The management of ~~subterranean~~ aphids and other ~~soil~~ NEST INHABITANTS ~~organisms~~ by the ant *Lasius flavus* (F.).

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ABSTRACT

An area of rough pastureland has been sampled regularly for Lasius flavus and other soil animals for three years. The density of ants found in these nests agrees well with estimates of other workers using mature nests from undisturbed sites.

The abundance of ants in the surface 10cm of the nest was correlated with twenty biotic and abiotic measurements to see which factors most heavily influenced ant captures. It was found that the model:

$$\text{Ant activity} = 17494 \times \text{larval brood dry biomass (g)} + 10654 \times \text{adult reproductives dry biomass (g)} + 0.1 \times \text{base area of nest mound (sq.cm)} + c$$

could predict the trends in ant activity with high accuracy ($0.0001<p<0.002$).

The relationship of subterranean aphids to ants was also investigated. Generally there were positive associations between Lasius flavus and regularly tended root aphids; but species which show obligatory host alternation e.g. Anoecia corni and aphids which are not ant tended e.g. Aploneura lentisci show marked negative associations with Lasius flavus. During periods of high larval biomass, the number of adult aphids was practically unchanged,

although many first instar aphids vanished from the nest, presumably due to predation. Only when the alate ants emerged were aphid numbers drastically reduced. This was attributed to the feeding up of the new queens, which subsequently fast until the development of their first brood. Despite the fluctuation of aphid numbers, no deliberate form of regulation by ants could be shown.

The distribution of aphids within the nest was studied and clump sizes for aphid species were calculated. These varied with sub-family, and showed that for most of the year different species intermingled within the nest, not forming separate mosaics. At high aphid density however, it was found that different aphid species became most abundant in certain parts of the nest; those most heavily sclerotized/waxy still possessing rudimentary siphuncles, furthest from the nest centre, and those without siphuncles and some with legs adapted for ant 'communication' near the centre of the nest. This is related to the degree of ant attendance towards each aphid.

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CHAPTER ONE

INTRODUCTION

1.1 Lasius flavus (F.)

The trophobiotic relationship between ants and aphids was first accurately described by Huber (1810) from his observations of Lasius niger and Aphis fabae although honeydew, manna, ros melleus or sugar lerp, has been known about from the earliest Greek philosophers. Since then ant tending behaviour has been observed in the majority of the groups of 'advanced' ants (Myrmicinae, Dolichoderinae, Formicinae) whereas amongst the primitive family Ponerinae it is unknown. The advanced groups are characterized by having nests which are moderately large, regular in design and architecturally complex. Pheromones are used to maintain communication throughout the nest and during foraging activities so that there is co-operation between workers. In the primitive groups, generally colony size is small, there is little co-operation between foraging workers, and even queens of some species in the absence of workers revert to colony founding and foraging behaviour.

Lasius flavus is a member of the Formicine ants and is one of the most widely distributed ants in Britain, occurring as far North as Caithness and the coast of Aberdeenshire and becoming extremely common in the South.

It is characteristic of old pastures and grassy hillsides. Its nest mounds are one of the most elaborate of our native species, and may reach a height of 38cm above ground level and have a base diameter of 165cm. It is probably also the most abundant ant species, on Staines moor reaching a density of 104 per 250 square metres, and Stavns fjord (Denmark) was recorded as having 191 nests per 625 square meters (Nielsen et al 1976). In maintaining a meadow ecosystem, regular grazing plays an important part in keeping down scrub and under these conditions Lasius flavus thrives. In the absence of this, brambles and hawthorn encroach, and L.flavus dies out, its mounds sometimes being taken over by parasitic members of the genus Lasius. Indeed there seems to be a succession between ant species, dependent upon the amount of vegetation cover above causing shading of the nest (A.J.Pontin personal communication). Lasius flavus is also favoured in locations which are prone to flooding. Staines moor is on the flood plain of the River Colne, and Stavns fjord is a tidal meadow. That they seem resistant to flooding for short periods of time, may be attributed to their nest galleries being lined with water repellant organic matter (Jakubczyk et al 1972) and normally having no open nest entrances at the soil surface (Boomsma and Isaaks 1982). Other similar localities from which L.flavus has been recorded include various European salt marshes and dune intertidal zones of Schiermonnikoog Island, Holland (Boomsma and de Vries 1980).

On Staines moor all colonies sampled (except for one) were mature, partly because the nests were selected to be of a certain size (average of 56 litres of soil above ground), and partly because Staines moor is one of the few sites in the Thames Valley which has not been ploughed in recorded history, at least for the last 300 years. The plants commonly found on these nest mounds were Yarrow (*Achillea millefolium* L.), Sorrel (*Rumex acetosella* agg.), Thyme-leaved sandwort (*Arenaria serpyllifolia* L.), Mouse eared hawkweed (*Hieracium pilosella* L.), Ribwort (*Plantago lanceolata* L.), Black medic (*Medicago lupuleria* L.) and the grasses *Festuca rubra* L., *Agrostis tenuis* Sibth., *Agrostis stolonifera* L. Of these *Arenaria serpyllifolia* was restricted to the nest mounds. Similarly there were plants on the pasture land which were not found on the nest mounds. These included White clover (*Trifolium repens* L.), Red clover (*Trifolium pratense* L.), Marsh buttercup (*Ranunculus repens* L.), Knapweed (*Centaurea scabiosa* L.), Birds foot trefoil (*Lotus corniculatus* L.), Ragwort (*Senecio jacobaea* L.), Thistle (*Carduus* sp.) and the grasses *Festuca ovina* L., *Alopeceurus pratensis* L., *Poa pratensis* L., *Holcus lanatus* L., *Lolium perenne* L., and *Dactylis glomerata* L. This fits in well with the observations of King (1975,1977a,1977b). There is little difference in the chemical composition of ant mound soil and soil from the surrounding pasture, except for a higher potassium concentration in ant mounds (King 1977a). Old nests are also reported to have a higher pH (Czerwinski et al 1971) which may be due to leaching of nutrients. Although it is tempting to postulate that ants themselves selectively nurture the plants useful to the aphids, this has never been observed and is unlikely as they cannot break down cellulose, although ant action is one of the factors responsible for the lack of some meadow plants on the nest mound. Soil excavated from the nest is deposited on the surface of the mound (usually after periods of rain), this soil covers growing seedlings and thus favours plants which can grow up through it e.g. _Agrostis stolonifera_ and kills many others (King 1975). Other factors which favour certain plants are related to the design of the ant nest; the galleries provide a higher proportion of air space within the nest soil, the mound provides a larger surface area to volume ratio than the surrounding pasture, permitting a greater exposure to solar radiation and wind action, thus causing wider temperature fluctuations near the surface of the nest. A combination of these effects make ant mound soils drier throughout the year and more susceptible to drought in Summer (King 1977a). Plants on top of ant mounds are cropped much shorter than the surrounding pasture, as rabbits preferentially graze, scratch and defaecate on the mounds, presumably due to the extra height given by the mound to survey the area for predators. This in turn is beneficial to ants, as tall grasses cause shading which can slow the development of the brood.

In mature _Lasius flavus_ colonies egg laying occurs throughout the Summer months and reaches a peak in late August-September. The larvae which develop from these early eggs overwinter at between 1-2mm long and are destined to become the new alate queens. It is reported that further eggs are laid throughout the Spring from which the alate males and workers develop (Talbot 1965), although none was ever found at this time. By mid-May the queen larvae have trebled their size and a new batch of small larvae are found, the males. By late May the queen larvae are full size, and by early June are pupating. At this time the queen larvae and male larvae still have two distinct size ranges (see appendix B3). By mid-June the male larvae are pupating and another group of small larvae are found, the new workers, which grow and pupate mid-late July. Queen larvae can grow up to 7.5mm and are commonly in the range 6-7mm when full grown. Male larvae are in the range 3.5-4.2mm when full grown, which is in the same range as the worker larvae (3.0-4.0mm), but the males are on the very upper limit of the range. The time when the pupae hatch is mainly temperature regulated, but commonly happens mid-July, first the alate females , then about a week later the alate males. Special flight chambers are excavated to accommodate the new alates. The alates do not fly for many days, in which time they consume great quantities of food; the females will not feed again until fed by their first worker brood.

The timing of the nuptial flight again depends upon external conditions, which vary for each species. Lasius flavus flies on sunny days in late July-August when the temperature is in the range 19-23°C in the late afternoon when the temperature is beginning to fall. There is little wind and medium to high humidity. It has been determined that global radiation and temperature seem to be the triggering factors (Boomsma 1981). The nuptial flights are often not perfectly synchronized, with some nests developing slower than others, often due to shading. In 1984 the flights were very staggered possibly because of the low humidity, resulting in the ground being so hard that the new queens could not burrow. Alates were still found in the nest in early November. Having mated, the queen removes her wings and searches for a new nest site. Usually L.flavus colonies are founded by a single queen, but on occasions when two or more queens colonize the same nest, multiple queens can occur.

The new workers do not emerge until about three weeks after the male alates, although in the laboratory, when ants were extracted by heat, this was hastened so that a few workers were found emerging with the alate males.

Soil is one of the most energy-rich terrestrial microhabitats, and Wilson (1971) cites this as one of the main reasons for the numerical pre-eminence of ants. However, Lasius flavus owes its extreme success not to this, but to the extent of the association between itself and aphids. This is the most intriguing aspect of the ecology of L.flavus which unlike some other native members of the genus Lasius, seldom forages above ground. The aphids it tends feed on the roots of grasses and composites found within the nest territory. The honeydew produced by the aphids is composed of the sugars glucose, fructose, melizitose, trehalose, sucrose, organic and phenolic acids, amino acids plus B-vitamins and minerals, and hence is a very good source of carbohydrate. In addition ants also require a protein source and this protein/carbohydrate balance is possibly a factor controlling the management of aphids. When workers are not tending brood it is possible that the amino acids from honeydew may supply their protein requirements; however, with rapidly growing brood the aphids themselves become a protein source (Pontin 1958), together with other soft bodied animals found in the nest.

1.2 Subterranean aphids

All root aphids show certain common adaptations to their subterranean lifestyle and their close association with ants. Most of these aphids lack pigment and have reduced eyes. There is a reduction in the length of antennae, legs and the absence of repugnatorial cornicles (except for rudiments in *Tetraneura ulmi* and *Anoecia* spp. which still produce globules of wax). Sclerotization is also reduced, only heavily present in *Anoecia corni* and *Anoecia furcata*. Saltatorial leg modifications are present in *Trama troglodytes*, where the hind legs are modified to such an extent for communication that they are of little use in locomotion. Many are very waxy, probably to prevent honeydew from fouling their bodies (Way 1963). They have all acquired a circlet of hairs surrounding the anus which retains the droplets of honeydew, an adaptation exclusively for trophobiosis. That a trophobiotic relationship exists between ants and aphids is clear, what is not so certain is the benefit acquired by the root aphid. In the presence of ants, aphids feed faster and produce more honeydew. This leads to a greater reproductive rate (El Ziady and Kennedy 1956) and a larger biomass of aphids. Ants may also generate some tranquilizing effect on the aphids, stopping them wandering, thereby saving energy for feeding and reproduction. By removing the honeydew, ants keep aphids cleaner and free of mould which is especially important with aphids which live in confined spaces such as root aphids. It has also been stated that ants increase the survival of aphids by warding off predators (El Ziady and Kennedy 1956). Under laboratory conditions this may be so, but in the field there are a number of predators which seem adept at avoiding ants e.g. Aphidiidae. Pontin (1960) found little difference in the degree of parasitism in tended and untended aphids. In Lasius flavus mounds far fewer 'guests' are found compared with the nests of L.brunneus and L.niger (Donisthorpe 1927). This may reflect their greater association with aphids, although the lack of entrances may have an even stronger influence. The attention with which aphids are treated also extends to their eggs. Lasius flavus collects eggs and stores them over Winter (Lubbock 1882) and has been observed licking them as it would its own eggs (Pontin 1960). In Spring the recently hatched aphids are placed upon the roots of plants.

Nineteen species of subterranean aphids have been recorded from L.flavus mounds in Britain, belonging to the five subfamilies listed below (Donisthorpe 1927, Pontin 1978, Paul 1980).

Anoeciinae: Anoecia furcata
Anoecia corni
Anoecia vagans
Paranoecia pskovica
Neanoecia krizusi

Traminae: Trama troglodytes
Trama rara
Neotrama caudata
Protrama radicis

Eriosomatinae: Tetraneura ulmi

Pemphiginae: Pemphigus bursarius

Fordinae: Baizongia pistaciae
Aploneura lentisci
Forda formicaria
Forda marginata
Geoica setulosa
Geoica utricularia
Smynthurodes betae
Paracletus cimiciformis

On Staines moor only ten species were recorded: *Anoecia furcata* (Theob.), *Anoecia corni* (Fabr.), *Tetraneura ulmi* (L.), *Trama troglodytes* von Heyd., *Baizongia pistaciae* (L.), *Aploneura lentisci* (Pass.), *Forda formicaria* von Heyd., *Forda marginata* (Koch), *Geoica setulosa* (Pass.), and *Geoica utricularia* (Pass.). They were identified using the keys of Zwolfer (1958) and Paul (1980). Distinctive features are listed which were apparent from the specimens preserved in 10% formalin solution.

Anoecia corni (Plates 1a-e).

Primary host: Dogwood (*Cornus* spp.)

Secondary host: a range of grasses, the preferred grass being *Agrostis tenuis* (Muir 1959).

Characteristic features: 6 antennal segments, red eyes, 7 pairs marginal tubercles, heavy sclerotization, medium length rostrum (0.52-0.85mm).

Anoecia furcata (Plate 2a).

Primary host: Dogwood (*Cornus* spp.)

Secondary host: Grasses. The majority of aphids are anholocyclic.

Characteristic features: 6 antennal segments, red eyes, 5 pairs marginal tubercles, heavy sclerotization, medium length rostrum.

Tetraneura ulmi (Plates 3a-e).

Primary host: Elm (*Ulmus* sp.)

Secondary host: a range of grasses, the preferred grass species being *Festuca rubra* (Muir 1959).

Characteristic features: pink/purple pigment, siphuncle rudiments present, 5 antennal segments (small), rostrum short.

Baizongia pistaciae (Plates 4a-e).

Primary host: *Pistacia terebinthus*

Secondary host: a range of grasses

Characteristic features: colour white, long hairs on anal plate arranged in two distinct rows, long hairs elsewhere arranged one per segment, 5 antennal segments (0.33-0.44mm), rostrum short (0.30-0.40mm).

Aploneura lentisci (Plates 5a-b).

Primary host: *Pistacia lentiscus*

Secondary host: a range of grasses

Characteristic features: colour white, body spindle shaped, rostrum short (0.17-0.27mm), 5 antennal segments (0.17-0.20mm).

Forda formicaria (Plates 6a-c).

Primary host: *Pistacia terebinthus*

Secondary host: a range of grasses, the preferred grass being *Agrostis alba* (Muir 1959).

Characteristic features: 5 antennal segments long (1.1mm), third antennal segment longer than the others, lack of thorn like cuticular sculpturing on head.

Forda marginata

Primary host: *Pistacia terebinthus*

Secondary host: a range of grasses

Characteristic features: 5 antennal segments short (0.5-0.64mm), third antennal segment longer than others, rostrum long (0.58-1.00mm), thorn like sculpturing of cuticle well developed on head.

Geoica setulosa (Plates 7a-b).

Secondary host: anholocyclic on a range of grasses

Characteristic features: colour white, 12-16 long hairs on anal plate arranged in two distinct rows, dense covering of hair, first instar larvae grey-green colour.

Geoica utricularia (Plates 8a-d).

Primary host: *Pistacia terebinthus*

Secondary host: a range of grasses

Characteristic features: colour white, 60+ short to medium hairs on anal plate, body has many spatulate hairs (in adult)

Trama troglodytes (Plates 9a-b).

Primary host: Compositae (e.g. Yarrow), anholocyclic

Characteristic features: 6 antennal segments, long, hind legs especially elongate, rostrum long.

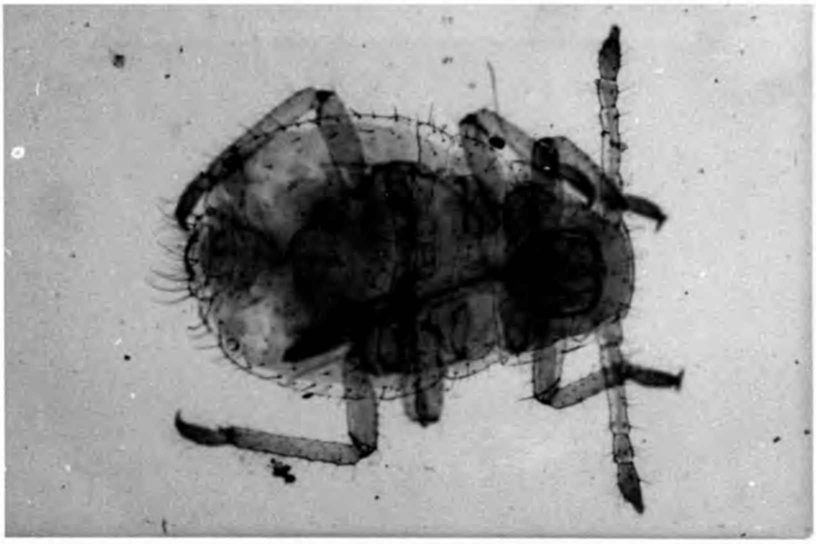


Plate 1a Anoecia corni; intermediate, 0.9mm.

Plate 1b Anoecia corni; sub adult, 1.6mm.

Plate 1c Anoecia corni; adult, 2.1mm.

Plate 1d Anoecia corni; intermediate alate, 1.3mm.

Plate 1e <u>Anoecia</u> <u>corni</u>; adult alate, 1.95mm.

Plate 2a Anoecia furcata; adult, 2.0mm.

Plate 3a _Tetraneura_ _ulmi_; first instar, 0.85mm.

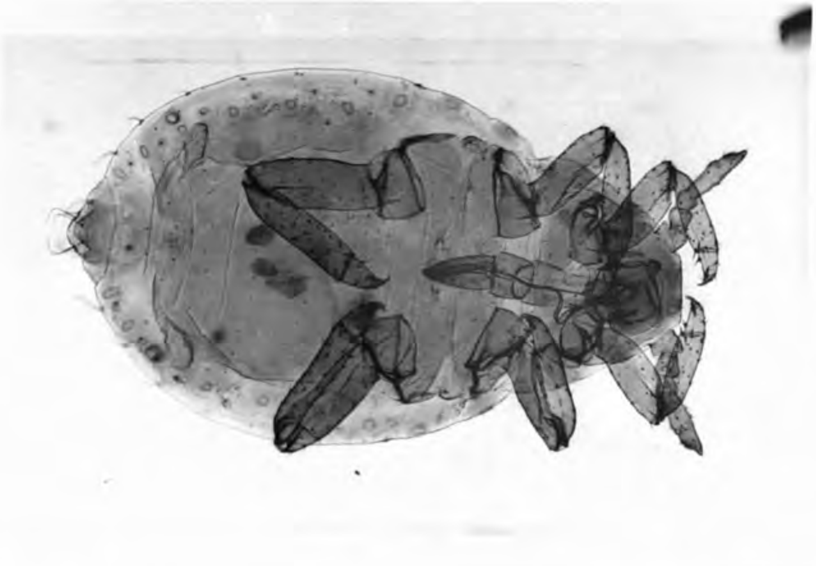


Plate 3b _Tetraneura_ _ulmi_; intermediate, 1.45mm.

