tradition, of course, the trails would not remain constant between May and November each year. During the active season, novice ants might learn the existing routes either directly from other ants - i.e., by following or being carried by individual foragers - or indirectly by following social cues along a trail e.g., the sight of the column of ants on a trail, or an odour on the trail, perhaps produced in small quantities by the large number of ants already on the trail. The laboratory results suggest a third possibility. Because each ant appeared to have learnt the journey to a food source by itself, a forage trail might exist because the individually-learnt routes of ants attending aphids on a number of trees share a common route either by chance, or because each ant learns a shortest-distance route. It must be remembered that the laboratory experiments demonstrated this individual learning over a distance of only 2 - 3 m. Schneirla (1943) showed that wood ants had to make a number of repeated journeys to a food source before they could learn to run a laboratory maze, relying on visual cues. Since the journey between the nest and aphid group in the top of a tree some 50 m away must represent a maze of awesome proportions, it is difficult to see how novice ants could learn to make repeated journeys to these distant aphid groups without using some information supplied by the veteran foragers.

At no time in either the field or laboratory were foragers seen carrying or being unmistakably followed by another ant. A great deal of carrying of brood was seen during Autumn 1977 on the inter-nest trail between nest 3 and the nests 120 m away (c.f. Mabelis, 1979a), but carrying did not occur on any of the forage trails. Rosengren (1971), however, has reported carrying as a means of recruitment in a number of wood ants species and witnessed 'tandem running' in _Formica_ _exsecta_ and _F._ _rufa_. If direct recruitment is not used in _F._ _lugubris_, any information which allows a novice ant to find a distant aphid group must come indirectly from the already experienced foragers or the trails. Rosengren (1971) suggested that foragers may be able to follow a route when visual cues are confusing by using the stream of ants or olfactory deposits on the route. Although he did not consider this behaviour in great depth, there is some evidence that it may be very important in indirect recruitment of novice ants.

Casual observation of ants using the nest 2 sapling trail in Spring suggested that they kept to the trail by staying within the area where other ants were also walking. In 1978, no ants were seen to make regular trips to and from birch saplings until June.

In May, several ants were observed when they departed from the birch on which they had been marked. None found their way back to the nest, but most wandered within 10 m of their tree. When one of these ants left the main trail, it would soon change from walking in a relatively constant direction, to meandering in a seemingly haphazard way. If, by chance, it reached the trail again, where there was constant traffic, the ant would resume walking in its original direction. On a forage trail, although interactions involving food exchange are rare, an ant is constantly surrounded by others walking in the same or the opposite direction, and may be jostled by this traffic. This potential navigational information would allow novices to reach very distant food sources simply by keeping within the area of heavy traffic. It is, of course, possible that low levels of olfactory information are also available on main routes, although this would be difficult to test. Nevertheless, a novice ant would quickly detect if it had deviated from the main trail, because it would be no longer surrounded by others, and could begin wandering in an attempt to return to the trail. The novice could thus follow the traffic all the way to a heavily visited tree, or depart at some point along its length (deliberately or accidentally) and wander until an aphid-supporting tree is found by chance. Many ants are, indeed, seen wandering apparently aimlessly in the areas between forage trails, but have usually been described as 'hunters' searching for insect prey (Sudd, 1967; Horstmann, 1973), though no hard evidence exists for such an assumption.

A novice ant could, therefore, reach a distant tree without any prior individual knowledge of the forage trail. The first return journey of such an ant would be a reversal of the outward route - haphazard wandering until a main trail is found by chance, and then it would keep in the main traffic until the nest was reached. A simple sun-compass or light response could be sufficient to let the ant know which direction to walk along a main trail in order to return to the nest. The first necessary cues to be learnt on subsequent journeys would be those allowing it to reach the tree from the trail. It would have to learn where to leave the trail and the course to take at that point (unless, of course, the tree was already heavily visited, in which case it could follow the others all the way). However, the main part of the journey along the forage trail would not have to be learnt. Since wood ants can use visual cues for navigation, it is probable that with repeated journeys, each novice could become less dependent on the social cues, and able to rely on visual cues. By Autumn, then, the veteran foragers would have sufficient knowledge of visual cues along its trail that these could be used the following Spring. Thus the spring traffic of visually navigating veterans would allow indirect recruitment of 'socially' navigating novices.

In recent experiments on F. polyctena Rosengren (1977a) found that recruits selected the foraging route which had the highest traffic rate. If baits were laid down between existing forage trails, new foragers were attracted to these in large numbers, whilst the 'veteran' foragers carried on using their existing trails. When the baits were removed, however, the 'recruits' to the bait returned to using the existing trails. Therefore, once the heavy traffic flow to the bait and the reward of the bait itself was gone, the 'recruits' returned to following heavily used existing trails. This implies that a novice forager will tend to select a heavily-used trail, but will also select the trail which gives the best reward at that time. Since, under normal circumstances, a heavily-used trail indicates that there are large and frequent honeydew rewards to be obtained somewhere along that route, this appears to represent an ideal strategy for a novice forager.