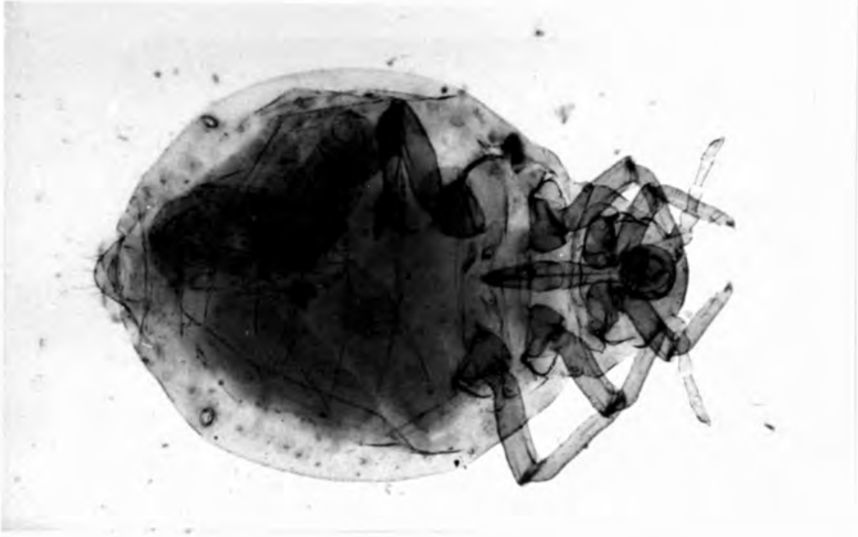


Plate 3c *Tetraneura ulmi*; adult, 1.85mm.

Plate 3d *Tetraneura ulmi*; intermediate alate, 1.75mm.

Plate 3e Tetraneura ulmi; intermediate alate, 1.85mm.

Plate 4a Baizongia pistaciae; intermediate, 0.9mm.

Plate 4b Baizongia pistaciae; intermediate, 1.35mm.

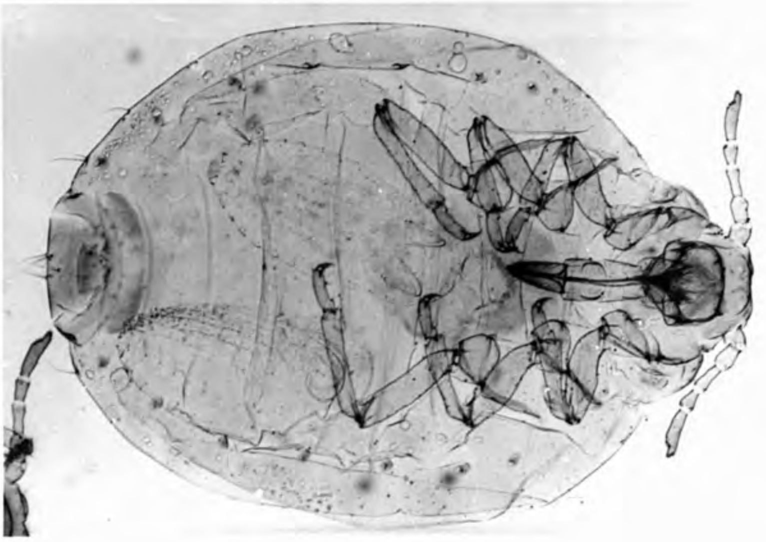


Plate 4c Baizongia pistaciae; adult, 1.7mm.

Plate 4d Baizongia pistaciae; sub adult alate, 1.6mm.

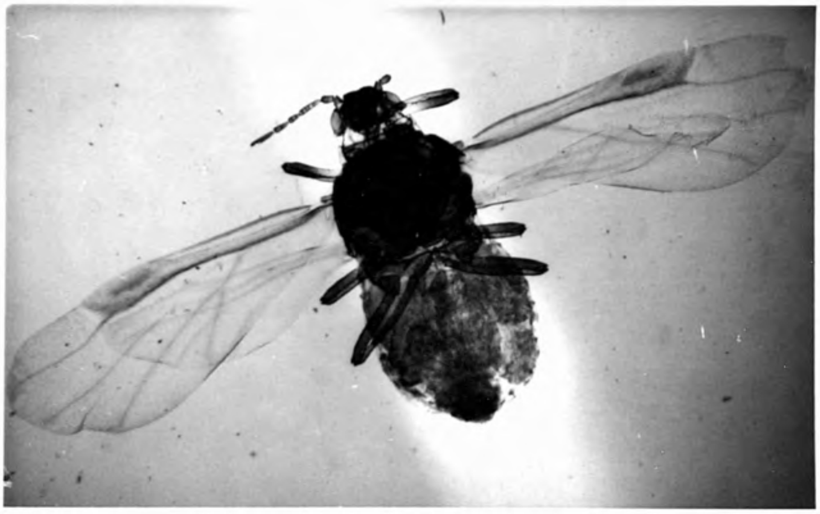


Plate 4e Baizongia pistaciae; adult alate, 1.25mm.

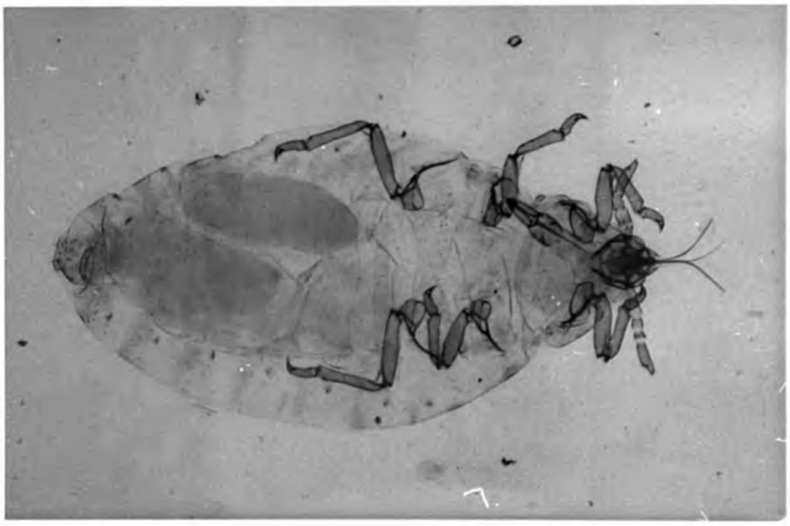


Plate 5a Aploneura lentisci; adult, 1.4mm.

Plate 5b Aploneura lentisci; adult, 2.0mm.

Plate 6a Forda formicaria; intermediate, 0.85mm.

Plate 6b Forda formicaria; adult, 2.65mm.

Some specimens ranged up to 2.75mm.

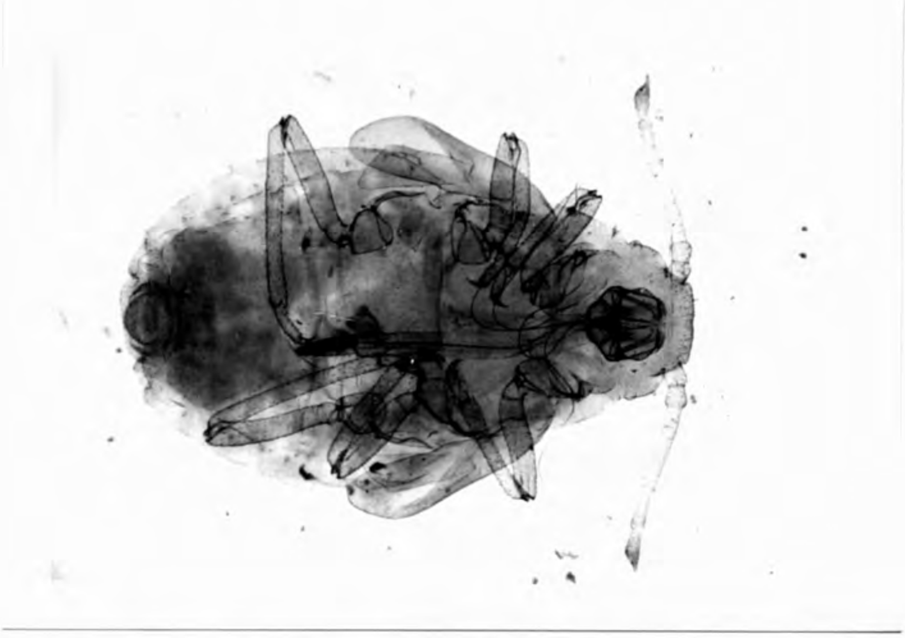


Plate 6c <u>Forda formicaria</u>; sub adult alate, 2.05mm.

Plate 7a Geoica setulosa; first instar, 0.8mm.

Plate 7b Geoica setulosa; adult, 1.9mm.

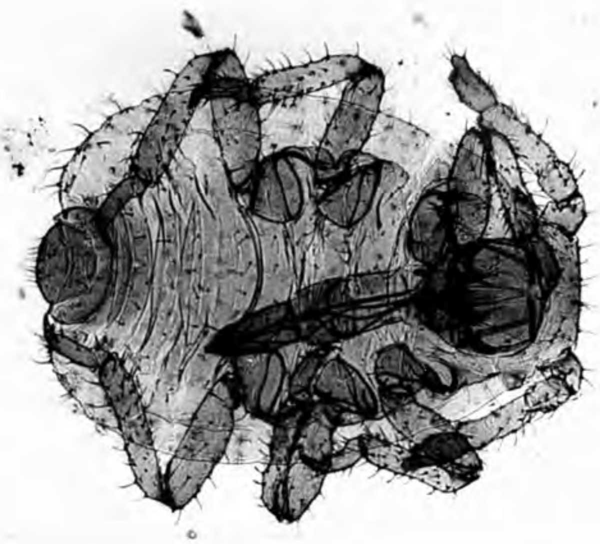


Plate 8a <u>Geoica</u> <u>utricularia</u>; first instar, 0.85mm.

Plate 8b <u>Geoica</u> <u>utricularia</u>; intermediate, 1.25mm.

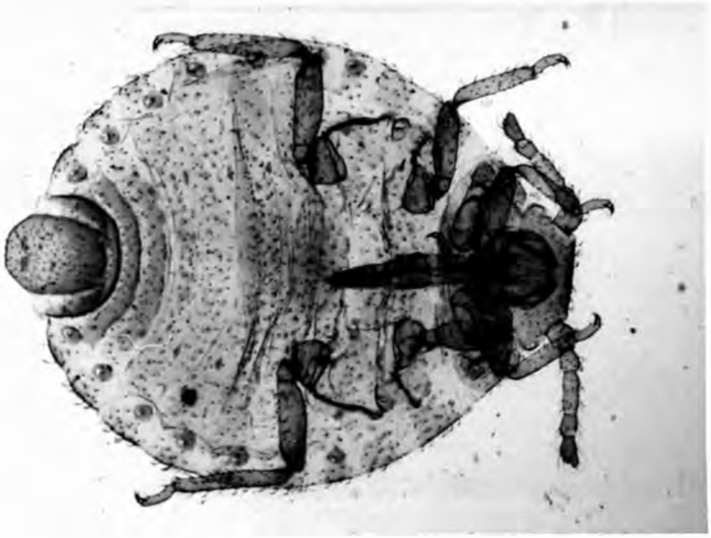


Plate 8c <u>Geoica</u> <u>utricularia</u>; adult, 1.75mm.

Plate 8d <u>Geoica</u> <u>utricularia</u>; adult, 2.05mm.

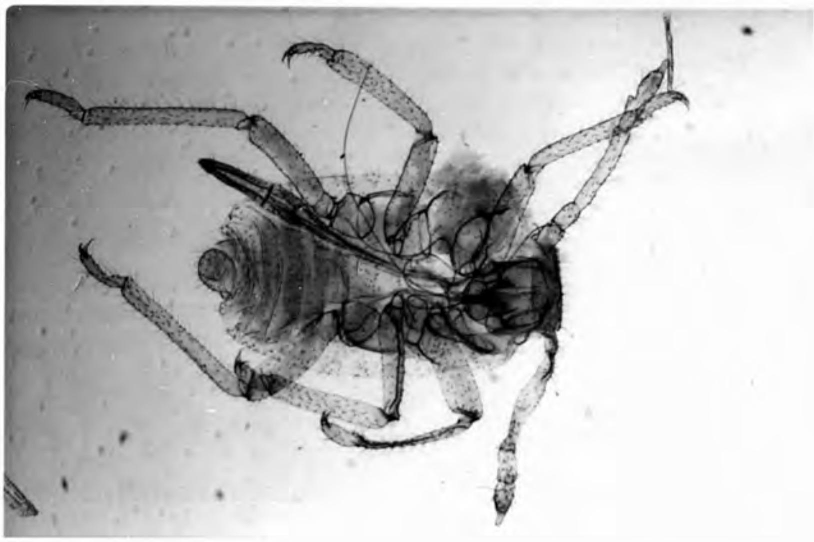


Plate 9a Trama troglodytes; first instar, 1.05mm.

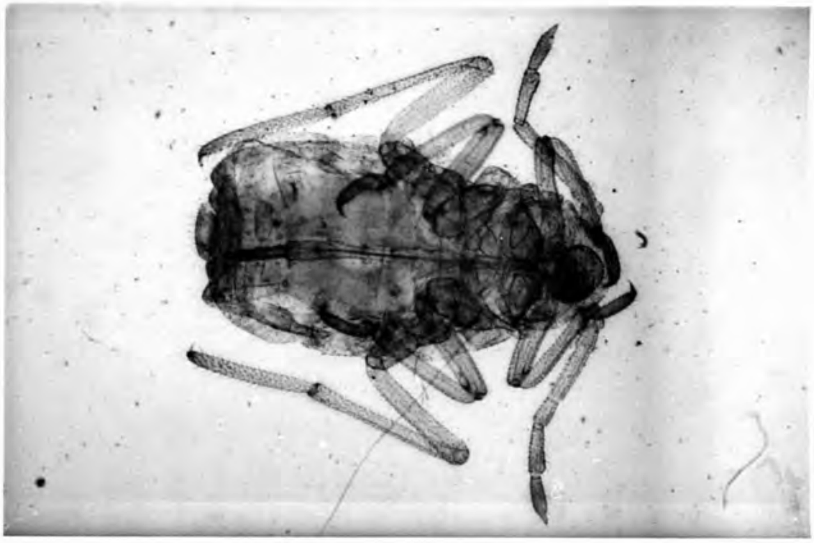


Plate 9b Trama troglodytes; adult, 2.15mm.

Some specimens ranged up to 3.15mm.

1.3 Other nest organisms

A Lasius flavus mound can be considered a partially isolated ecosystem (Wilson 1975). It is a permanent structure which has a slightly higher temperature than the surrounding soil. It is a good source of refuse in the form of dead ants and pupae exuviae plus an abundant source of food in the form of larvae and pupae. Some species abound in ant nest neither harming nor benefiting the hosts, and are just casual visitors, quite capable of completing there life cycles elsewhere e.g. Mirid and Coreid bugs, Psocoptera. Other species are obligate myrmecophiles for part or all of their life cycle. Wassman (1894) classified these species into four groups:

True guests (Symphiles)
Indifferently tolerated lodgers
Hostile persecuted lodgers
Ecto and endo parasites.

The greatest number of species of myrmecophiles are found with host species that form large mature, long lived colonies. Very few are known from Ponerine and Dacetine ants, presumably because most symphiles are tolerated because they have 'broken' the pheromone code, this becomes harder when no such code is used!

Over half the myrmecophiles known belong to the Coleoptera. Carabids have been recorded from Lasius nests (Lindroth 1966). Clavigeridae are found in the nests of L.flavus, and are the most symphilic of beetles, soliciting honeydew from the workers. Staphylinids are by far the most common group of beetle guests, living in ant nests by virtue of their preference for moist, hidden environments. They are predators as well as scavengers.

The next most abundant group are the mites. They can gain easy access into the nest on account of their small size, and are tolerated due to their inconspicuous life-style. Most are scavengers, but some are ectoparasites of ants e.g. Antennophorus.

Myriapods are also common. They tend to occupy habitats where there is a balance between rapid water drainage (therefore not immobilized by surface tension) and high humidity (Blower 1956). Symphyla make up the majority of the soil myriapod population and are characteristic of the upper soil layers. They cannot make their own burrows but use existing cracks, hence they are most abundant in soils with an open structure and good organic content (Edwards 1956). Some feed on growing roots, others on fungi.

Soil collembola are the major soil decomposition animals. They are attracted to ant mounds by the higher soil temperature and high humidity.

Amongst the less common animals were Diplura, which are predatory upon small soft bodied soil animals e.g. Collembola, and even some hard shelled mites. Two species of Mymaridae (Hymenoptera) were also found, which are parasites of ant eggs.

Of more dubious status were those animals could have arisen from the surface vegetation. Grasshopper nymphs were found, and have been recorded as forming temporary burrows.

Froghoppers were quite common, mostly as nymphs again these are mainly epigeic, but root feeding forms are known. Very common was the Tingid bug *Acalypta platychila* (Fieber). It is a well known meadow species where it is recorded as feeding on mosses. Mosses were present on ant mounds, but uncommon on Staines moor, and their abundance belies the food plant. I feel it significant that Tingidae are the closest group phylogenetically to the Reduviid (assassin) bugs.

1.4 Aims

The association between ants and aphids has been widely documented. However, authors differ in their opinions of the benefit afforded to aphids by ants. Nixon (1951) concluded that aphids derived little benefit from the association, the main benefit; protection from predators being due to the aggressive response of ants to any fast/erratically moving organism. Way (1963) regarded the main benefit to subterranean aphids to be the shelter provided from Winter conditions. Banks (in Way 1963) and Pontin (1960) cast further doubts on the effect of ant protection. Pontin (1958,1978) attempted to rationalize the management of aphids by *Lasius flavus* according to a protein/carbohydrate balance.

The 'mutualism' exhibited between *Lasius flavus* and subterranean aphids has been developed to such an extent that the aphids become the major carbohydrate and protein source. In this country most of these aphid species are found in no location other than the company of ants. Moreover *Lasius flavus* mounds normally have no open nest entrances at the soil surface, thus creating a practically closed system. To further complicate the association, nine species of aphid are commonly found in *L.flavus* mounds, which interact with each other as well as the ants.

The objective of this research was to determine how nine aphid species with such similar ecological requirements manage to coexist in the nest. To achieve this it was important to see how the individual aphid populations interacted, and whether there were any subtle differences in the environmental tolerances of each species. Thus it was necessary to quantify the effect of ants and other soil organisms upon aphids as well as abiotic factors.

From these parameters it was hoped to be able to construct some model relating ant and aphid abundance throughout the year. It was also hoped that this could be used to demonstrate the degree of aphid population regulation by <u>Lasius flavus</u> and quantify the ways in which subterranean aphids profited from this association.

CHAPTER TWO

MATERIALS AND METHODS

2.1 Sampling sites

STAINES MOOR. This is rough pastureland based on alluvial soil from the River Colne. The soil is approximately four inches deep (less in some places), beneath which is a stony subsoil and then gravel. The pasture has not been ploughed (at least for 300 years) and is regularly grazed by cattle and horses. In 1983 the North-East quarter of Staines moor was used as the sampling site, the same area as used by Dr.A.J.Pontin in 1974. The density of ant nests in this area was 104 per 250 square meters, with an average size of 58.3 litres above ground level. The area around the ant nests was heavily water-logged for much of the year, and it was not until late August that the River Colne receded and resumed its course. The changes in water level did not correspond to recent bouts of rain, 1983 was not even a particularly wet year. It is my contention that the gravel pit workings next to Staines moor were altering the watertable. Hence in 1984 and 1985 a different, drier area of Staines moor was sampled, the North-West quarter. The density of ant nests in this area was less, 85 per 250 square meters and the average volumes of nests sampled was slightly smaller at 47.3 litres.

ALDERHURST. In the grounds of the Zoology department of Royal Holloway College there is an area of grassland called the Small Paddock. The area is regularly grazed by sheep and rabbits. The soil is sandy (Bagshot sand overlying London clay). The density of nests is 40 per 324 square meters (77 per 625 square metres), and the average nest size is 57.6 litres, indicating a long period without cultivation (King 1981). Unlike Staines moor many nests have been taken over by Lasius niger, there are also two nests of Myrmica scabrinodis.

In part of the study area, the nest mounds are partially covered by 9"x9" concrete slabs. These slabs warm up faster and retain more heat than the rest of the nest, and in Summer the larvae, pupae and alates congregate underneath. These observation nests were used in the feeding experiments.

2.2 Pilot study

This was carried out in the grounds of Alderhurst mid-October to December 1982.

SOIL CORERS. Different size corers were tried to optimize the sample size, within the constraints of the extraction apparatus. Corers of diameters 2", 4" and 5" were used. To sample a comparable volume of the nest with a 2" corer required 24 samples. This produced too many samples to handle and it gave too many null counts of aphids each week

(50%). The 5" corer reduced the number of samples taken and had far fewer null counts, but there was a technical problem that the sample filled the extractor almost completely thus leaving only a very small gap around the sample for air to circulate. The air gap is important when extracting animals by heat to achieve an equal rate of drying throughout the soil core. As a result a four inch corer was selected as it gave a sufficient air gap, and the same proportion of null counts as the 5" corer. More samples could be taken with this corer than with the 5" corer without destroying the nest, therefore replicate samples were possible.

Twelve cores were taken per nest, to a depth of 10cm which was the maximum depth possible on Staines moor away from the nest mound. This sampled 65% of the area of the nest mound (25% of the whole nest territory). 9.4 litres of soil were sampled each week which accounted for 12% of the nest mound. Soil cores up to a depth of 20cm were taken during the pilot study, but these did not give an increase in aphid numbers, although it did give a 12% increase in ant numbers.

EXTRACTION METHODS. Extraction of soil animals is commonly by flotation or by heat. Both methods were tried to optimize the number of animals extracted and the time taken to do so.

Ladell (1937) first developed a flotation stage during extraction using magnesium sulphate to separate soil from organic matter including arthropods. Salt and Hollick (1944) further modified this by incorporating an oil separation stage using benzene to separate arthropods from organic debris. Unfortunately this method has four serious setbacks when tackling samples from old pasture:

(i) the grass roots are so intertwined that total removal of soil is very hard

(ii) the design can only really deal with small numbers of samples at a time

(iii) the final separation of arthropods from vegetative matter was always incomplete, even when the benzene layer was frozen to remove the animals.

(iv) many samples were needed to cover the nest area, therefore extraction time was long and laborious.

The other common method of extraction is by desiccation via some sort of Tullgren funnel. Burkards of Manchester supply banks of twelve funnels. Using these, my method was a refinement of that used by Pontin (1978). The problems he found with extraction related to the aphids breeding in the extractor, as an example quoting a 40:1 ratio of Tetraneura ulmi first instar nymphs to adults. To counteract this I used a slightly cooler lamp (25W) with a greater air flow around the samples. If small gaps only are left, then ants have the habit of using damp soil to form galleries on the walls of the sample container and when this happens ants are more likely to ascend the container and escape, whilst some aphids still remain in the galleries after the rest of the sample is dry. For Summer samples which only took three days for complete extraction, the ratio of T.ulmi first instar to adult is only 25:1 and this is comparable to the rate found in the laboratory. Other problems with this method related to aphid predation during extraction. No measure was taken, but again was probably reduced by a lower temperature and a quicker extraction time. Arthropods were collected in 10% formalin. Detergent was added to break the meniscus so that soil would not accumulate on it and the arthropods on top of that.

Many aphids especially the smaller more active ones are driven out of the sample normally. Larger or trapped aphids are removed by the ants. Chambers are made to collect brood and aphids successively lower down the sample until they drop out the bottom. There is a great deal of aphid carrying by the ants, many died with them in their jaws, and it is commonly seen in artificial nests.

To assess the efficiency of this method, samples were hand sorted afterwards checking for ants. No live ants were ever found, but on average one or two dead ones were found per nest, possibly crushed during sampling. Very few ants were trapped thus, especially when ants were at low density (Winter), but the number increases in Summer to about 0.007% of the total for the nest (see appendix A1). Aphids were also checked for, but when desiccated were very hard to identify, and none was ever found. This method resulted in a high efficiency of extraction; Nielsen et al (1976) using similar methods claimed an efficiency of 98%.

2.3 Field experiments

1983 The pilot study suggested that there were differences in the distribution of aphid species within the ant nest (see table 1). Therefore, to check this, to find how the size of the ant population influenced aphid numbers, and to see how both varied with season, a sampling program of one nest per week was carried out in 1983. The sampling site was Staines moor where there were more L.flavus mounds than Alderhurst, and fewer had been taken over by other ant species.

A random sampling pattern was not followed because I was interested in finding which aphids were present at set distances from the centre of the nest mound. The sampling pattern is shown in figure 1a. Samples were taken at 70cm because this is the outer limit of the ant territory on this area of Staines moor (Pontin 1978). Samples at 35cm were at the edge of the nest mound. Samples were taken at 20cm and at the centre to provide a contrast with the other areas of the nest and so that transects through the territory could be drawn. Twelve samples were taken as this is the number of extractor funnels in a Burkard extractor. When investigating the abundance of species across an environmental gradient, it is quite proper to sample along a transect. The idea of a linear transect was rejected because it did not allow for replicates to be taken in different compass directions. It is known that some areas of the ant mound receive more solar radiation than others and this may have influenced the number of ants and aphids.

Species	Proportion of total aphids at each location			Kruskal-Wallis Test	
	70cm	35cm	20cm	K	p
Anoecia corni	0.51	0.20	0.29	0.30	N/S
Anoecia furcata	0.15	0.27	0.58	6.24	0.05
Tetraneura ulmi	0.38	0.32	0.29	15.55	0.001
Baizongia pistaciae	0.01	0.03	0.96	1.95	N/S
Forda formicaria	0.21	0.49	0.30	0.48	N/S
Geoica setulosa	0.51	0.06	0.43	2.42	N/S
Geoica utricularia	0.21	0.18	0.61	10.37	0.01
Trama troglodytes	0.28	0.23	0.49	19.40	0.001
Aploneura lentisci	0.36	0.26	0.38	10.19	0.01

Table 1. The results of the pilot study, to determine whether there were differences in the spatial distribution of aphids.

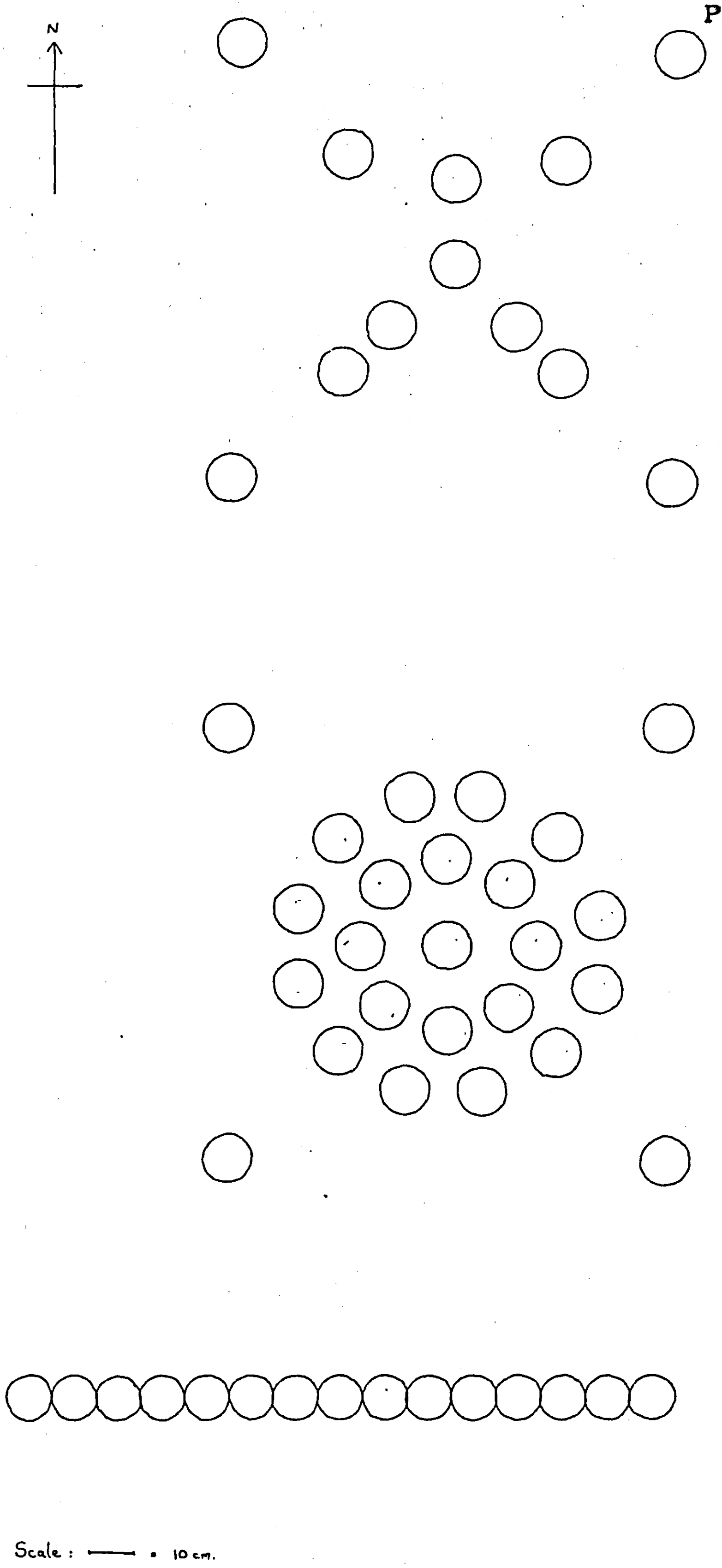


Figure 1. The different sampling patterns used during this study.

On five occasions 25 samples were taken from the ant nest (see figure 1b). This covered 85% of the surface of the nest mound (30% of the volume), and provided a more accurate count of the numbers of ants and aphids and investigated whether aphids formed a mosaic of species (see appendix A2). In mid-November central cores were taken from ten large nest mounds to assess whether the lack of aphids experienced in other mounds was a widespread phenomenon (see appendix A3).

All samples were taken mid-afternoon (14.30-15.30) when the temperature was highest. Air and ground temperatures were recorded together with nest size measurements and the plants found on the nest mound. Variation between nests was kept to a minimum by sampling nests from the same locality, which were selected to be of a certain size and covered by a characteristic ant mound flora.

Once extracted, numbers of ants, aphids, coccids, collembola, Coleoptera (staphylinids, wireworms and others), mites, myriapods (geophilomorph centipedes and symphyla), Psocoptera, spiders, and other Hemiptera and Hymenoptera were recorded. All the aphids were mounted in Berleze's medium (Beirne 1955), identified to species and split into three age categories; first instar, intermediate and adult. Soil Coleoptera, Hemiptera and Hymenoptera were preserved in 10% formalin for later identification.

<u>1984</u> The sampling method of 1983 was repeated on a different area of Staines moor to test whether the trends observed in 1983 were predictable. The sample site was changed because of repeated flooding of the area around the ant nests. As

before, all aphids were identified and put into age classes, but no slides were made as this was too time consuming. Twenty-five core samples were not taken, but in the weeks approaching the nuptial flight, two adjacent nests were both sampled to see if they showed similar trends in the number of animals present and whether they were at the same state of brood development (see appendix A4).

At Alderhurst in mid-December, the temperature of an ant nest was continually recorded. Temperature probes were inserted; in the top of the ant mound (approximately 1/2" under the surface), halfway up the mound (approximately 4" into the nest), at the base of the mound (approximately 6" into the nest). Another probe was placed amongst the grass roots away from the nest mound, but within the nest territory.

1985 More results were gathered on the distribution of aphids. The pattern of core samples was changed to a linear transect (see figure 1c). The benefit of this was that the results could be analysed by statistics regularly applied to plants (Kershaw 1973), thus indicating the clump size of aphid species, the degree of interspecific association and the formation of mosaics. The orientation of the transect was designed to minimize any North-South differences in species abundance due to differential solar radiation. Fifteen samples were required to span the area previously covered by samples.

The animals were extracted and recorded in the manner of 1984.

Although many factors had been monitored over the year, it became apparent that important factors were often interlinked. More specific field experiments were carried out at Alderhurst, and further observations made assess the extent to which these factors influenced ant and aphid numbers.

1. Temperature (May). Two nests were selected of approximately the same size (volumes 46.61, 49.61), and close together both unshaded by trees. Temperatures were recorded at their surface (approximately 1cm into the soil), half-way up the side of the nest and at ground level. The surface of one nest was then heated for four hours, raising the surface temperature to a steady 30-32°C. The other nest was left as a control. Final temperatures were recorded and four samples taken from each nest at a radius of 20cm from the nest centre and extracted as normal. A week later temperatures were recorded and four more samples were taken from each nest at 20cm from the nest centre. Ant and aphid numbers are analysed in appendix A4.

2. Temperature (July, August). Daily measurements were taken of internal and surface nest temperatures, ground temperature and air temperature. The abundance of workers and alates were also noted to assess the effect of high temperature on ant numbers. Records were taken using the observstion nests in Alderhurst grounds (see appendix B1).

3. Carbohydrate (August). During this period, aphid numbers in nest mounds reach their lowest level and then start to recover. By feeding excess carbohydrate (1.5M sucrose and melizitose in ratio 19:1) to the ants, it was investigated whether instead of recovery, even more were

eaten to maintain a protein/carbohydrate balance. Twenty successfully reproducing mature Lasius flavus colonies were randomly selected; in half of the nests 2cc of sugar solution was added in a 3"x1" vial everyday, in the other half an equal amount of tap water was added. At the end of August a central core was taken from each nest and the animals recorded as usual (see appendix A5).

4. Larval predation (January-April). Once it became clear that aphid density in the nest was kept below the level of interspecific competition by worker predation (to feed the queen and brood), larvae were removed from five nest mounds at Alderhurst. This decreased the predation pressure upon aphids, and thus it was possible that they would attain high densities and show interspecific competition at a time of year when this was usually undemonstrable. Samples were taken at 20cm (as no difference in species had been found between 0 and 20cm), 35cm and 70cm in April to May, when larval biomass was known to be high in control nests. Soil organisms were extracted as usual.

On Staines moor, the vegetation on top of the nest mounds was always surveyed. Occasionally, instead of the usual mix of plants, some nests were dominated by one species, most commonly Hieracium pilosella. Four samples from these nests were taken at 20cm radius from the centre to see if they favoured any species of subterranean aphid. (see appendix A6). Further samples were taken at high aphid density to find the most abundant aphid species.

2.4 Laboratory experiments

APHID REARING. To assess competition between aphid species, the ideal experiment would be to rear single species cultures and measure reproductive rates, then contrast these with mixed cultures. Replacement series (Williamson 1971) could then be constructed to determine a hierarchy of aphid 'competitiveness'. Various methods were used and are discussed in appendix A7.

ARTIFICIAL NESTS. Newly hatched alate female ants were taken in July 1985. These were put in nests with and without workers from the same nest mound. Worker pupae were also given to both nests to tend. The ants were fed on sugar solution as described in section 2.3, *Aphis fabae* were also added. The nests consisted of 4"x3" plastic boxes containing small quantities of soil and saturated tissue to provide a high humidity. Observations are recorded in appendix A8.

CHAPTER THREE

THE SEASONAL ABUNDANCE OF LASIUS FLAVUS

3.1 Introduction

The purpose of this chapter is to give a complete description of the variations in ant number over the year, to draw similarities between years and compare the trends. A number of factors are thought to influence these trends, and their interrelationships are discussed. Finally using this knowledge of ant distribution in the nest, colony size is estimated and compared with the results of other workers.

3.2 Nest mounds

The nests sampled in 1983 gave an overall mean diameter of 0.83m +/- 0.04m (mean +/- 95% Confidence limits), with an interquartile range of 66-84cm. In comparison Dr.A.J.Pontin using the same site in 1974 found a mean diameter of 0.83 +/- 0.03m (Pontin 1978). This similarity although not surprising is reassuring. That the mean nest size has not increased implies that the populations may have reached a stable size, presumably related to competition between neighbouring nests. King (1981) showed that long established Lasius flavus mounds from chalk grassland increased at the rate of 1.04 litres per year and suggested that this rate was constant with age and soil type. An increase in the volume of these mounds is possible, as no measures of volume were taken in 1974.

On the 1984/5 site, the mean diameter of the nests was 0.75 +/- 0.03m and the mean volume of the nests was also smaller. The density of the nests was lower at 85 per 250 sq.m. compared with the 1983 site (104 per 250 sq.m.). The 1984/5 site did show the occasional nest which was much larger than average, one having a volume of 319 litres, hence this area of Staines moor was not newly colonized. The lower density of ant nests is related to the thinner layer of topsoil in this part of Staines moor, and the ground being much drier, suggesting that the ants require larger territories to support the colony and brood.