Although this discussion has so far considered how wood ants follow forage trails and why the trails remain largely unchanged over many years, the straightness of the trails which did not follow topographical features under forest cover should be examined. It is known that wood ants tend not to make turns of more than 90° unless necessary when foraging. This has been termed 'behavioural inertia' by Rosengren (1971). However, some of the trails in Langdale Forest were straight for distances of 15 - 20 m or more, and 'behavioural inertia' cannot fully explain trail straightness over such long distances. Gradual small-scale straightening of bends over many years (Rosengren, 1971) undoubtedly contributes to the situation, and one such process was observed on the nest 2 sapling trail over the experimental period. In 1977, a 90° bend was made by wood ants on the nest 2 sapling trail as they reached the drainage ditch (marked 'c' in Figure 3), as shown diagramatically in Figure 26. This area was cleared of undergrowth so that return journeys between the birch and the nest might be easily observed. Although this clearing did not affect the foraging behaviour, by 1978 a gradual straightening of the bend had occurred, and by late 1978, a much straighter route was used (see Figure 26). Thus, over a year, a 90° bend forced upon the foragers by inpenetrable undergrowth, was straightened when the obstruction was removed. Since the Langdale Forest study colony was probably between 10 and 30 years old, sufficient time had elapsed for the main trails to have become straight through the combined effects of many local straightenings. It would, therefore, be interesting to study the development of trails in an area newly colonised by wood ants, to discover whether trails are straight even when newly established, or whether local straightenings over a number of years are necessary to develop the trail

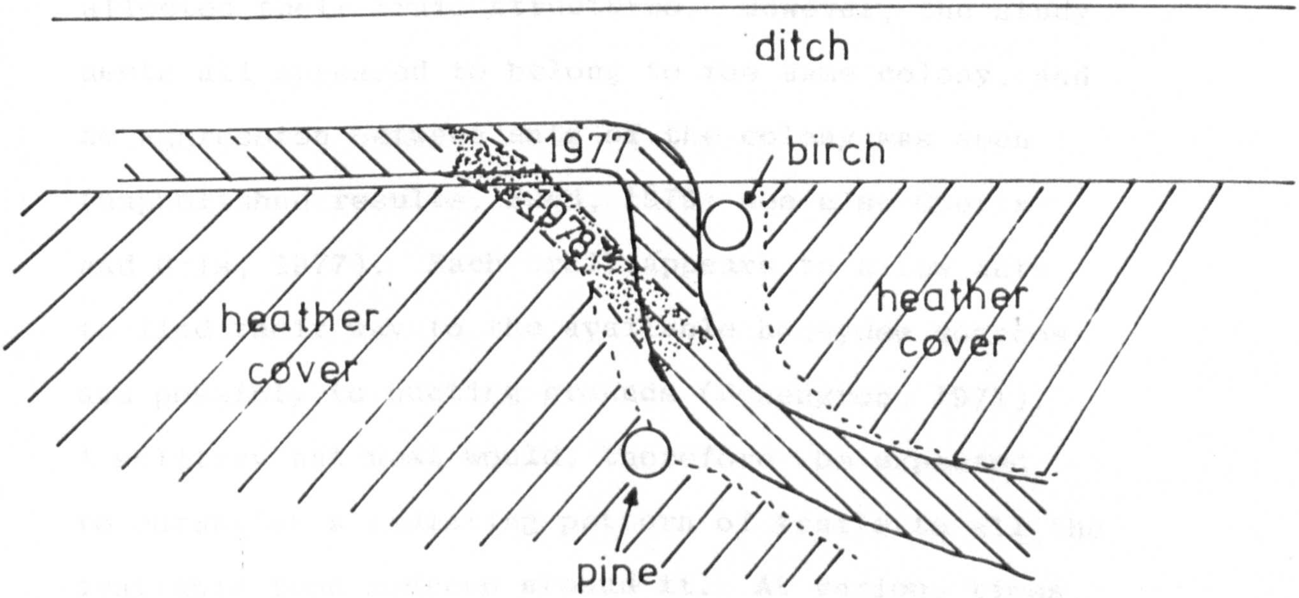
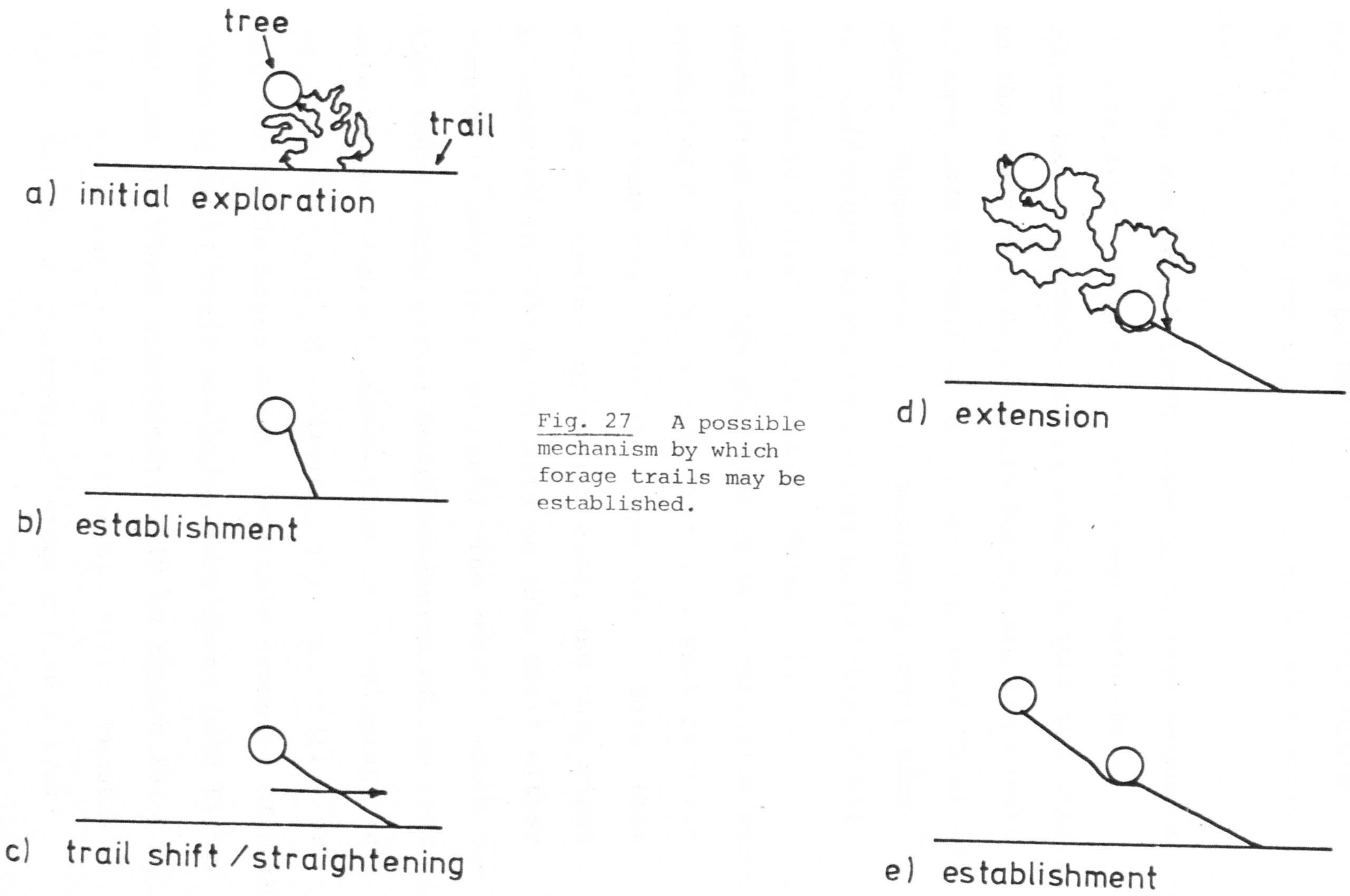