The diameters of the nests were measured from North to South and East to West. The mounds were approximately circular, the mean nest covering an area of 5548 sq.cm +/- 634 sq.cm. The only consistent exceptions to mound shape were those in which Lasius flavus were being displaced by Myrmica scabrinodis. Myrmica was found in 31% of the nest mounds, but were only established in two. In each case the symmetry of the nest had been lost, it was much flatter and had been extended in the opposite direction to the invading Myrmica. The distribution of mound size was both skewed and peaked, (skewness = 1.61, kurtosis = 2.80), although the reason for this is not clear. The nests were selected to be within a certain size range in an effort to standardize my observations, and this distribution probably reflects the true variation within my chosen limits. The size of the ant mound was not significantly correlated with the number of ants extracted from it.

When the North-South and East-West diameters were compared (see table 2), it was found that in 82% of the nests, the East-West diameter was greater than the North-South. This was not significant, but fits in well with Hubers records of Swiss <u>L.flavus</u> mounds (reported in Wheeler 1910, p.205), in which the ants extend the nest in an easterly direction, where they are most abundant. In such nests the East-West direction was so disproportionately elongate that they were used as a compass by mountaineers! On Staines moor in general it is to be expected that ants would be more abundant on the South side of the mound, which gains greater exposure to the sun, and to a lesser extent on the West side. The latter case is complicated however, by the effects of the predominantly South-westerly winds which in late Winter-Spring tend to warm the nest, but in Summer and Autumn tend to cool it. When such ant abundance is compared (see table 3), no conclusive statistical difference is found in either the 1983 or 1984 results. In the 1983 results there is a weakly significant difference between the number of ants found on the Northern and Southern most edges of the ant territory ($p<0.1$), and more ants were found at the South-Eastern limit of the territory, than in any other 70cm sample ($p<0.05$). The 1984 results also show a slight difference between the number of ants found on the Northern and Southern slopes of the ant mound ($p<0.1$).

EAST-WEST DIAMETER (cm)	NORTH-SOUTH DIAMETER (cm)
72	69
73	75
90	77
85	76
89	78
71	69
74	72
72	67
70	68
75	68
73	79

Mann-Witney U-test; U = 42.5 U(11,11) = 30, therefore not significant

Table 2. The difference in nest diameters (1985 data).

	t-test	Probability
1983		
West vs East (35cm)	0.11	N/S
North vs South (35cm)	0.77	N/S
West vs East (70cm)	0.51	N/S
North vs South (70cm)	1.73	0.1
S-E vs N-W (70cm)	1.56	N/S
S-E vs N-E (70cm)	2.01	0.05
1984		
West vs East (35cm)	0.28	N/S
North vs South (35cm)	1.82	0.1
West vs East (70cm)	0.34	N/S
North vs South (70cm)	0.89	N/S

Table 3. The difference in ant abundance at the different compass points of the nest.

Null hypothesis	d-value	Probability
1983		
0 cm = 20 cm	0.87	N/S
20 cm = 35 cm	4.82	0.001
35 cm = 70 cm	7.90	0.001
1984		
0 cm = 20 cm	0.25	N/S
20 cm = 35 cm	2.27	0.05
35 cm = 70 cm	6.45	0.001

Table 4. The differences in ant abundance at different distances from the nest centre.

The distribution of ant numbers throughout the territory is heavily influenced by the nest mound (see table 4). In 1983 no difference was found between the numbers of ants near the centre of the mound (0cm and 20cm samples). Significantly less were found near the edge of the nest mound ($p<0.001$), and even fewer in the outlying territory ($p<0.001$). The 1984 results follow this trend, except that the difference between the 20cm and 35cm samples was not so extreme ($p<0.05$). This is because the Winter and early Spring results in which such differences are most apparent were not collected, which implies that the variation in the ant distribution further varies with season.

3.3 Dispersion of ants in the nest

Various indices of dispersion exist to describe the degree of aggregation of a population, examples are given in table 5. The suitability of each measure to describe my results and its limitations, is subsequently discussed.

The coefficient of dispersion and the clumping index of David and Moore (1954) are strongly influenced by the number of individuals in the sample. As a result, they are not a good measure of the degree of clumping in populations unless the sum and mean have the same values in each sample (Elliot 1977 p.74). Given these restrictions, David and Moores clumping index becomes a very good measure, because values between species can be readily contrasted.
The coefficient b from Taylors Power Law (Taylor 1971), is indepedent of number of samples, mean of samples and sum of animals, but is not independent of quadrat size. It is derived from the gradient of the 'best fit' line, when different values of mean and variance are plotted for a population. It varies from 0 (regular distribution), through 1 (random distribution), through 2 (clumped distribution) to infinity showing very highly clumped populations. It provides a fairly constant value for species and therefore is useful for interspecific comparisons.
Lloyds indices (Lloyd 1967) convey two different types of information; the mean crowding index provides a measure of mean density per quadrat sample, however, it assumes that each quadrat must be as good a habitat for animals as any other, and is heavily dependant upon the abundance of animals. Furthermore when samples are taken a wide distance

	1983	1984	1985
b (Taylor Power Law)	1.80	1.72	1.92
Variance/Mean ratio (Coefficient of dispersion)	78.4	61.6	
Index of clumping (I) David & Moore 1974	77.4	60.6	
Lloyds indices:			
Mean crowding (m*)	130.7	112.7	
Patchiness (m*/m)	2.45	2.16	

Table 5. Measures of ant aggregation.

apart (as in this case), the biological concept of it ceases to be applicable, but overall comparisons are still valid (George 1974). The index of patchiness is independent of density and shares the same range of values (and interpretation) as Taylors coefficient b. Like b, both Lloyds indices vary with quadrat size.

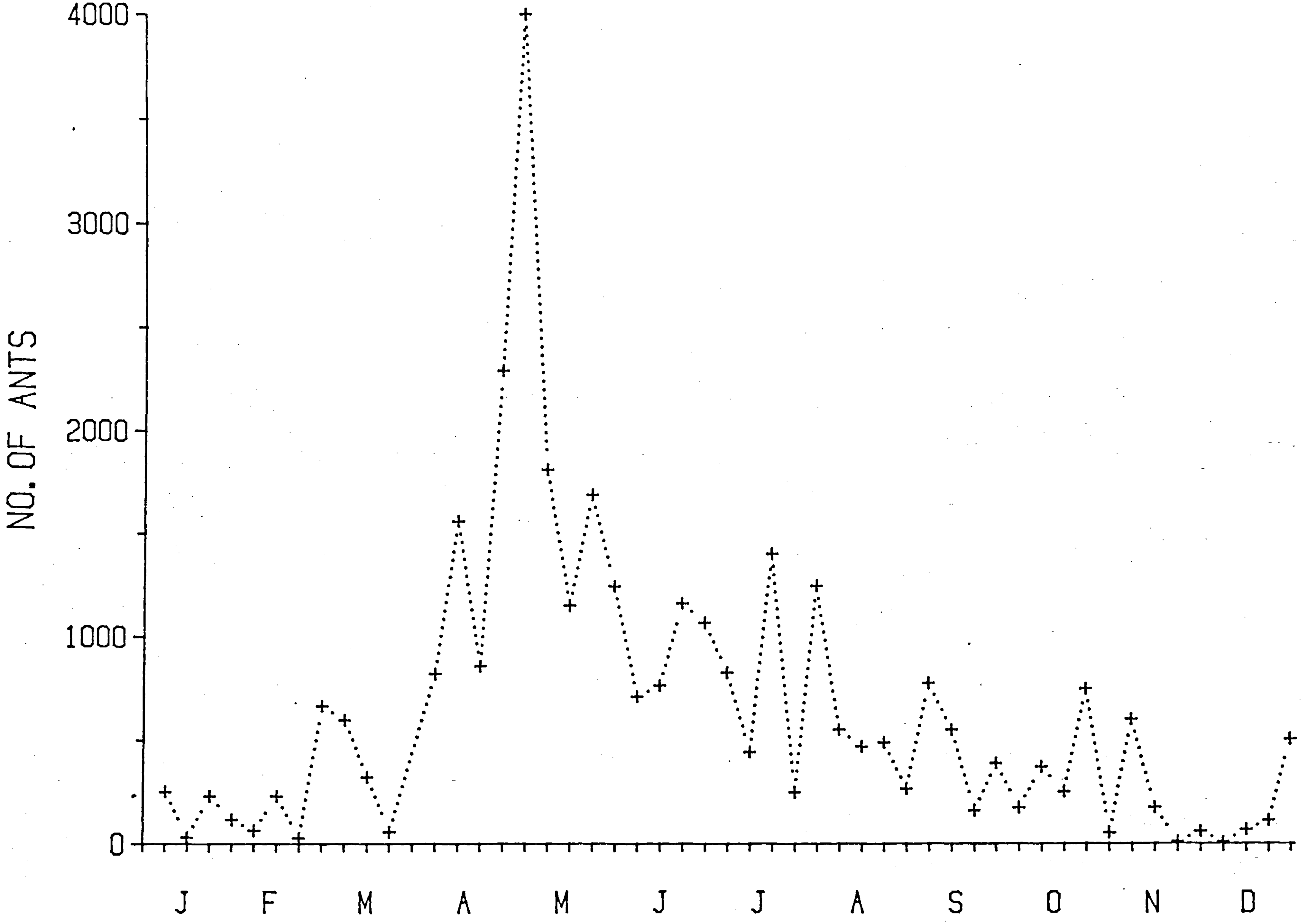
The coefficient of dispersion and the index of clumping show little more than that fewer ants were found in 1984 than 1983. Lloyds mean crowding index is no more valid, but gives values of the mean number found, and again shows that ants were more abundant in the 1983 site. Both Lloyds index of patchiness and Taylors coefficient b show a deviation from a random distribution. Lloyds index depicts it as a clumped distribution and Taylors index shows it approaching a clumped distribution. When the 95% confidence limits are considered, it shows that the values of b over successive years are not significantly different. A contagious distribution is to be expected from Lasius flavus, as it is known that the mound is honeycombed with chambers connected by very short galleries (Talbot 1965), hence the ants are most likely to be encountered in discrete clumps in chambers.

In subsequent chapters the only measure of clumping used is Taylors coefficient b. This is chosen because it is independent of the number of cores taken, as long as the core size remains constant. It is also a value which has extreme importance in transforming data, thus it has a relevance to the results which is more readily apparent than Lloyds index of patchiness.

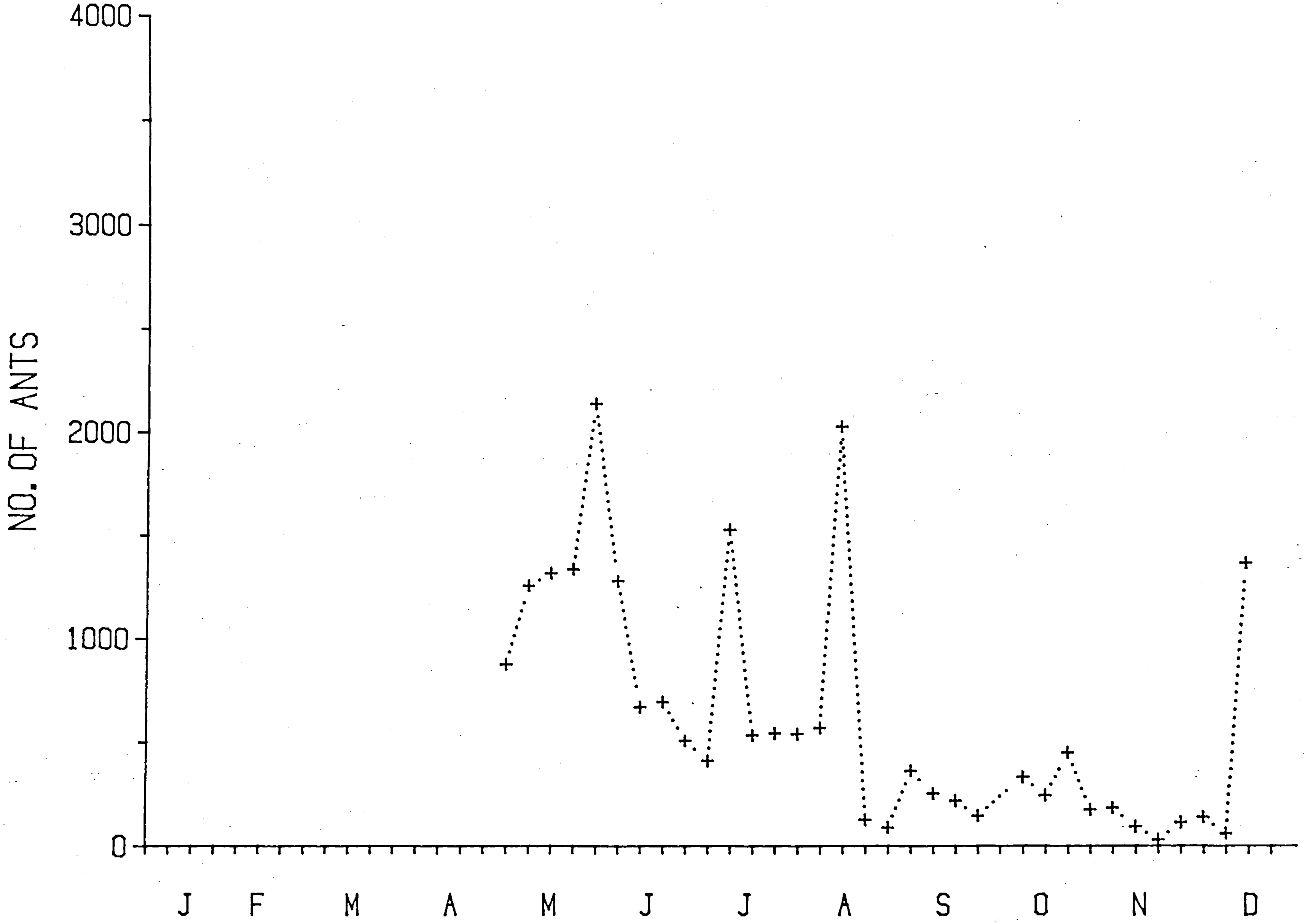
3.4 Seasonal fluctuation in ant numbers

The number of ants extracted from each nest varied over the year (see graphs 1-3). Captures were lowest in Winter, then began to rise in March. From April to May the number of ants steadily rose, reaching peak values in late May-June. The extreme peak in May 1983 was also due to large nest size (third largest nest sampled). Worker numbers then decline slightly until late July-early August, when there is a noticeable increase and then decline. From August-late October/November the number of captures was further reduced, and return to Winter levels in late November-December. On some days in December however, captures were high.

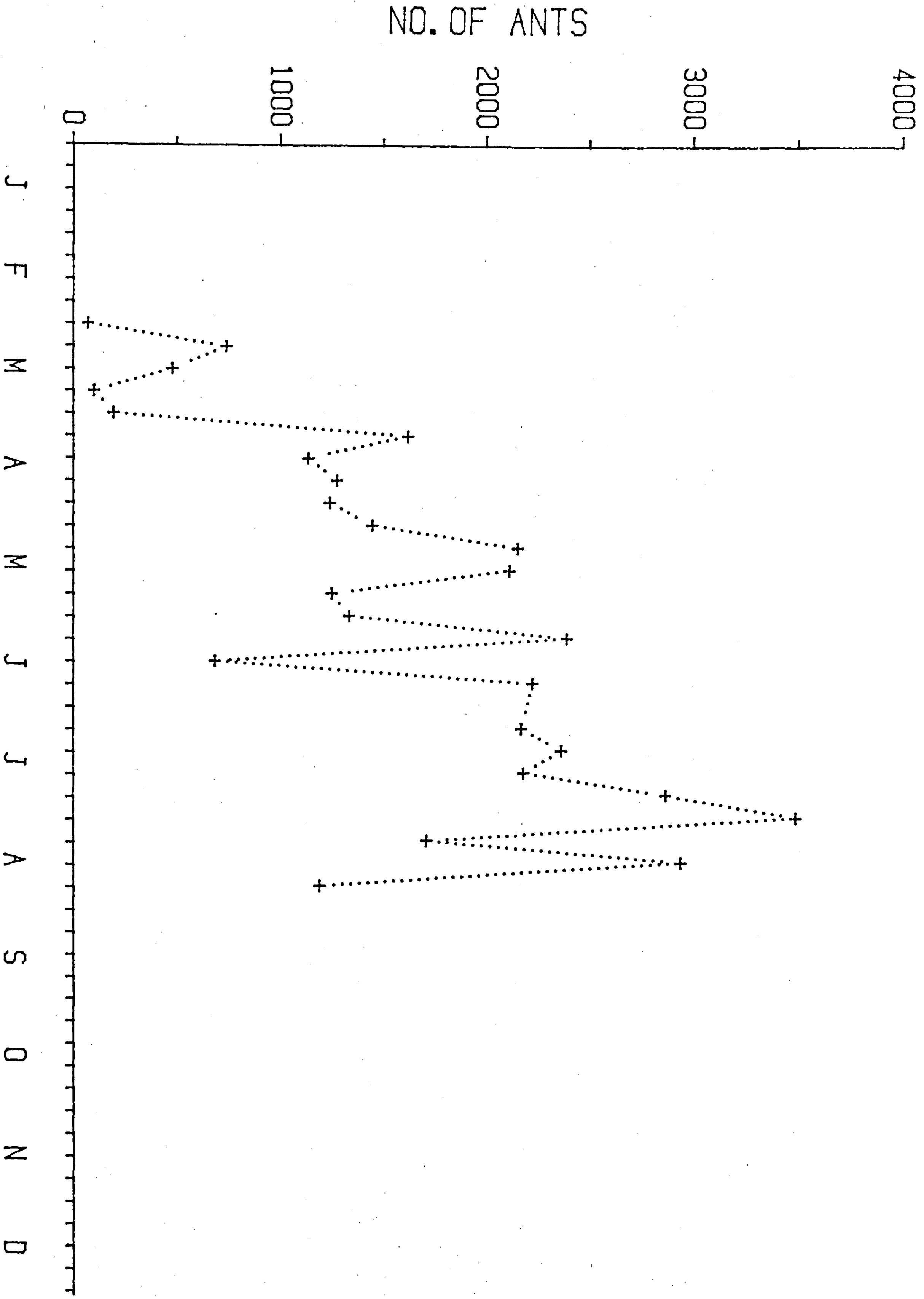
These patterns of worker abundance which are similar for all three years, are at odds with what is known about the biology of Lasius flavus. Although there is quite high mortality of worker ants over Winter, there is no subsequent emergence of new workers to increase ant numbers to the May levels. New workers do not emerge until late July to September, a feature which goes almost unmarked on the graphs (except for slightly higher numbers in September). The declines observed over June and July, and August-November might well be due to worker mortality. No data were available on the lifespan of Lasius flavus workers, but newly emerged workers in August-September (distinguished by their lighter colour) make up to a third of the total worker population suggesting at least a three year lifespan. Workers of Lasius niger have been kept in the laboratory for three years and Leptothorax workers for five years (A.J.Pontin personal communication) which supports this observation. _Lasius flavus_ queens may live up to 22 years (Prescott 1973).



Graph 1. The abundance of Lasius flavus workers over the year (1983).