Fig. 26 Diagram of observed trail straightening along the nest 2 forage trail : 1977 - 78.

structure seen in mature colonies.

A feature of the trails of mature colonies which is more difficult to understand is their non overlapping radiation. A number of researchers have investigated aggression between conspecific colonies of wood ants (e.g., Breen, 1977; Mabelis, 1979b), and this competition between adjacent colonies has clearly affected their trail structures. However, the study nests all appeared to belong to the same colony, and no aggression between ants of the colony was seen (unpublished results, Sudd, 1979; see also Cherix and Gris, 1977). Each trail appears to allow ants to find their way to the available honeydew sources and possibly to hunting grounds (Rosengren, 1971). A solitary ant nest would, therefore, be expected to establish a radiating pattern of trails to all the available food sources around it. At various times, a nest will bud-off daughter nests at points along one or more established forage trails (Mabelis, 1979a; Rosengren, 1969). Their choice of sites for new nests is unclear, but most new nests which were found in Langdale Forest were established in areas which received direct sunlight for a few hours each day. Wood ants nests are rarely found in very exposed or totally shaded areas (Sudd <u>et al</u>, 1977). As a daughter nest creates a new nucleus of activity, further exploitation of the surrounding area is possible by establishing a new set of radiating trails from the daughter nest. However, some mechanism must prevent the new nest from establishing trails into the area already served by trails from the parent nests. It is useful, at this point, to consider the process involved when a new trail is pioneered. Although over two or three years the structure of the forage trails of a wood ant colony will show little change, the structure is dynamic, with some trails dying out, and new branches becoming established, and this change probably reflects the movements of aphid colonies which die out on some trees and become dispersed onto others. Of course, changes in prey density in the foraging grounds may also have an effect. Figure 27 shows a proposed mechanism for trail establishment in diagrammatic form, where a previously unattended tree is colonised by aphids through dispersal of alates from an adjacent tree. The first ants will arrive purely by chance; they will possibly be wandering novice ants, or, if such a group exists, ants hunting for prey. Field observations showed that a tree without aphids is not regularly visited, but Figure 18 showed that one or two ants may be found on uninfested trees from time to time. With more ants continually reaching this newly colonised tree by chance, a new trail will eventually become established, linking it to the nearest trunk trail. Experiments by Rosengren (1971) (see his p. 41) would suggest that a new route would be



a) initial exploration

b) establishment

c) trail shift /straightening

d) extension

e) establishment

Fig. 27 A possible mechanism by which forage trails may be established.

unlikely to be angled at more than 90° to the trunk route, and over a period of time the trail would shift to reduce the trunk trail/branch angle still further.

The new branch trail could be further extended by ants discovering additional trees onto which aphids had dispersed. It is possible that the trails in the study area of Langdale Forest are the result of many such extensions and branchings over 20 or so years. Suppose now, that a developing trail from one nest began to extend towards an existing trail from another nest of the same colony. If, as postulated above, the pioneers of this extension were wandering ants, they would eventually walk onto the nearby trunk trail from the other nest. Here, they would be overwhelmed by social cues, and they might be expected to follow the ants on this trail either towards or away from the nest. The result would be that there would either be no extension of one trail onto another - all pioneers from the developing trail would be lost onto the existing adjacent trail - or the two trails might merge. Possible examples of both these types of trail evolution were found (see Figure 25) and are shown diagrammatically in Figure 28. Crossing of two trails would be unlikely: because there must be a 'pioneering' stage before a trail becomes established, the ants doing the pioneering would have to walk across a busy existing trail and

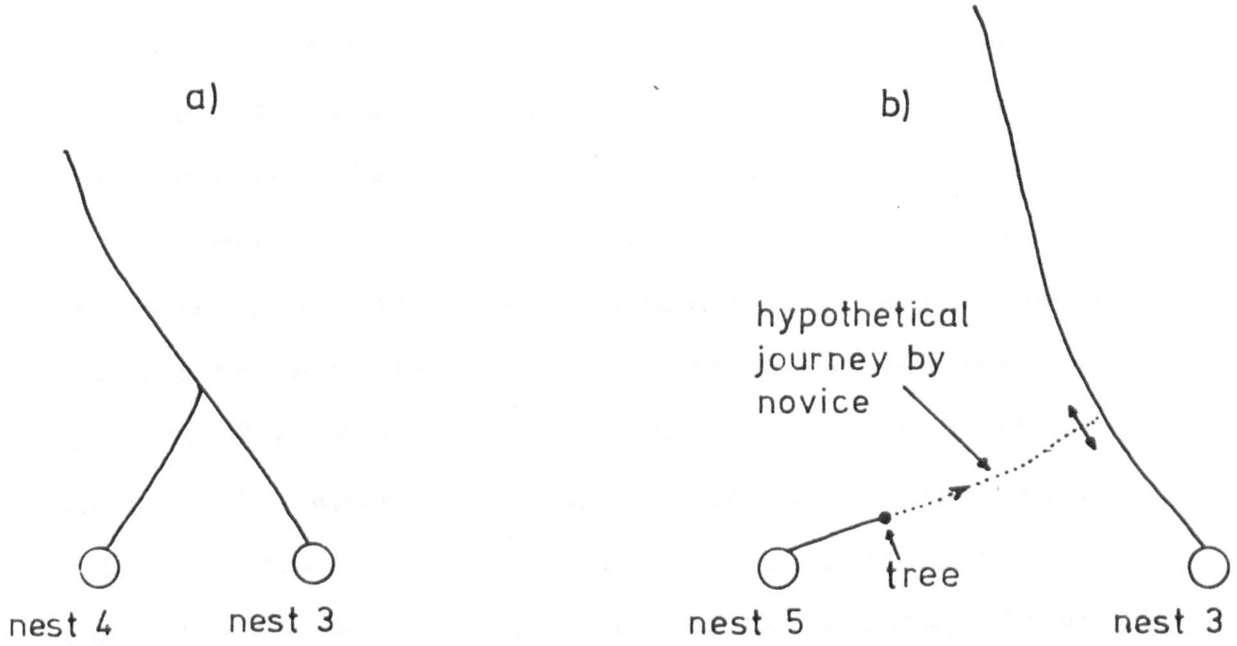


Fig. 28 Diagrammatic representation of two types of trail evolution, based on observed trails.

a) The trail from nest 4 becomes incorporated into the trail from nest 3.

b) Because most ants from nest 5 reach the tree, wandering novices reaching the nest 3 trail will never return to nest 5, so no connection of the trails will occur.

return over it again many times before such an extension could be established. The evidence on the response to social cues on trails suggests that this process would be very unlikely to occur.

There is one final point about wood ant forage trails which must be considered. It is only possible to plot a trail when it is visible as a column of ants running purposefully in an obvious direction. Close to the nest, the trails are plainly visible because they are worn away as well as being very busy. However, the further away from the nest one looks, the fewer the numbers of ants on the trail, and a point is reached where it is impossible to ascertain whether the trail actually exists or not. Similarly, a trail might connect the nest to a tree visited by 10 ants. These 10 ants must use a trail of some sort to reach the tree, but it will be impossible to find it without watching a number of ants making the journey. In essence, a simple search through the undergrowth would not reveal a trail used by only a few ants. Figure 25 therefore shows only the most obvious trails, and it is impossible to know the true extent of the trail network. The large number of ants which are found between trails may, in fact, be following specific trails, but without intensive study of the journeys taken by ants in a fixed area between trails, it is impossible to understand where these ants are going, or why they have left the main trails at all.

In Britain, the wood ant colonies which have spread into Forestry Commission plantations are really quite young. In most compartments of a forest, all the nests probably belong to the same colony, or originated from the same parent nest. There must be few areas where two or more separate colonies have begun to compete. As the colonies spread through the forests, this will begin to occur. In the colony studied here, the habitat for hundreds of metres around it was unoccupied by other competing colonies. It is, therefore, difficult to compare the forage trails of F. lugubris in Langdale Forest directly with many of the continental colonies, because these will be influenced by inter-colony competition for the available resources (Mabelis, 1979b). When two colonies of F. lugubris do finally begin to compete in Langdale Forest, it will be extremely interesting to study the effect on the forage trails. At the present rate of colony spreading, however, this is unlikely to occur for many years.

CHAPTER 9

GENERAL DISCUSSION

Aphids are extremely important to wood ants. Bradley and Hinks (1968) have shown that when all the aphids on trees close to a nest were killed by spraying, the foraging territory of *Formica obscuripes* increased dramatically. It would seem, then, that the configuration of forage trails is very dependent on the location of aphid-infested trees. Because these trees may support aphids for many years, a strategy in which permanent routes are established with little change over very long periods is clearly advantageous. However, there is sufficient flexibility in the foraging behaviour to allow wood ants to pioneer new trails when more resources become available, and this enables them to discover new aphid colonies formed as a result of alate dispersal onto previously uninfested trees. In North Yorkshire, *F. lugubris* has been able to encroach into at least the boundaries of newly planted forests from its original habitat of deciduous woodland and appears to be spreading continuously inwards. The aphid species available in the new coniferous plantations are generally very different from the species which had been available previously, yet the wood ants have been able to exploit a number of them. Five species of aphid (*Cinara pini*, *C. kochiana*, *C. piceae*, Symydobius oblongus and Periphyllus testudinaceus) were attended on 6 species of tree (Scots pine, Japanese larch, Sitka and Norway spruce, birch and Sycamore respectively). Only birch and sycamore occurred in the deciduous valleys where F. lugubris had originated. All these aphid species seemed to be attended in much the same way, and all the aphids responded to the ants by producing honeydew. This implies that there has been behavioural adaption by those species of aphids which are attended by ants, so that they all respond in the same way. Of course, by attracting ants in this way, they receive the benefits of protection from predators and disease (Nixon, 1951; Kloft, 1959), and indeed there is some evidence that neighbouring species of attended aphids actually compete for the services of ants (Addicott, 1978).