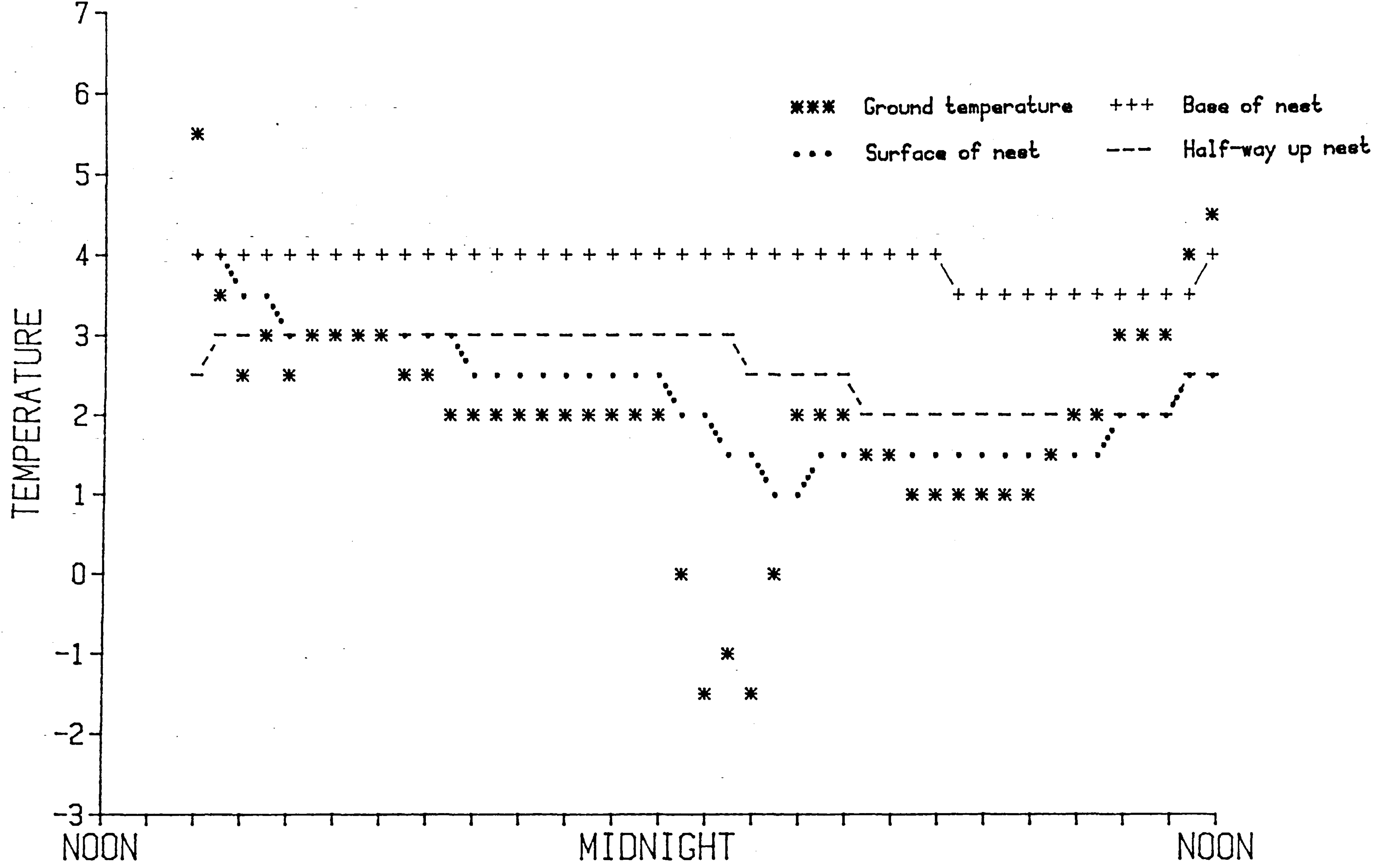
Graph 2. The abundance of *Lasius flavus* workers over the year (1984).



Graph 3. The abundance of *Lasius flavus* workers over the year (1985).

Worker abundance correlated with:	r	p
Temperature	0.29	N/S
Low temperature (1-10°C)	0.60	0.05
High temperature (23-35°C)	-0.80	0.01
Mid-range temperatures	0.08	N/S

Table 6. The correlation between worker abundance and various temperature ranges.



Graph 4. The temperature variation at different depths of an ant nest in early Winter (1984).

Two major factors are considered to influence the number of ants captured from a nest, namely temperature and brood. Temperature is of obvious importance to poikilothermic animals. The ant mound structure itself is designed to absorb solar radiation, and has been called "an incubator for ants' brood" (Donisthorpe 1927). Once the ant mound has been heated up, then due to lack of external openings and large volume (including insulating air pockets), it retains warmth much longer than the surrounding soil. When ground temperature is correlated with ant numbers (see table 6), at low temperatures (range 0-10^{o}C) there is a slight positive relationship between temperature and ant numbers ($p<0.05$). Thus low temperatures can explain the trends found in January-March. At this time of year the ants are concentrated near the bottom of the nest mound and therefore out of range of the core samples. The benefit of this location becomes clearer when one considers the continuous temperature recordings taken in mid-December 1984 (see graph 4). At this time of year, the maximum surface temperature of the ant mound was always lower than the maximum ground temperature (whereas in Summer the surface of the ant mound may rise up to 6^{o}C above the ground temperature). By early afternoon the temperature on top of the mound rises to within a degree of the temperature of the surrounding grass. As the ground temperature drops, the temperature of the nest mound declines more slowly, reaching its lowest level just before dawn. With sunrise, the temperature on top of the nest mound is at approximately the same level as the ground temperature, but whereas the ground temperature had usually fallen below 0^{o}C, the temperature on top of the ant nest was always one or two degrees above this. The temperatures recorded from mid-way up the ant mound reflect the same trends, but here the temperatures rose and fell more slowly, lagging behind the surface of the mound. These 'mid-way' temperatures seldom rose as high as those on the surface and usually kept 3-4°C above the coldest ground temperatures. The temperatures at the base of the mound lagged even further behind the rise and fall of the ground temperatures and at this time of year showed a constant 4-4.5°C, which was 6°C above the coldest ground temperatures. These temperatures were recorded from the onset of Winter, and it is suggested that during days of permanent frost (as experienced that Winter) the ants would be located in the centre of the nest mound, probably even below ground level.

At very high ground temperatures (in excess of 23°C), there is a negative correlation between the number of ants found and the increasing temperature ($p<0.01$). This suggests that as the temperature of the nest mound reaches a certain threshold, the ants begin to move (with the brood) to cooler, lower regions of the mound. During the field observations taken in July and August 1985 (see appendix B1), numbers of ants started to decline at a temperature of 27-28°C, and by 30°C very few L.flavus were found at the surface of the nest. It was also recorded that workers of Lasius niger were still abundant at the surface at these temperatures, and numbers only noticeably started to decline when the temperature reached 34°C. These changes in vertical distribution are thought to account for the low number of ants found in some nest in July and August. However, at this time of year the upper layers of the nest mounds also become much drier, and humidity may be an equally important factor. This would partially explain the difference in threshold temperatures between L.flavus and L.niger; L.niger frequently forages above ground and would therefore be expected to be more tolerant of lower relative humidity than L.flavus, which only comes above ground during nest building after periods of rain and during the nuptial flight.

In May 1985 an experiment was conducted to see whether temperature or humidity was the most important factor. High temperature was induced in a nest at a time of year when humidity was also high (see section 2.3, appendix B2). After using a number of non-parametric statistical tests, no significant difference was found between the irradiated and non-irradiated nests. This implies that the vertical migration of ants observed at high temperatures is not due to temperature itself, but its effect on reducing humidity below a certain level.

The majority of ground temperatures recorded in 1983 fall in the temperature range 11-22^{o}C. No significant correlation exists between this range of temperatures and ant numbers, therefore once the nest mound has warmed up to a certain level, ants are abundant in the top 10cm of the nest. Peakin (1960) in considering the reaction of Lasius flavus to humidity levels, divided temperature up into four classes and recorded the L.flavus response:

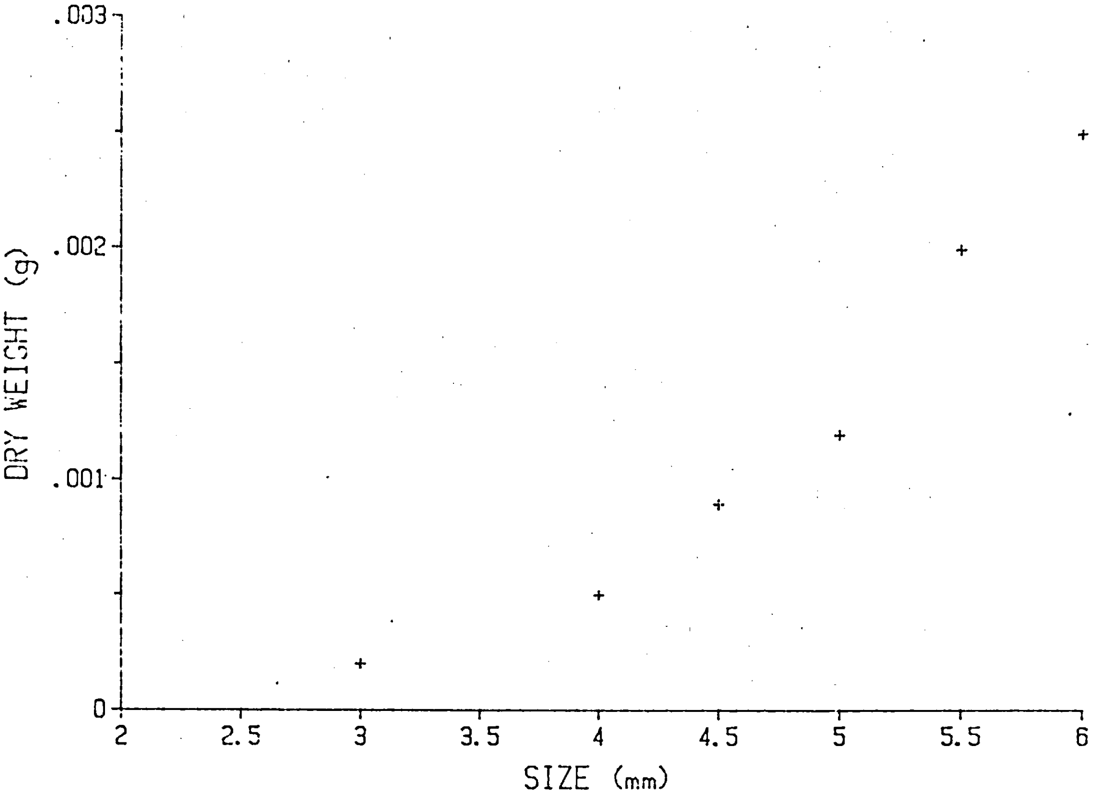
5-8^{o}C; slow, low activity
11-23.5^{o}C; hygropositive responses
27-28^{o}C; variable responses
33.5-35^{o}C; hygropositive responses, tend to descend

to lower regions of the nest.
This agrees well with my observations and emphasises the effect of humidity.

This leaves the higher number of ants found April to early June unexplained. The state of the brood is considered to be the other major factor influencing ant captures. To correlate the number of larvae against ant numbers would be misleading as the size of larvae varies, and the pupae may require far less attention. Therefore all brood numbers were reduced to dry weight. The graph of dry weight against larval size (see graph 5) shows an almost exponential weight increase with size, i.e. most weight is gained in the final instar in common with other insect larvae. Larvae longer than 6.0mm were found, queen larvae ranged up to 7.2mm (further observations on the development of larval brood are included in appendix B3). Large larvae thus cause a greater strain on nest resources in the form of food and ant labour, than either smaller larvae or pupae, and it is suggested that the larger the weight of dry larval brood, the more ants that are found. Indeed the largest number of ants were found with high brood biomass, and a significant correlation between these was found in all three years (see table 7). Pupae were excluded from the biomass totals, thereby giving a measure of 'active' biomass; that biomass of brood that draws upon the resources of the nest.

The brood containing alate sexuals and worker larvae were considered separately on the grounds that these would have had a quantitatively different effect on the nest resources. Also at this time year, high temperatures/low humidity interfered with the number of ants found at the surface of the nest. Despite this, again in 1984 and 1985 a significant correlation was found between the number of ants and the active biomass of the brood. The 1983 results do not show this correlation as clearly, differences being attributed to the length of time the alates remained in the nest. The shorter the time period the less noticeable the drain upon nest resources; also the fewer observations led to higher experimental error.

Therefore the increase in ant numbers in April-June is related to the maturation of the ant larvae, and the reduction of ant captures in June is related to the smaller larval biomass as more pupate. The slight increase in worker numbers is related to the



Graph 5. The rate of increase in dry weight with size of ant larvae.

Worker abundance correlated with:	Spearmans RHO	p	Kendalls Tau	p
Larvae (1983)	0.78	0.001	0.64	0.001
Larvae (1984)	0.56	0.075	0.46	0.05
Larvae (1985)	0.59	0.05	0.54	0.01
Alates (+ remaining worker larvae),(1983)	0.32	N/S	0.21	N/S
Alates etc (1984)	0.89	0.001	0.72	0.001
Alates etc (1985)	0.75	0.05	0.52	0.05

Table 7. The correlation between worker abundance and larval and alate biomass.

hatch of alates, and the subsequent drop in ant captures is linked with the alates leaving the nest and high temperatures. In September there is a slight increase in worker numbers due to the hatch of the new worker brood. From October-November, the brood is very small, and the temperature declining until the frosts start in late November. Ants with brood then retire to the deeper parts of the nest where they are less accessible, except for warmer spells when they briefly return to the surface of the nest. From the above trends it is clear that the samples which have been taken from the ant nests do not give a realistic estimate of numbers of ants in a colony. By sampling just the top 10cm of the ant nest, what has been recorded is some measure of ant activity, and from this viewpoint the association between ant numbers, temperature and brood becomes more meaningful.

Based upon these main factors of temperature and brood development, the year can be split up into seven biologically meaningful sections (see table 8); and therefore the differences between sections can be quantified, as well as the differences between years (see table 9). Non parametric tests (U-tests) were used throughout 1983 and 1985 due to the difficulties in transforming the ant data (see appendix B4). In 1983 there is a significant increase in ant activity from February to March ($p<0.01$), and a further increase from April to May ($p<0.001$). Once the workers have reached high ant activity tending the large larval brood, there is no further marked change in ant activity until the temperature starts to fall in Autumn, implying that the June decline is an artifact of sampling. From the time of the nuptial flight to mid-October, there is a mixture of high temperature and lower Autumn temperatures, which results in a decline in ant activity ($p<0.05$). From mid-October to the onset of Winter there

Section	Dates 1983	1984	Characterized by
I	12/1-22/2		Low temperature
II	1/3-20/4		Low temperature and small to medium sized larvae
III	29/4-22/6	28/4-6/6	Large larvae (high brood biomass)
IV	30/6-22/7	15/6-8/8	Pupae and alates present (includes nuptial flight)
V	29/7-17/8	15/8-29/8	High temperature, last few alates in nest
VI	24/8-19/10	5/9-17/10	Temperature falls to Autumn levels
VII	26/10-29/12	24/10-12/12	Low temperature, frosts begin

Table 8. The biologically different sections of the year.

Section	1983		1984	
	d value	Probability	t-test	Probability
I				
	2.40	0.01		
II				
	3.80	0.001		
III				
	0.002	N/S	1.49	N/S
IV				
	0.90	N/S	3.88	0.001
V				
	2.09	0.05	1.22	N/S
VI				
	4.26	0.001	1.92	0.1
VII				

Table 9. Differences between the sections of the year (1983 and 1984 results).

Section	Comparison of 1983 and 1984 ant abundance	
	t-test	Probability
I		
II		
III	0.92	N/S
IV	2.48	0.05
V	5.06	0.001
VI	3.23	0.01
VII	0.16	N/S

Table 10. Comparison of ant abundance between the years 1983 and 1984.

is a further decline in ant numbers ($p<0.001$).

In 1984 sampling did not start until the ants had reached high activity. Once again there is no significant decline in activity in June. After the nuptial flight there is a significant drop in ant numbers, due to successive high temperatures ($p<0.001$). From this level there is no further change in ant activity in Autumn and only a hint of a decline from the Autumn to Winter levels ($p<0.1$).

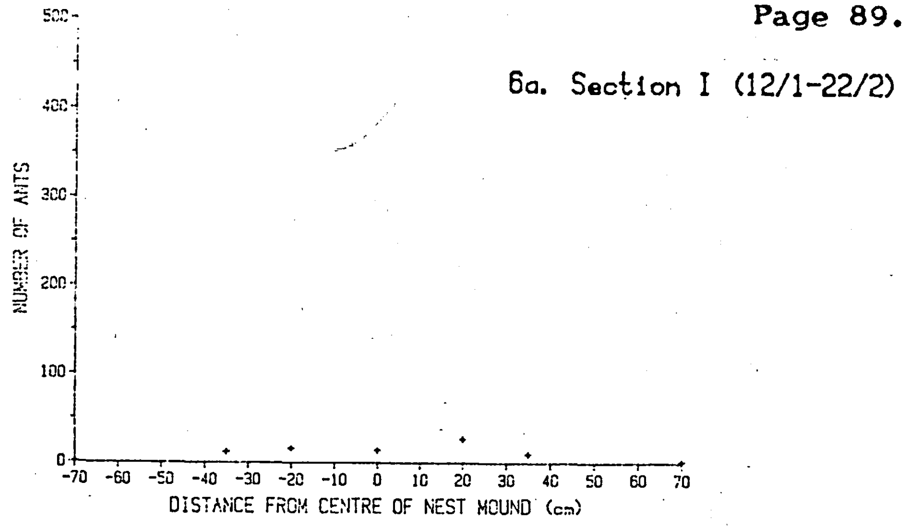
In 1985 sampling started towards the end of Winter. Because of a warm spell in early Spring, ant activity rose quickly and there is no difference in ant numbers between early Spring and late Spring, through to early Summer levels when the larval biomass was largest. As with the other years there is no June decline in numbers and no significant difference in ant activity from the time of large larval biomass until the nuptial flight.