The introduction of F. lugubris to Canadian forests has resulted in a dramatic increase in the numbers of aphids in the forest (McNeil, Delisle and Finnegan, 1977). Many species of aphids which had not been known in these forests (but were perhaps already present in very low numbers) soon became very common close to wood ant nests, and a similar process appears to have occurred in Langdale Forest. Cinara kochiana, for example, is a very rare british aphid (Eastop, personal communication). In Langdale Forest, however, it is very common on larch trees close to ant nests. Bradley and Hinks (1968) have shown that Jack pine aphids (Cinara gracilis and C. banksiana) require ant attendance to survive. Both the aphids and the ants, it seems, are highly dependent upon each other, and the view that wood ants are primarily forest predators is perhaps a misconception, despite the large numbers of insects which they capture. For example, several marked honeydew-collecting ants were seen either chasing or catching weevils on birch trees. The weevils were immediately transported back to the nest if caught, but the ants later returned to their original task of honeydew-collecting. Horstmann (1973) concluded that ants in trees find mainly honeydew, but take prey where they can find it, and estimated that 50% of prey came from trees. Most researchers (e.g., Sudd, 1967; Rosengren, 1971; Horstmann, 1973) consider that prey is generally caught by a population of workers which specialise in hunting for prey. Although Ayre (1960) showed that a diet of honeydew alone is insufficient to allow the rearing of brood, the evidence for a strict partitioning of tasks is far from convincing. Horstmann (1973) showed that marked prey carriers (not coming from trees) were significantly more likely to be rediscovered carrying prey than controls, but of prey carriers coming from trees, only 23% were discovered with prey. He suggested that on the ground there was no distinct grouping of prey carriers and nest material carriers, and that in the trees, specialist prey carriers could not be shown. In trees, then, insect prey seems likely to be caught by chance, as an additional 'bonus', by ants which normally collect honeydew. This is probably only to be expected: a specialist hunter which searched for insects in a tree would waste a great deal of time. If insects were a bonus instead, then each ant in a tree could collect or transport honeydew in the times between catching insects. A tree without aphids is as likely if not more likely to contain insect prey as a tree with aphids. The results in Figures 18 and 19 show that during the Spring virtually no ants visit trees without aphids. Observations throughout the study period suggested that this was the case all year round. For example, during May - June large numbers of adult weevils infest the birch saplings. Although these are kept under control on birches supporting aphids through predation by wood ants, other birches without wood ants (often adjacent to attended trees) are attacked by large numbers of weevils and suffer a great deal of damage to their leaves. If a specialist group of hunters did exist, they would be expected to exploit this regular seasonal outbreak within the birch trees. Instead, those weevils which are captured are apparently found by honeydew collectors. On the ground, there is little evidence for or against a distinct hunter population, and it could be argued that here, too, the capture of prey is more by chance that intention. Until the behaviour of the ants which run about between the trails is understood, it is impossible to know whether these are ants which are deliberately searching for insect prey or nest material or whether they are novice ants whose exact task is flexible until they discover a tree at which they can collect honeydew. That prey collectors on the ground are more likely to return again with prey may simply be because they are unable to find an aphid-infested tree. This is clearly an area of study which demands closer examination.

Whilst it remains to be seen whether insect prey is captured by a distinct group of specialist hunters, the behaviour of honeydew-collecting wood ants is now fairly clear. The results of this study show that each ant which collects honeydew has a high degree of fidelity to the tree in which it attends aphids. Depending on the tree size and distribution of aphids within the tree, considerable fidelity to a particular aphid group may also exist. Each ant usually collects its own cropload of honeydew directly from aphids, by moving around within an aphid group and, where aphid groups are small but close together, by moving between aphid groups. When a load is collected, an ant returns directly to the nest without regurgitating or accepting any more en route, and, having given up its honeydew within the nest, it returns to the tree it had previously left, again without any trophallaxis along the trail. Tree fidelity appears to be unaffected by the size of the tree or by the nest-tree distance, and there seemed to be little change in the overall honeydew-collecting behaviour during the active period. An occurrence of chain transport was recorded, but the extent or importance of this behaviour in wood ants is uncertain. It was demonstrated, however, that wood ants are capable of establishing a strategy in which one group of ants collects honeydew from aphids, whilst another group transports this honeydew back to the nest. The 'collectors' remain at a single aphid group, whilst the 'transporters' move between the aphid groups collecting a number of second-hand loads of honeydew from 'collectors' along with a small amount of aphid-produced droplets. The environmental factors which initiated this behaviour are unclear, but it is possible that the rate of honeydew production, the ratio of ants to aphids and the dispersal of aphids within the tree influence honeydew collection. However, because chain transport could only be found on one tree, and because it only occurred for 3 - 4 weeks, the conditions were probably quite unusual.

The foragers which last attend the trees in Autumn leave the nest the following Spring, stimulated by a rise in air temperature. Foragers which attended trees close to the nest in Autumn are likely to return to the same tree in Spring, but this over-winter tree-fidelity decreases with increased nest-tree distance. Whether this is a result of diminished memory of visual cues during hibernation or because of the establishment of 'Elementary Search Ranges' could not be ascertained. Over-winter trail fidelity has been shown by Rosengren (1971) to be very high, and explains why the trail structure of a colony shows very little change between subsequent seasons. The foraging tradition is maintained during the active season by novice ants learning to follow existing routes to sources of honeydew and perhaps to hunting grounds. *Formica lugubris* shows little evidence of direct recruitment of these novices, and it seems likely that they are indirectly guided to the sources of food by use of social cues.

The evidence that insect prey from trees is only captured in large numbers by honeydew-collecting foragers suggests that the effectiveness of *F. lugubris* as a biological control of forest pests would be limited to a radius of perhaps 50 - 100 m around a colony, and protection would be afforded to only those trees which contained honeydew-producing aphids. Whether the trees suffer damage through infestations of ant-attended aphid species remains to be seen, but clearly any assessment of the economic value of *F. lugubris* in planted forests must take into account the importance of aphid-produced honeydew in its behaviour and ecology.