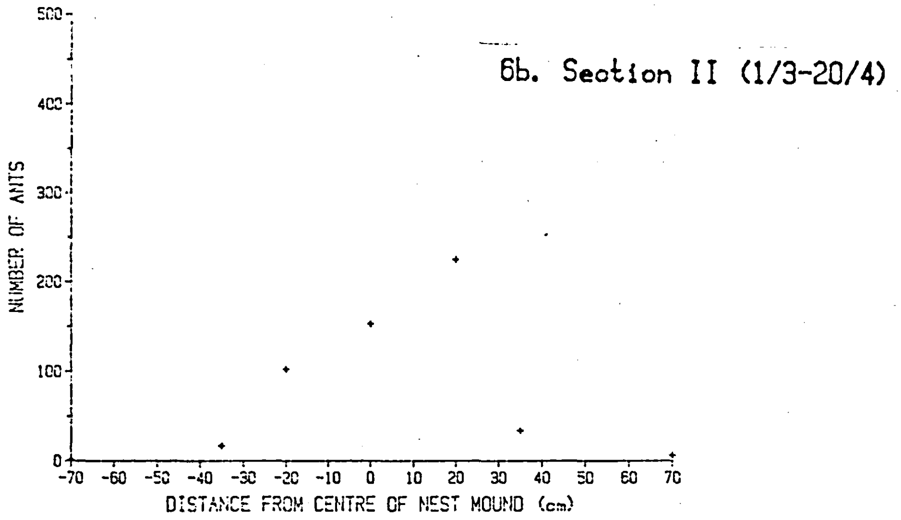
Comparing the sections between 1983 and 1984 (see table 10), it becomes clear that there is more ant activity from the 1983 site. At times when there is high moisture content in the soil i.e. April-June and October-December, there is no significant difference between years, but during high Summer when the ant mound is drying out there is a significant difference between the number of ants. This is not surprising on two counts; 1984 was a much dryer year than 1983, also the 1983 site was on slightly lower lying land and surrounded by much damper areas. This again emphasises the importance of humidity.

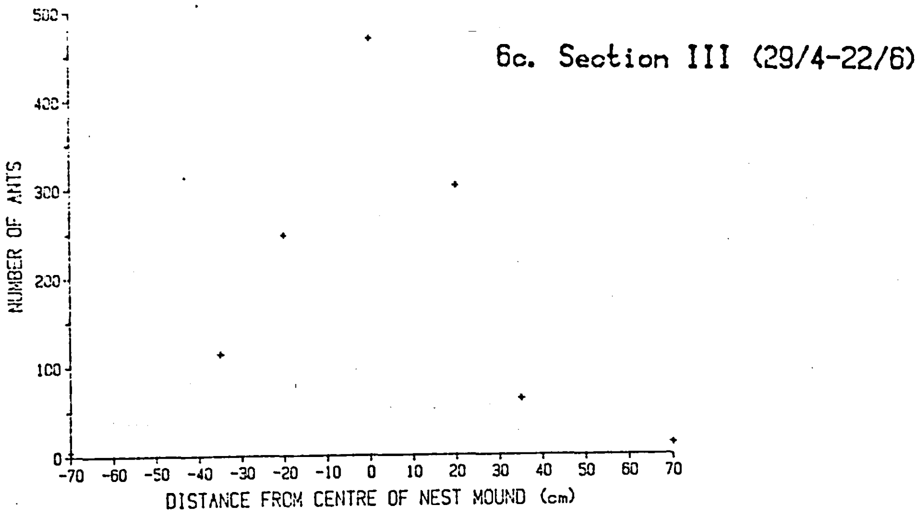
In addition to varying with season, ant activity may also vary with location in the nest. It has been stated that on average over the year, ant numbers are distributed equally between 0 and 20cm samples, with less ants at 35cm, and even fewer at 70cm. East-West profiles of ant numbers were drawn to show any variations in ant activity with location (see graph 6a-g). Each diagram represents mean values for each of the seven sections of the year. Significance tests were then carried out between locations and between sections (see tables 11-14).

Generally worker distribution over the nest territory is concentrated in the nest mound, moreso in the centre and conforms to the pattern 0=20>35>70*. No difference can be found between the number of workers in the centre and at 20cm from the centre of the nest throughout the year. This pattern breaks down during the Winter (sections I and VII), when equally few ants are extracted from all areas of the nest mound, due to the majority being below the level of sampling, and in the period from alate hatch to the nuptial flight (section IV), (but not in 1984).

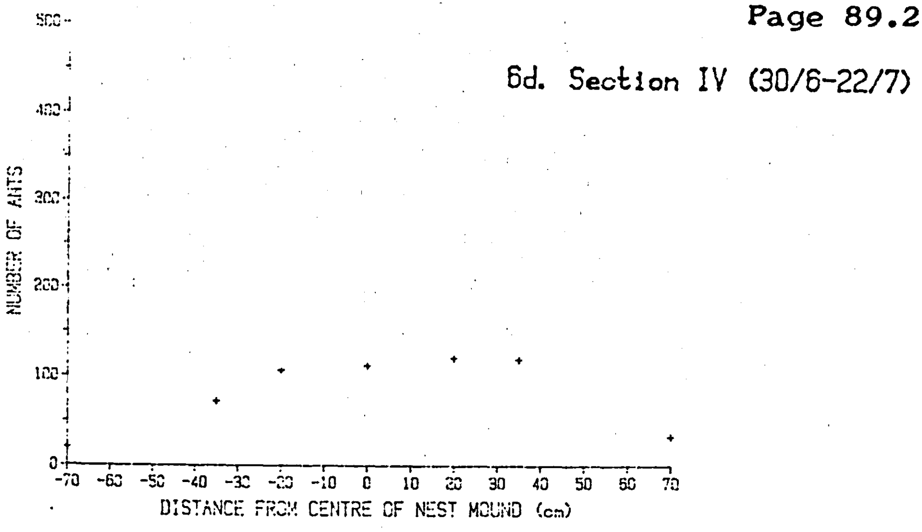
*0=20>35>70 is an abbreviation to represent the relative abundance of worker ants at set distances (in cm) from the centre of the nest mound.

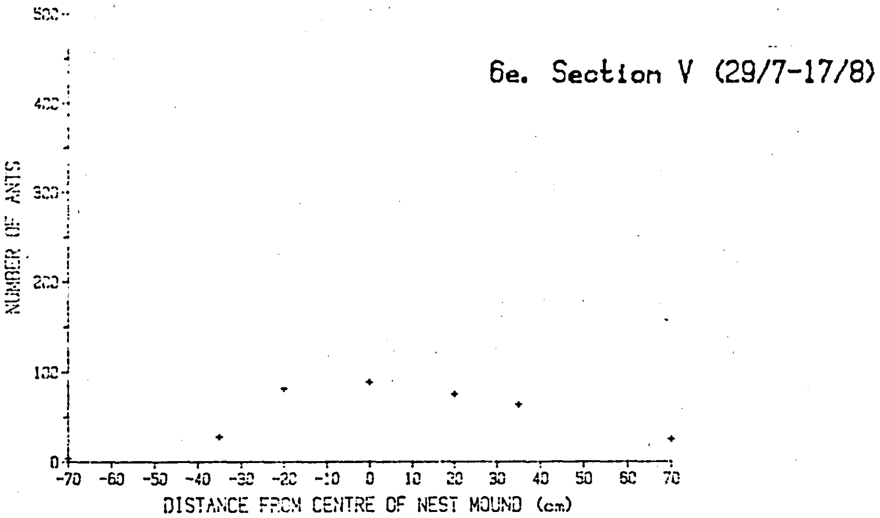

6a. Section I (12/1-22/2)

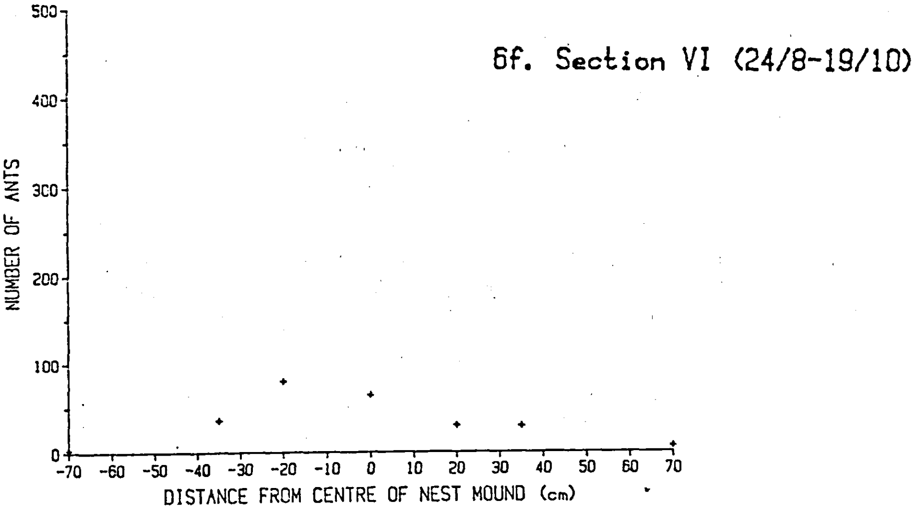

6b. Section II (1/3-20/4)


6c. Section III (29/4-22/6)

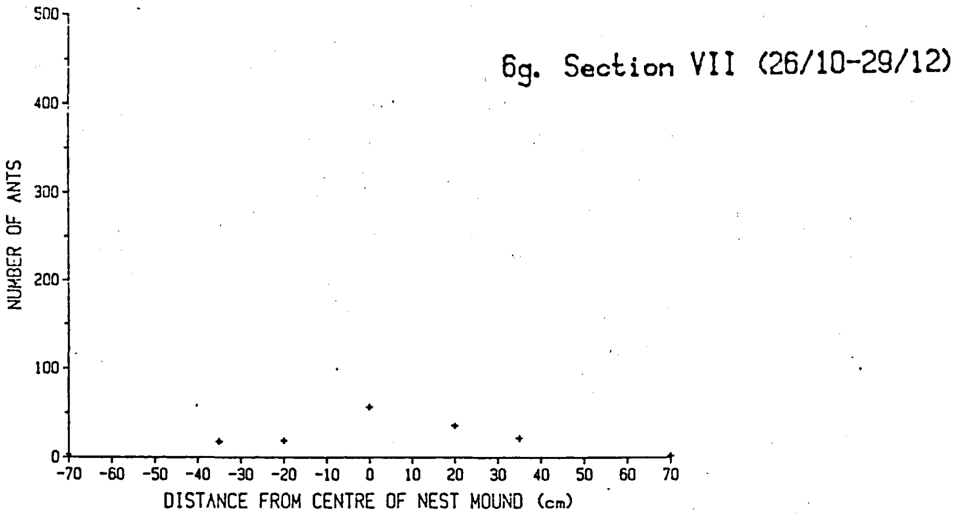
Graph 6. Nest profiles during the seven sections of the year, 1983 results.


6d. Section IV (30/6-22/7)


6e. Section V (29/7-17/8)


6f. Section VI (24/8-19/10)

Graph 6. Nest profiles during the seven sections of the year, 1983 results.



6g. Section VII (26/10-29/12)

Graph 6. Nest profiles during the seven sections of the year, 1983 results.

Section of year	Difference between nest locations						Conclusion
	0-20		20-35		35-70		
	t-test	p	t-test	p	t-test	p	
I	0.40	N/S	1.24	N/S	3.65	0.001	0=20=35>70
II	0.37	N/S	2.74	0.05	5.47	0.001	0=20>35>70
III	1.57	N/S	4.30	0.001	5.27	0.001	0=20>35>70
IV	0.20	N/S	1.53	N/S	3.69	0.01	0=20=35>70
V	0.31	N/S	2.30	0.05	3.15	0.01	0=20>35>70
VI	0.25	N/S	2.46	0.05	6.21	0.001	0=20>35>70
VII	0.30	N/S	1.01	N/S	5.02	0.001	0=20=35>70

Table 11. The variation of worker distribution in the nest over the year 1983.

Comparison of sections:	Nest locations (cm from nest centre) 0		20		35		70	
	t-test	p	t-test	p	t-test	p	t-test	p
I-II	2.75	0.05	2.39	0.05	1.40	N/S	0.43	N/S
Conclusion	0 > 0		20 > 20		35 = 35		70 = 70	
II-III	2.32	0.05	1.90	N/S	2.43	0.05	2.44	0.05
Conclusion	0 > 0		20 = 20		35 > 35		70 > 70	
III-IV	6.51	0.001	2.78	0.05	1.82	N/S	2.41	0.05
Conclusion	0 < 0		20 < 20		35 = 35		70 > 70	
IV-V	0.44	N/S	0.84	N/S	2.55	0.05	0.38	N/S
Conclusion	0 = 0		20 = 20		35 < 35		70 = 70	
V-VI	0.49	N/S	1.79	N/S	1.36	N/S	2.06	0.05
Conclusion	0 = 0		20 = 20		35 = 35		70 < 70	
VI-VII	1.41	N/S	3.62	0.01	3.42	0.01	2.92	0.01
Conclusion	0 = 0		20 < 20		35 < 35		70 < 70	

Table 12. The variation in ant activity at different nest locations over the year (1983).

Section of year	Difference between nest locations						Conclusion
	0-20		20-35		35-70		
	t-test	p	t-test	p	t-test	p	
III	1.44	N/S	3.14	0.01	9.09	0.001	0=20>35>70
IV	0.40	N/S	3.07	0.01	8.51	0.001	0=20>35>70
V	1.11	N/S	0.04	N/S	3.07	0.01	0=20=35>70
VI	0.43	N/S	0.19	N/S	8.08	0.001	0=20=35>70
VII	0.78	N/S	2.06	0.05	4.92	0.001	0=20>35>70

Table 13. The variation of worker distribution in the nest over the year 1984.

Comparison of sections:	Nest locations (cm from nest centre)							
	0		20		35		70	
	t-test	p	t-test	p	t-test	p	t-test	p
III-IV	2.28	0.05	1.54	N/S	2.37	0.05	0.66	N/S
Conclusion	0 < 0		20 = 20		35 < 35		70 = 70	
IV-V	1.54	N/S	3.20	0.01	3.01	0.01	1.78	N/S
Conclusion	0 = 0		20 < 20		35 < 35		70 = 70	
V-VI	0.02	N/S	1.22	N/S	1.68	N/S	0.15	N/S
Conclusion	0 = 0		20 = 20		35 = 35		70 = 70	
VI-VII	0.04	N/S	0.39	N/S	2.50	0.05	0.11	N/S
Conclusion	0 = 0		20 = 20		35 < 35		70 = 70	

Table 14. The variation in ant activity at different nest locations over the year (1984).

When the differences in ant activity between sections are considered more closely (table 12), it is seen that as the nest temperature rises, activity first increases in the nest mound. As the larvae mature, activity rises throughout all areas of the nest territory, indicating increased foraging and brood care. When alates are present in the nest, there is a further increased abundance in the outlying territories, but far fewer workers are found in the nest mound, and it is this which accounts for the observed distribution. The number of worker captures from the nest mound is comparable to the level prior to large brood biomass, which implies that adult alates require less attention than larvae. Space may also become limiting for workers (and other soil organisms) at this time of year, owing to the large number of alates in the nest mound. Even the larvae are moved from central nest positions to chambers near the edge of the nest mound, emphasising the lack of space and possible predation of larvae by new queens. After the nuptial flight worker activity remains about the same levels during Autumn temperatures, with slight reductions at 35 and 70 cm. When the frosts start and Winter temperatures return, less ants are found in all parts of the nest, significantly so at 20, 35 and 70cm from the centre of the nest mound, indicating that the centre of the nest mound is the last area of the nest to cool.

In 1984 sampling began when the nests already contained high larval biomass, hence ant activity was high, and the pattern of ant distribution was 0=20>35>70. Ant numbers again dropped in the nest mound, with the lack of brood and alate emergence, but not enough to change the overall distribution pattern. Activity levels in the outlying territory were unchanged. In the three weeks immediately after the nuptial flight worker abundance in the nest mound dropped further, but this may be meaningless due to the limited number of results. Ant abundance then stabilized during Autumn temperatures, dropping first at 70cm (although not statistically marked), and then at 35cm. Samples were not collected so late into the Winter and as a result there is no further drop in ant activity, and the final distribution is 0=20>35>70.

The distribution of ants at different locations in the ant nest does indeed vary. In all cases more ants are found in the nest mound than in the outlying territory. But at low temperatures when the ants are almost out of sampling range, there is no significant difference between the number of ants sampled from different places in the nest mound. As ant activity increases, the standard pattern of distribution resumes, but during the period from pupation until after the nuptial flight, less ants are found near the centre of the nest mound, and far more are found in the nest territory indicating a greater degree of foraging. This declines as the Winter temperatures begin. The variation in ant captures at the various distances from the centre of the nest mound over the year is summarized in graph 6. Determining the varying distribution of ants in the nest is important in assessing the total ant population in a colony, and equally important in understanding the relative abundance of aphids (see chapter 4).

3.5 Estimates of ant colony size

Various factors have to be taken into consideration; temperature, state of brood, nest size and ant distribution patterns. Therefore estimates of colony size were restricted to results gathered from May-August showing mid-range ground temperatures. The nest territory was judged to extend in a circle (70cm radius) from the centre of the nest mound, based on the inferences of Pontin (1961,1978). Thus the colony size was calculated by using the observed density at each distance from the nest centre in a series of concentric rings.

$$\text{Total per colony} = \pi(70^2) \times \frac{\bar{x}\text{ of 70cm ants}}{78.5} - \text{nest mound base surface area} \times \frac{\bar{x}\text{ of 70cm ants}}{78.5}$$

$$+ \text{nest mound base surface area} \times \frac{\bar{x}\text{ of 35cm ants}}{78.5} - \pi(35^2) \times \underline{\bar{x}\text{ of 35cm ants}}$$

$$+ \frac{\pi(35^2) \times \bar{x}\text{ of (35 + 20cm) ants}}{78.5}$$

$$- \frac{\pi(20^2) \times \bar{x}\text{ of (35 + 20cm) ants}}{78.5}$$

$$+ \frac{\pi(20^2) \times \bar{x}\text{ of (0 + 20cm) ants}}{78.5}$$

The value of 78.5 is the volume (in cc) of soil taken per sample. This calculation is extended for the 1985 results where the samples were taken at more nest locations.

In 1983 the results gave a mean value of 17454 +/- 7255 (95% confidence limits) ants per nest, which is comparable to Pontins estimate (1978) for a circular territory, of 18,500 +/- 7000 ants, both sets of results being gathered from the same area of Staines Moor. The estimate for the 1984/5 site is 15,854 +/- 10285 ants, lower than 1983, but not significantly so. These values are thought to heavily underestimate the true total, as only the top 10cm of the nest mound was counted, which only accounts for half of the mound volume.

Source	L.flavus per sq.m.	% L.flavus in nest mound	Nest counts maximum	Nest counts mean
Pickles (1940)	13		6000	
Odum & Pontin (1961)	1130		11100	6600
Waloff & Blackith (1962)	5210		24500	
Pontin (1969)			14400	10200
Nielsen (1976)	7290	92.6	100000	22100
Pontin (1978)	3700	66.7		18500
J.L. (1983)	5560*	79.4	45000	17500
J.L. (1985)	5050*	82.2	27700	15900

* Assuming same nest territory as Nielsen

Table 15. Comparison of colony size estimates for Lasius flavus.

Population estimates of Lasius flavus nests from other workers are given in Table 15. There is general agreement on the density of L.flavus with the exception of Odum and Pontin who sampled young nests, and Pickles. In the estimates of the proportion of L.flavus in the nest mound, all authors noted and assessed the reduction in numbers of workers away from the mound. My results for 1985 sampled this feature more thoroughly and thus probably provide a more accurate figure. The reasons for these discrepancies are manifold, the largest factors including different sampling techniques, habitat age and soil type. There is also variation in calculating territory size, my results follow the assessment of Nielsen.