SUMMARY

The honeydew-collecting behaviour and the foraging system of the wood ant was studied using natural populations of _Formica lugubris_ in Langdale Forest, North York Moors. The results are summarised as follows:-

1. Honeydew-collecting wood ants show a high degree of fidelity to trees regardless of the distance from the nest. The level of fidelity to aphid colonies depends on the tree size and the distribution of colonies.

2. Observations over 2½ seasons showed that each ant generally collected all its honeydew directly from aphids. Where aphid colonies were large and far apart, each visiting ant collected at a single colony, whilst several colonies were visited if they were small and close together. Ants with full crops returned to the nest without any trophallaxis en route. After regurgitating their honeydew inside the nest, they returned to their tree again.

3. Although individual collection and transport of honeydew was the norm, chain transport occurred briefly on a tree in 1977. One group of workers ('collectors') collected droplets from the aphids. A second group ('transporters') collected the

majority of their honeydew by trophallaxis with several 'collectors'. When full, they returned to the nest with their second-hand loads without any further trophallaxis en route. Laboratory experiments suggested that the rate of output and accessibility of honeydew and the dispersal of aphids within a tree might be important in inducing chain transport.

4. Foragers in Spring tend to return to the trees they visited the previous Autumn, though this effect decreases with distance from the nest. This may be due to incomplete memory of visual cues, or the establishment of 'Elementary Search Ranges'.

5. Temperature seems more important than the hatching of aphids in stimulating the arrival of ants onto trees in Spring. Although there may be trail activity near the nest, before any aphids hatch, ants reach most trees with aphids up to 50 m from the nest at roughly the same time.

6. The foraging trails of <u>F. lugubris</u> showed little change over 2 years. The over-winter trail fidelity maintains trail structure between years, and it is preserved through the year by novice ants learning the existing routes, probably using social cues. The trails emanate radially from each nest without overlapping onto the trails of adjacent nests of the same colony.

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References

Abbott, A. (1978) Nutrient dynamics of Ants in "Production Ecology of Ants and Termites". Ed.M.V. Brian. International Biological Programme; 13, Cambridge University Press.

Addicott, J.F. (1978) Competition for Mutalists: aphids and ants. Can.J.Zool. 56, (10) 2093-2096.

Auclair, J.L. (1963) Aphid feeding and nutrition. Ann.Rev.Ent. 8, 439-490.

*Ayre, G.L. (1960) Der Einfluss von Insektennahrung auf das Wachstum von Waldameisenvoskern. Naturwiss. 47, (21) 502-503.

Bradley, G.A. & Hinks, J.D. (1968) Ants, aphids and Jack Pine in Manitoba. Can.Ent. 100, 40-50.

Breen, J. (1977) Inter-Nest Battles of Formica lugubris in Ireland. Entomologists Record and Journal of Variation. 89, (11) 296-298.

Breen, J. (1979) Worker populations of Formica lugubris Zett. nests in Irish planation woods. Ecol. Ent. 4, 1-7.

de Bruyn, G.J., Goosen-de Roo, L., Hubregtse-Van den Berg, A.I.M., & Feijen, H.R. (1972) Predation of ants by woodpeckers. Ekologia Polska. 20, (9) 83-91.

de Bruyn, G.J. & Kruik-de Bruin, M. (1972) The diurnal rhythm in a population of Formica polyctena Först. Ekologia Polska. 20, 117-127.

Chauvin, R. (1962) Observations sur les pistes de Formica polycenta. Insectes Sociaux. 9, 311-321.

Cherix, D. & Gris, G.Ch. (1977) The Giant Colonies of the Red Wood Ant in the Swiss Jura. (Formica lugubris Zett.). Proc.VIII Int.Congr. IUSSI p296.

Collingwood, C.A. (1964) The identification and distribution of British ants (Hym, Formicidae) I. A revised key to the species found in Britain. Trans. Soc.Brit.Ent. 16, 93-121.

Cotti, G. (1963) Bibliografia Ragionata 1930-1961 de gruppo Formica rufa in Italiano, Deutsch, English. Min.Agr.For. Collana Verde. 8, 1.413.

Douglas, J.M. & Sudd, J.H. (1980) Behavioural coordination between an aphis (Symydobius oblongus von Heyden, Hempitera-Callaphidae) and the ant that attends it (Formica lugubris Zett. Hymenoptera-Formicidae); an ethological analysis. Animal Behaviour. (in press).

Elgert, B. & Rosengren, R. (1977) The guest ant Formicoxenus nitidulus follows the scent trail of its wood ant host (Hym, Formicidae). Memoranda Soc. Fauna Flora Fennica. 53. 35-38.

Finnegan, R.J. (1974) Ants as predators of Forest Pests. Entomophaga Mem.Hors.Ser. 7, 53-59.

Finnegan, R.J. (1977) Predation de Choristoneura fumiferana (Lepidoptere : Tortricides) par Formica lugubris (Hymenoptere : Formicides). Rev.Bimes de Rich. 33, (1) 1.

*Gösswald, K. (1951) Die rote Waldemeise im Dienste der Waldhygiene. Fortwirtschaftliche Bedeutung, Nutzung, Lebensweise, Zucht, Vermehrung und Schutz. M. Kinau Verlag. Lüneburg.

*Gösswald, K. (1959) Einig zur Zusammenarbeit für die Gesundung des Waldes! Waldhygiene 3, 2-36.

*Gösswald, K. & Kloft, W. (1960) Untersuchungen mit radioactiven Isotopen an Waldameisen. Entomophaga. 5, (1) 33-41.

Henquell, D. (1976) Sur l'existence d'une piste chimique chez Formica polyctena dans les conditions de vie semi-naturelle. Insectes Sociaux. 23, (4) 577-583.

Higashi, S. & Yamauchi, K. (1979) Influence of a supercolonial ant Formica (Formica) gessensis Forel on the distribution of other ants in Ishikari coast. Jap.J.Ecol. 29, 257-264.

Hill, M.O. (1973) Reciprocal Averaging : an eigenvector method of ordination. J.Ecol. 61, 237-249.

Holldöbler, B. (1971) Recruitment behaviour in Camponotus socius (Hym : Formicidae). Z.vergl.Physiol. 75, 123-142.

Holldöbler, B. (1976) Recruitment behaviour, Home Range, Orientation and Territoriality in Harvester Ants Pogonomyrmex. Behav.Ecol.Sociobiol. 1, 3-44.

Holldöbler, B. (1978) Territoriality in ants. Proceedings of the American Philosophical Society.

Holt, S.J. (1955) On the foraging activity of the wood ant. J.Anim.Ecol. 24, 1-34.

*Horstmann, K. (1970) Untersuchungen über den Nahrungserwerb der Waldameisen (Formica polyctena Förster) in Eichenwald. I. Zusammenstezung der Nahrung, Abhängigkeit von Witterungsfaktoren und von der Tageszeit. Oecologia (Berl) 5, 138-157.

*Horstmann, K. (1973) Untersuchungen zur Arbeitsteilung unter der Aussendienstarbeiterinnen der Waldameise Formica polyctena. Z.Tierpsychol. 32, (5) 523-543.

*Horstmann, K. (1976) Über die Duftspur - Orientierung bei Waldameisen (Formica polyctena Foerster). Insectes Sociaux. 23, 227-242.

*Horstmann, K., Bitter, A., Ulsamer, P. (in press). Nahrungsalarm bei Waldameisen (Formica polyctena Förster). Insectes Sociaux. 27,

*Horstmann, K. & Geisweid, H.J. (1978) Untersuchungen zu Verhalten und Arbeitsteilung von Waldameisen an Rindenlauskolonien. Waldhygiene. 12, 157-168.

*Jander, R. (1957) Die optische Richtungsorientierung der Roten Waldameise (Formica rufa L.). Z.vergl.Physiol. 40, (2) 162-238.

Jander, R. (1963) Insect Orientation. Ann.Rev.Ent. 8, 95-114.

King, R.L. & Walters, F. (1950) Population of a colony of Formica rufa melanotica Emery. Proceedings of the Iowa Academy of Science. 57, 469-473.

*Kloft, W. (1959) Versuch einer Analyse det trophobiotischen Beziehungen von Ameisen zu Aphiden. Biologisches Zentralblatt. 78, 863-870.

Kruk-de Bruin, M., Röst, L.C.M. & Draisma, F.G.A.M. (1977) Estimates of the number of foraging ants with the Lincoln-Index method in relation to the colony size of Formica polyctena. J.Anim.Ecol. 46, (2) 457-470.

Kunkel, H. (1973) Die Kotabgabe der Aphiden (Aphidina, Hemiptera) unter Einflus von Ameisen. Bonner Zoologische Beiträge. 24, (1) 105-121.

*Lange, R. (1960) Modellversuche über den Nahrungsbedarf von Völkern der Kahlrückigen Waldameise Formica polyctena Förster. Z.angew.Ent. 46, (2) 200-208.

*Lange, R. (1967) Die Nahrungsuerteilung unter Arbeiterinnen des Waldameistenstaates. Z.Tierpsychol. 24, (5) 513-545.

Mabelis, A.A. (1979a) Nest Splitting by the red wood ant (Formica polyctena Foerster). Netherlands Journal of Zoology. 29, (1) 109-125.

Mabelis, A.A. (1979b) Distribution of Red Wood Ants (Formica polyctena Först) over the foraging area of their Nest, and the influence of a Conspecific Neighbouring population. Netherlands Journal of Zoology. 29, (2) 221-232.

McNeil, J.N., Delisle, J. & Finnegan, R.J. (1977) Inventory of aphids on seven conifer species in association with the introduced red wood ant, Formica lugubris (Hym : Form). Can.Ent. 109, 1199-1202.

McNeil, J.N., Delisle, J. & Finnegan, R.J. (1978) Seasonal predatory activity of the introduced red wood ant, Formica lugubris (Hym : Form) at Valcartier, Quebec in 1976. Can.Ent. 110, 85-90.

Möglich, M. & Holldöbler, B. (1975) Communication and orientation during foraging and emigration in the ant Formica fusca. J.comp.Physiol. 101, 275-288.

Möglich, M., Maschwitz, U. and Holldöbler, B. (1974) Tandem calling : a new kind of signal in ant communication. Science. 186, 1046-1047.

Nichols, S. (1977) On the interpretation of Principal Components Analysis in ecological contexts. Vegetatio. 34, (3) 191-197.

Nixon, G.E.J. (1951) The association of ants with aphids and coccids. Commonwealth Institute of Entomology London. 36pp.

Noy-Meir, I. & Whittaker, R.H. (1977) Continuous Multivariate Methods in community analysis : some problems and developments. Vegetatio. 33, 79-98.

*Otto, D. (1958) Über die Arbeitsteilung in Staate von Formica rufa rufo-pratensis minor Gössw und ihre verhaltensphysiologischen Grundlagen : Ein Beitrag zur Biologie der Roten Waldameise. Wissenschafliche Abhandlungen der Deutschen Akademie der Landwirtschaftwissenschaften zu Berlin. 30, 1-169.

*Pavan, M. (1959) Arrivita italiana per la lotta biologica con formiche del gruppo Formica rufa contro gli insetti dannosi alle foreste. Min.Agr.For., Collana Verde. 4, 1-80.