Nielsen et al (1976) also proposed a model relating ant numbers to the colony size:

Total colony size = 609 x mound volume + 303

Despite the poor accuracy of my colony estimates, the larger ant colonies in 1985 do fit this line. Therefore this model seems to be valid and the larger ant counts do provide fairly accurate estimates of ant colony size.

3.6 Conclusion

(i) Colonies on Staines moor have reached a stable density.

(ii) Nest mounds were approximately circular with no overall North-South or East-West bias, although more ants were found in the South east sector than in any other area of the nest territory.

(iii) The pattern of *L.flavus* distribution throughout the territory is heavily influenced by the position of the mound. Ants are of similar abundance in the middle of the nest mound, fewer near the edge of the nest mound and even fewer in the surrounding territory.

(iv) *Lasius flavus* had a consistently clumped distribution over the years.

(v) The number of ants extracted gives some measure of ant activity, not population size. Two factors heavily influence this, namely temperature and the biomass of the brood.

(vi) The abundance of ants at the locations outlined in (iii) is modified by temperature and brood. High abundance in the outlying territory indicates increased foraging.

(vii) Mean colony size was estimated at 17500 +/- 7300.

CHAPTER FOUR

THE SEASONAL ABUNDANCE OF APHIDS AND COCCIDS

4.1 Introduction

One of the most interesting features of *Lasius flavus* mounds is the variety of species of subterranean aphids that live together. Moreover the majority of these aphids feed on the same range of grass roots (*Dactylis*, *Agrostis*, *Holcus*, *Festuca*, *Poa*, *Alopecurus*), with the exception of *Trama troglodytes*, which feeds on Compositae. That these aphids do coexist suggests that they are not complete competitors, therefore species were analysed to determine the differences in lifestyle between them. Muir (1959) discovered that some aphids seem to prefer certain grasses (see chapter 1.2) Pontin (1963) observed subterranean aphids feeding on different parts of the plant. My analysis includes measures of clumping and clump size; spatial distribution in the ant nest with consideration of the degree of association between species; and differences in temporal abundance between species, with further measures of interspecific association.

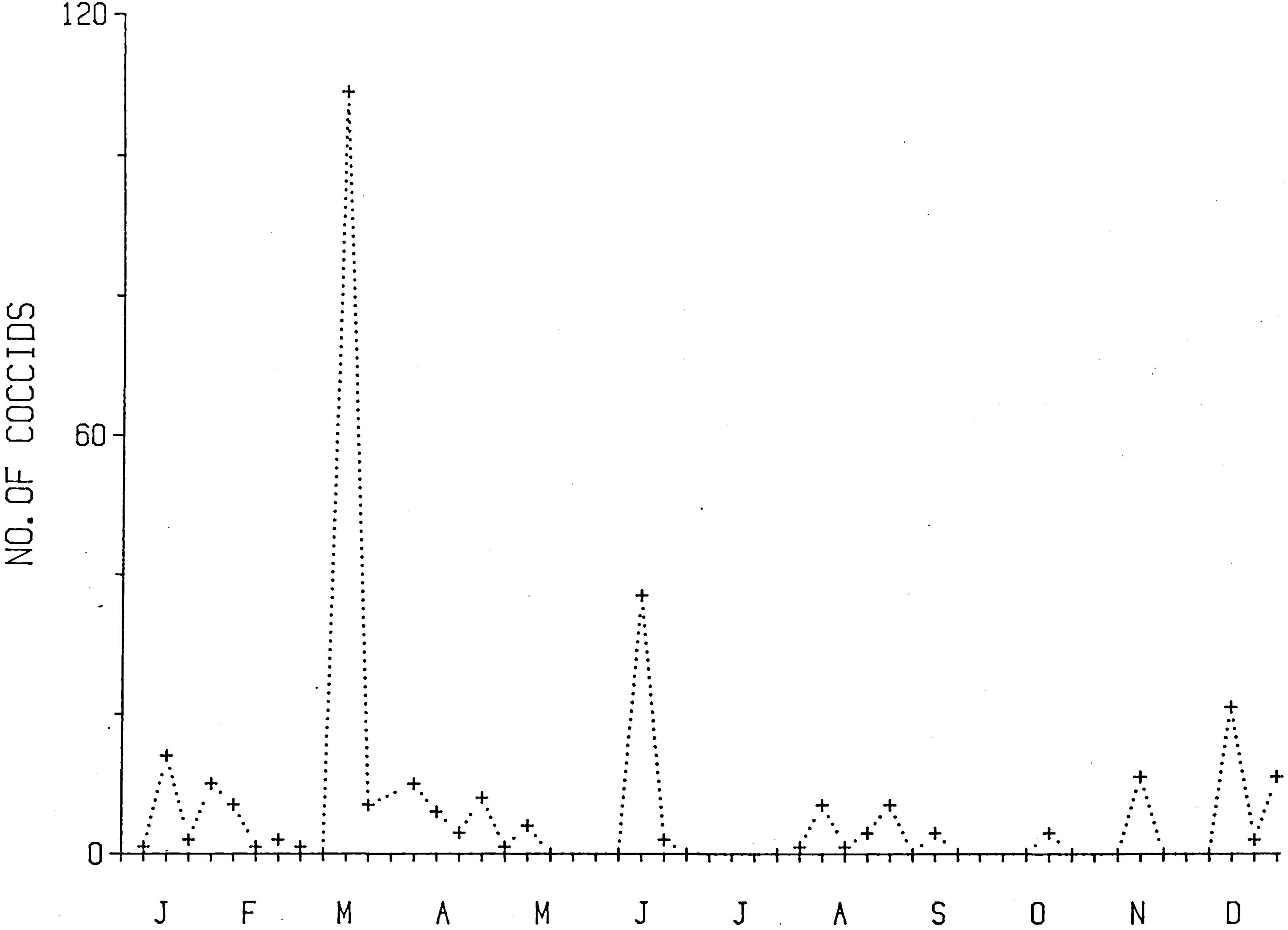
4.2 The seasonal fluctuation in the abundance of trophobionts

Coccids.

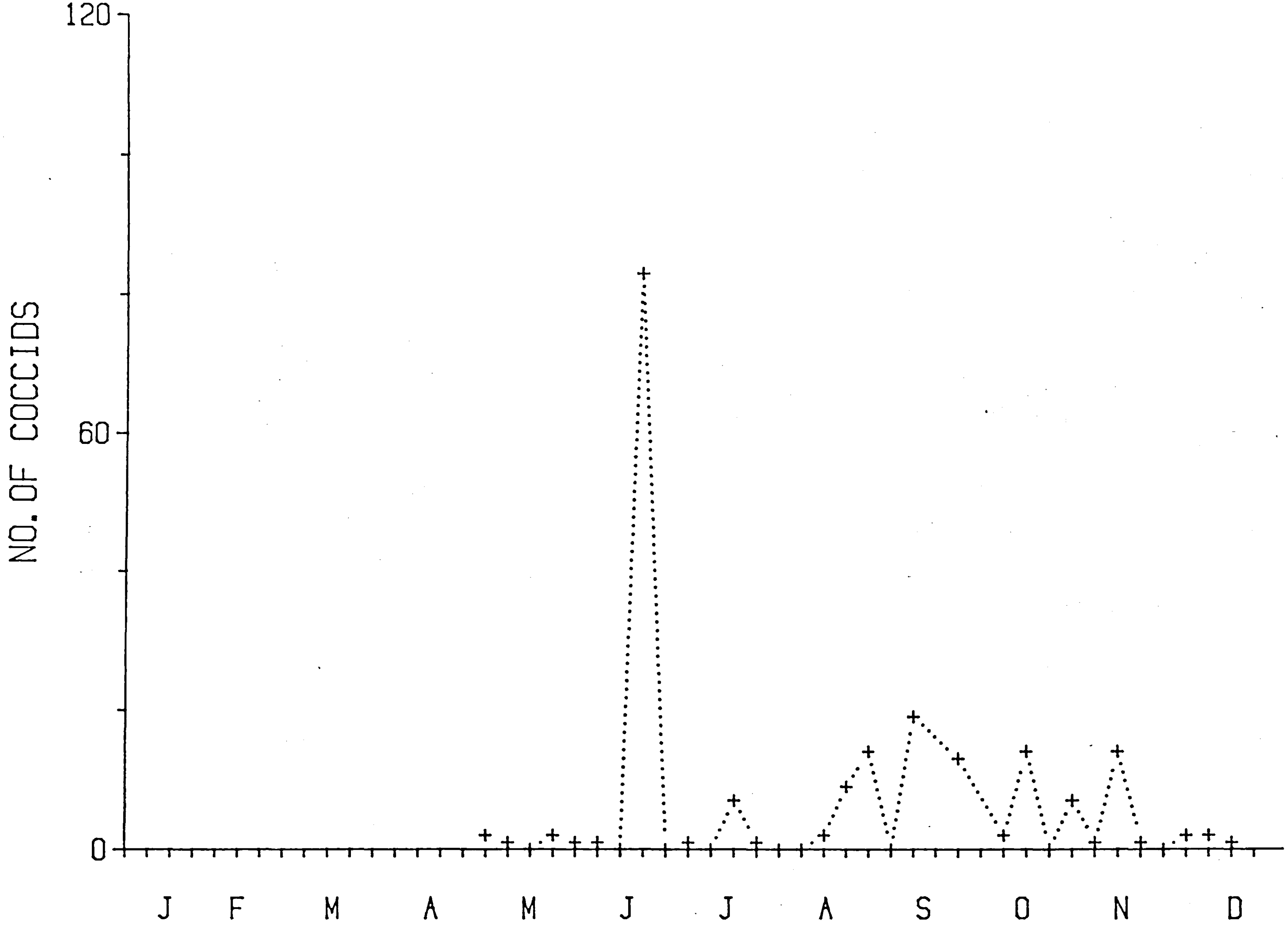
Low numbers of coccids are found throughout the year (see Graphs 7-9). The high peaks found in these graphs occur when adult coccids (usually only one) are surrounded by large numbers of first instar larvae. From the graphs it appears that the main breeding periods are early Spring and early to mid Summer.

Aphids.

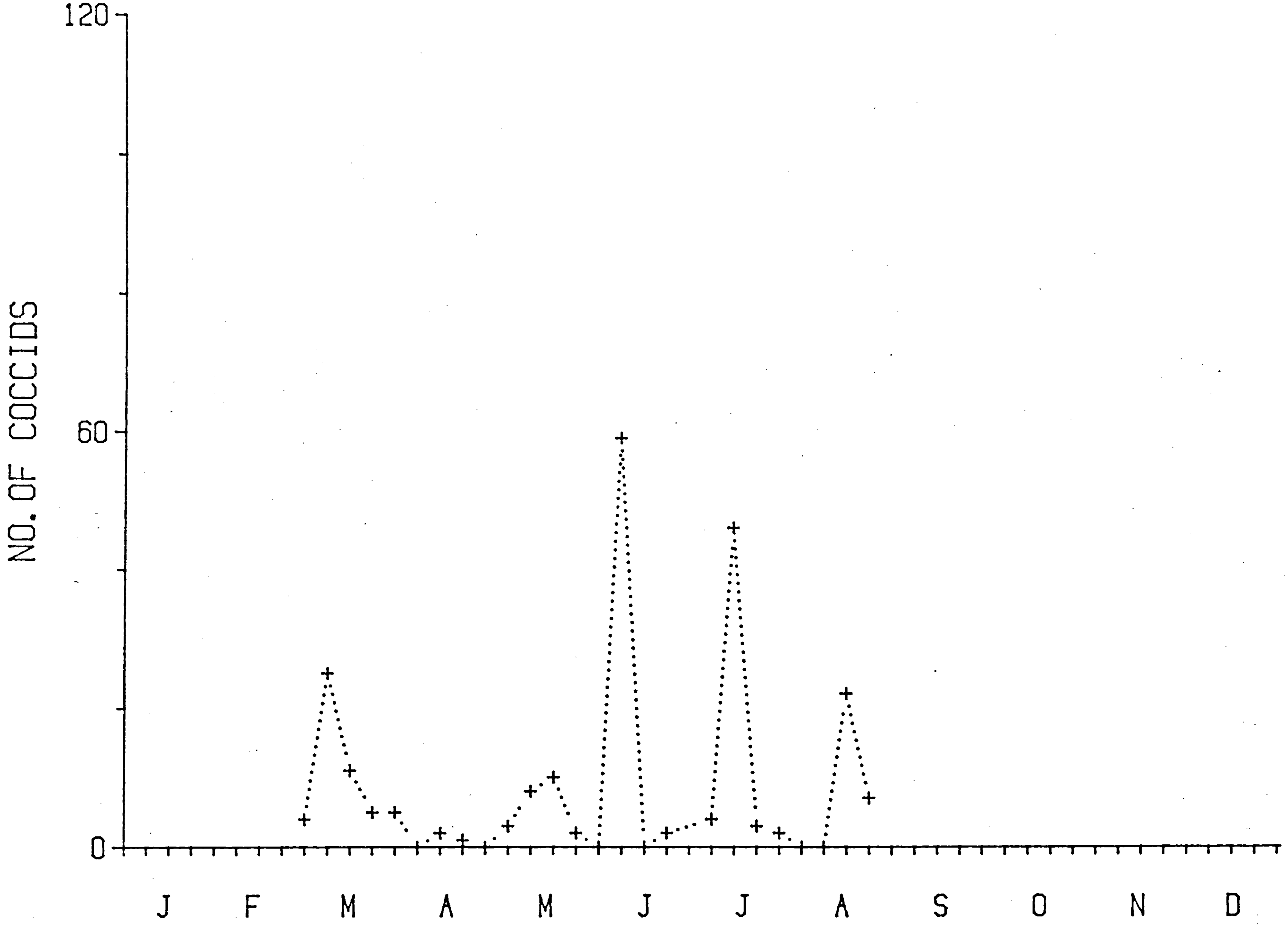
Graphs 10-12 show combined totals of aphids per week. All years show the same trends, so they will be considered together. January to mid February shows high counts of aphids, which then decline until March. From March onwards there is a steady increase in aphid numbers, reaching a subsidiary peak in late April to May. A decline in numbers begins in late May which continues through June and reaches lowest levels in July, when aphids vanish from the nest mound, but are still present in the surrounding territory. From August to October there is a slight recovery in aphid numbers, although this recovery was slow to pick up in 1984, possibly due to the dry Summer. From November to December there is a further rapid increase in aphid numbers, resulting in levels similar to the January counts. Hence for the purpose of comparisons, the year can be split up into four sections, signifying Winter levels, the Spring increase and decline in late July, the 'recovery' period until October, and the return to Winter levels in November



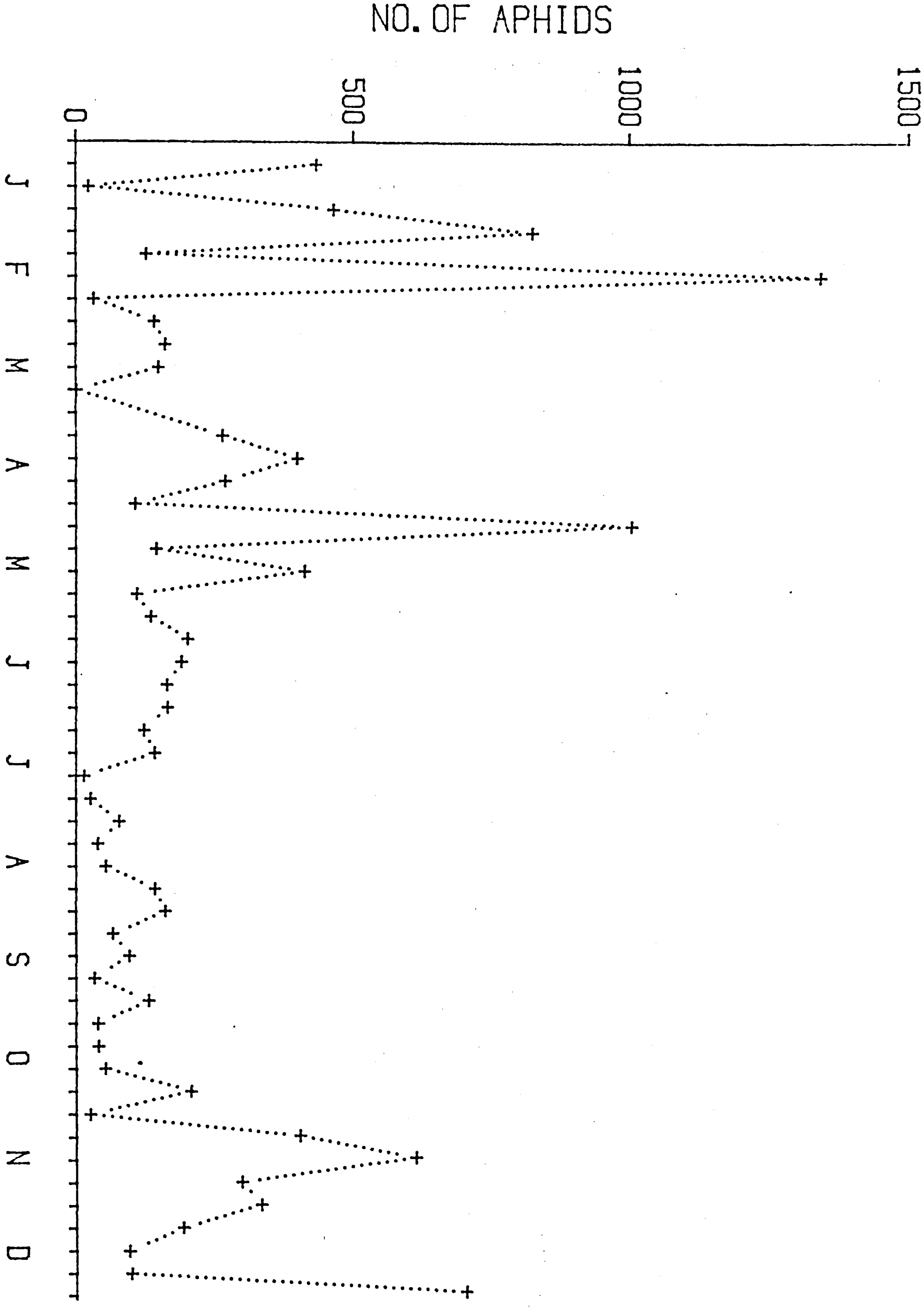
Graph 7. The abundance of coccids throughout the year (1983).