Ritchie, W., Tate, D.A., Wood, M. & Wright, R. (1977) Mapping for Field Scientists : a problem solving approach. David & Charles Newton Abbott 327pp.

Rosengren, R. (1969) Notes regarding the growth of a polycalic nest system in Formica uralensis Ruzsky. Notulae Entomologicae. 49, 211-230.

Rosengren, R. (1971) Route Fidelity, Visual Memory and Recruitment behaviour in foraging wood ants of the genus Formica (Hym : Form). Acta Zoologica Fennica. 133, 1-106.

Rosengren, R. (1977a) Foraging strategy of wood ants (Formica rufa group) I. Age polyethism and topographic traditions. Acta Zoologica Fennica. 149, 1-30.

Rosengren, R. (1977b) Foraging strategy of wood ants (Formica rufa group). II. Nocturnal orientation and diel periodicity. Acta Zoologica Fennica. 150, 1-30.

Rosengren, R. (1978) Effect of winter timber felling on the behaviour of foraging wood ants (Formica rufa group) in early Spring. Memorabilia Zoologica. 29, 143-155.

Schneirla, T.C. (1943) The nature of ant learning II: The intermediate stage of segmented maze adjustment. J.comp.Psychol. 35, 149-176.

*Stammer, H.J. (1937) Eine Riesenkolonie der roten Waldameise (Formica rufa L.). Z.angew Ent. 24, 285-290.

Sudd, J.H. (1967) 'An Introduction to the Behaviour of Ants'. London : Arnold 200pp.

Sudd, J.H., Douglas, J.M., Gaynard, T., Murray, D.M., & Stockdale, J.M. (1977) The distribution of wood ants (Formica lugubris Zett.) in a Northern English Forest. Ecol.Ent. 1977 2, 301-313.

Verron H. & Barreau, S. (1974) Une technique de marquage des insect de petite Taille. Bulletin Biologique 108, (3) 259-262.

Vowles, D.M. (1955) The foraging of ants. Brit.J.Anim. Behav. 3, 1-13.

Vowles, D.M. (1965) Maze learning and Visual Discrimination in the wood ant (Formica rufa). Brit.J. Psychol. 56, 15-31.

Vowles, D.M. (1967) Interocular transfer, Brain lesions and maze learning in the wood ant, Formica rufa. in 'Chemistry of Learning : Invertebrate Research' pp 425-451 Plenum Press : New York.

Wallis, D.I. (1961) Food sharing behaviour of the ants Formica sanguinea and Formica fusca. Behaviour 17, 17-47.

Way, M.J. (1963) Mutualism between ants and honeydew - producing Homoptera. Ann.Rev.Ent. 8, 307-344.

Welch, C. (1978) Changes in the distribution of the ants of Formica rufa L. at Blean Woods National Nature Reserve, Kent, during the decade following coppicing. Insectes Sociaux. 25, (2) 173-186.

*Wellenstein, G. (1952) Zur Ernährungsbiologie der Roten Waldameise (Formica rufa L.). Zeitschrift für Pflanzenkrankheiten. 59, 430-451.

Wilson, E.O. (1971) The Insect Societies. Cambridge, Mass : Harvard University Press 548pp.

Wisniewski, J. (1967) An analysis of animal remnants occurring in anthills of Formica polyctena Forst (Hym : Formicidae). Polskie Pismo Entomologiczne. 37, (2) 385-390.

*Zakharov, A.A. (1973) Experimental studies of intra-colonial exchanges in Formica lugubris (Hym :Form). Zool.jurnal (Moscow). 52, (5) 714-720.

*Zakharov, A.A. (1978) Individual territory competition in ants. Jurnal obtshey biologii, Moscow. 39,(3) 445-451.

*Zoebelein, G. (1956) Der Honigtau als Nahrung der Insekten Teil II. Z.an.Ent. 39, 129-167.

Those references marked * have been read in abstract or English summary only.

Appendix

Inventory of aphids and coccids found in Langdale Forest 1976 - 79

1) Aphids on *Pinus sylvestris*

Cinara pini (L)

Attended by *Formica lugubris* and very common. A small aphid which formed large colonies on the smaller branches of pine trees. Eggs laid on pine needles.

2) Aphids on *Larix leptolepis*

Cinara Kochiana (Borner)

Very common on larch trees close to nests of *F. lugubris* and heavily attended. Colonies are large, normally found on the undersides of the main branches, but some colonies can form on the stem. Eggs laid in the cones of larch trees, and larch trees without cones do not support *C. kochiana* until alate dispersal. This is considered a very rare British species, the last British specimen in the British Museum (National History) dating from 1847. Voucher specimens of this aphid from Langdale Forest are housed in the B.M.

Adelges laricis (Vallot)

Fairly common and attended by *F. lugubris* in Spring. Once colonies of *C. kochiana* are established, few wood ants continue to attend *A. laricis*.

3) Aphids on *Betula* spp.

Symydobius oblongus (v. Heyden)

Very common and heavily visited by wood ants. It forms colonies on the branches throughout the trees and eggs are laid at the base of the buds in Autumn.

Euceraphis punctipennis (Zett.)

A small green aphid which forms colonies on the undersides of the leaves. Not attended. Eggs are laid on the branches.

4) Aphids on *Picea abies* and *P. sitchensis*

Cinara piceae (Panzer)

Common on spruce trees close to *F. lugubris* nests. Heavily attended. Eggs laid on the ends of the branches, at the base of the needles.

Cinara bogdanowi (Mordvilko)

Cinara stroyani (Pasek)

Little is known about these two species in Langdale Forest. Both are rare British species and further investigation would be worthwhile. They may be attended, but the only examples found were laying eggs at the end of the season when ant numbers in the tree were very low.

Elatobium abietinum (Walker)

Fairly common. Not attended.