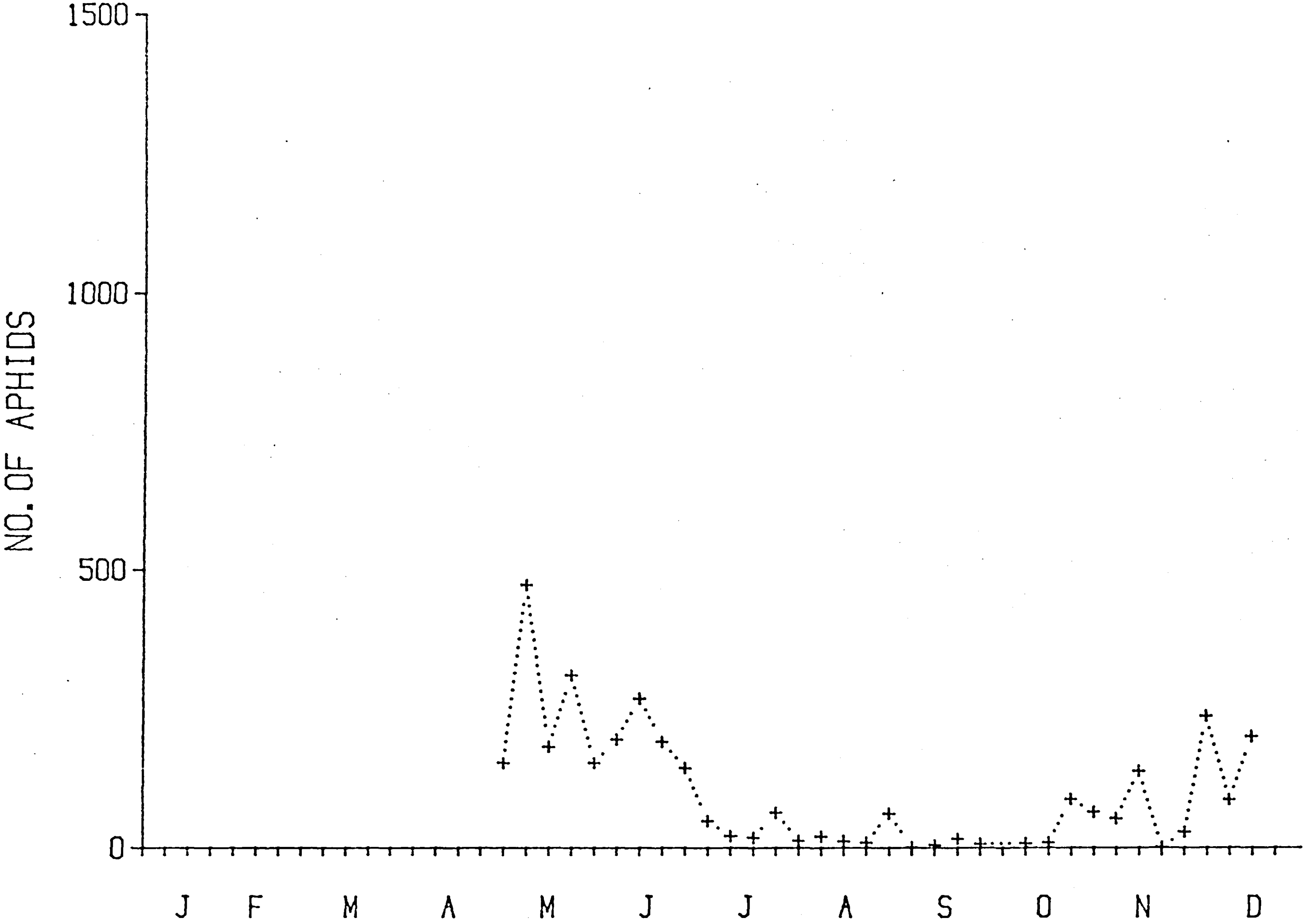
Graph 8. The abundance of coccids throughout the year (1984).



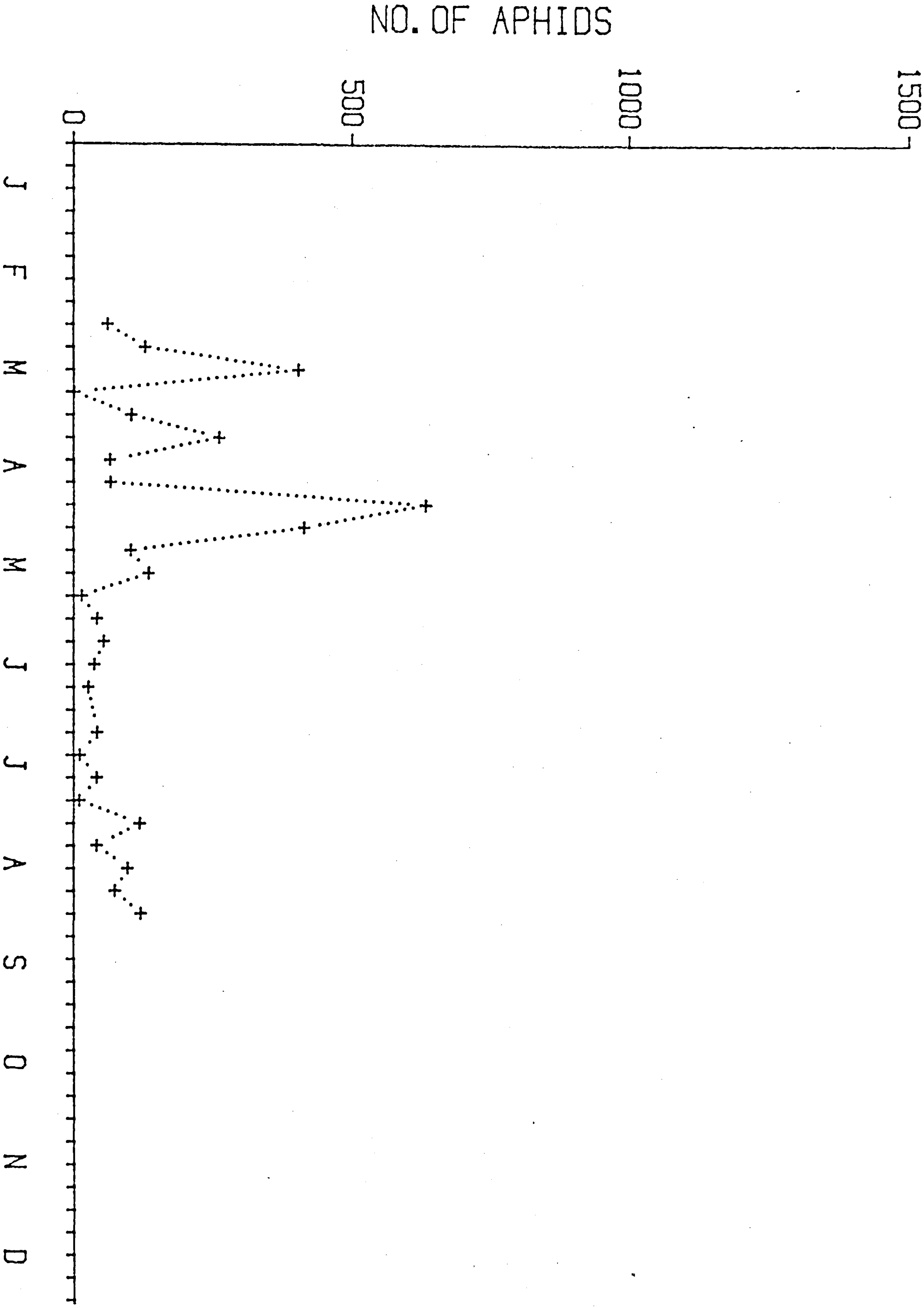
Graph 9. The abundance of coccids throughout the year (1985).



Graph 10. The abundance of aphids throughout the year (1983).



Graph 11. The abundance of aphids throughout the year (1984).



Graph 12. The abundance of aphids throughout the year (1985).

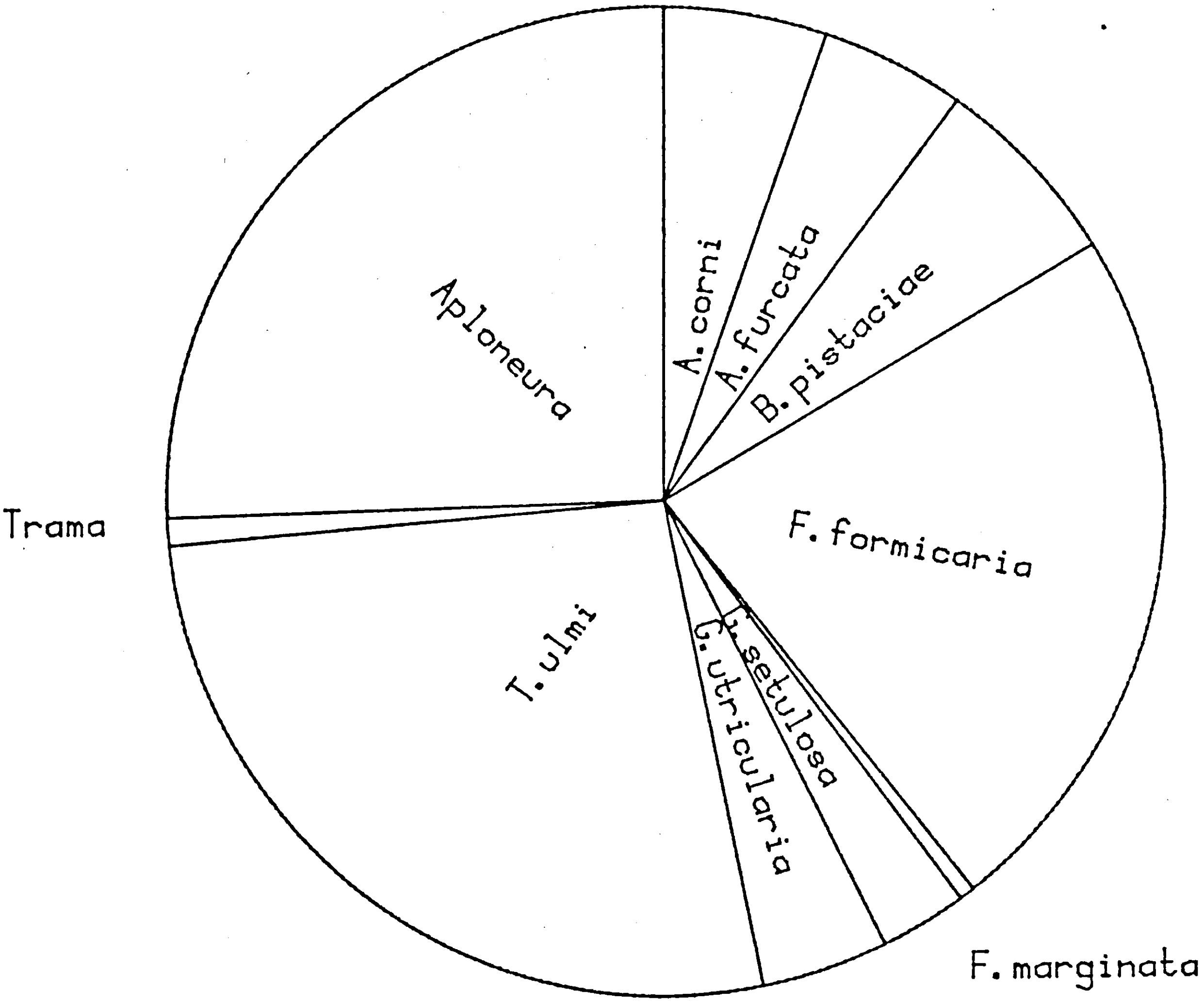
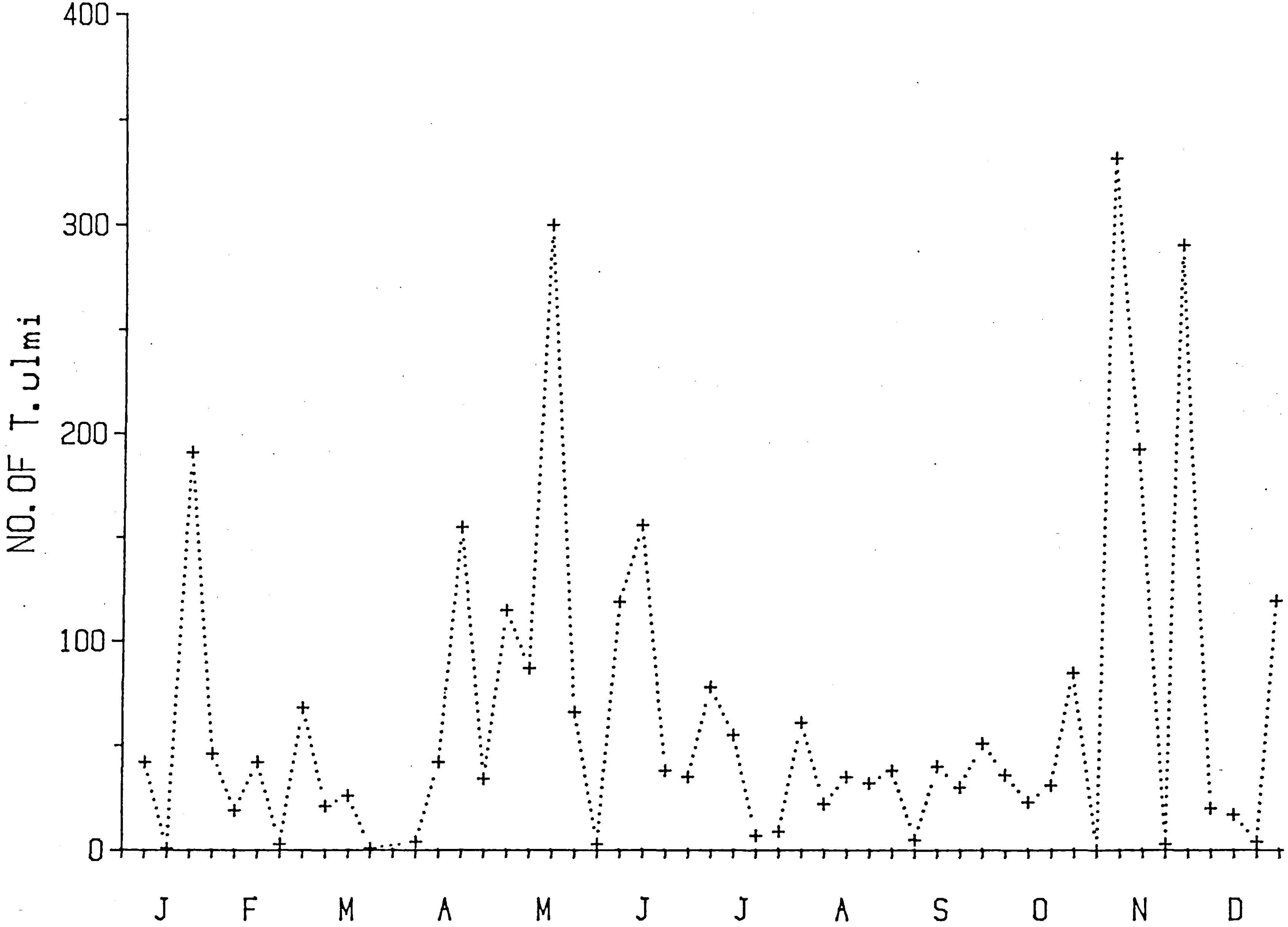
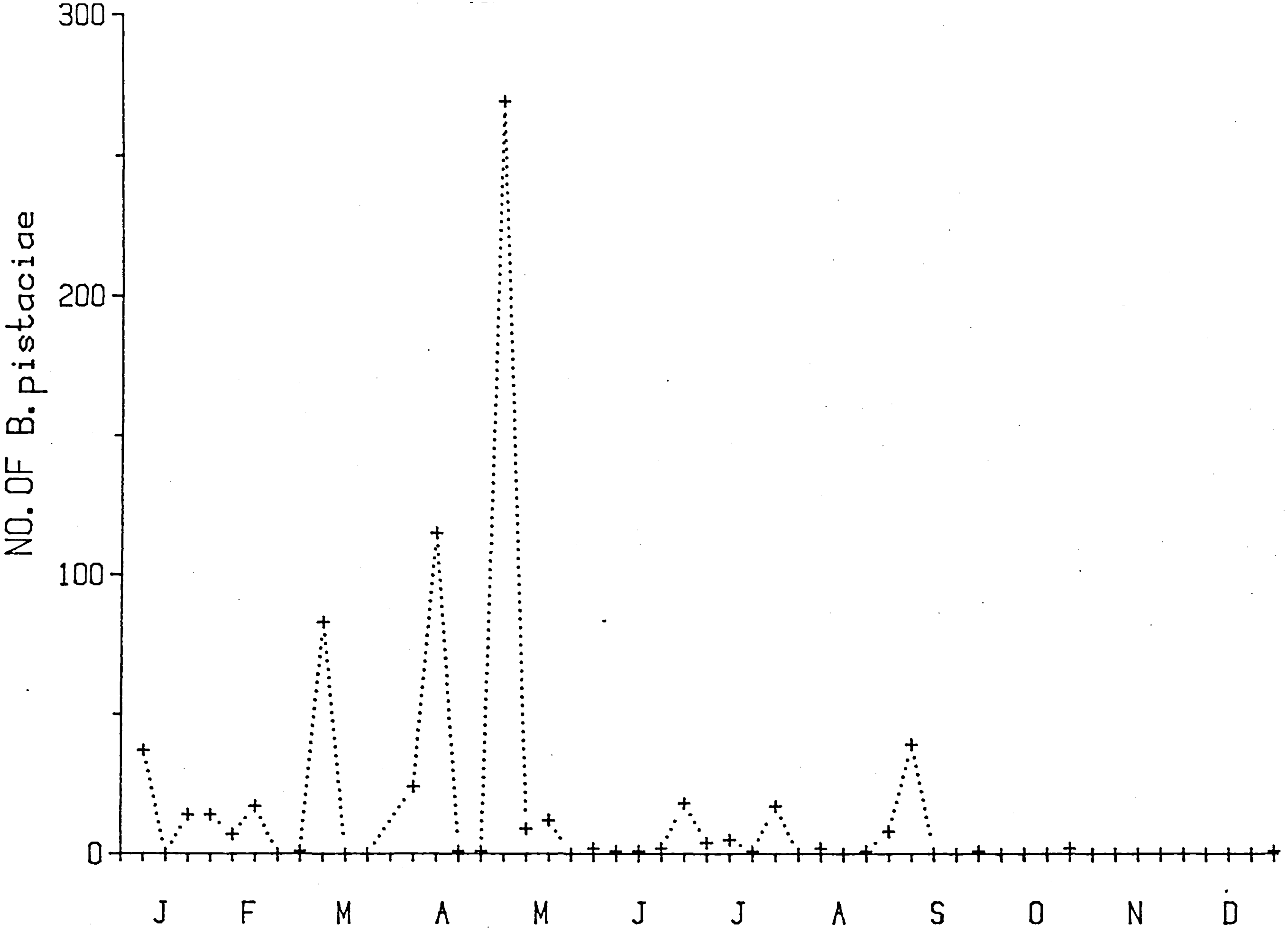


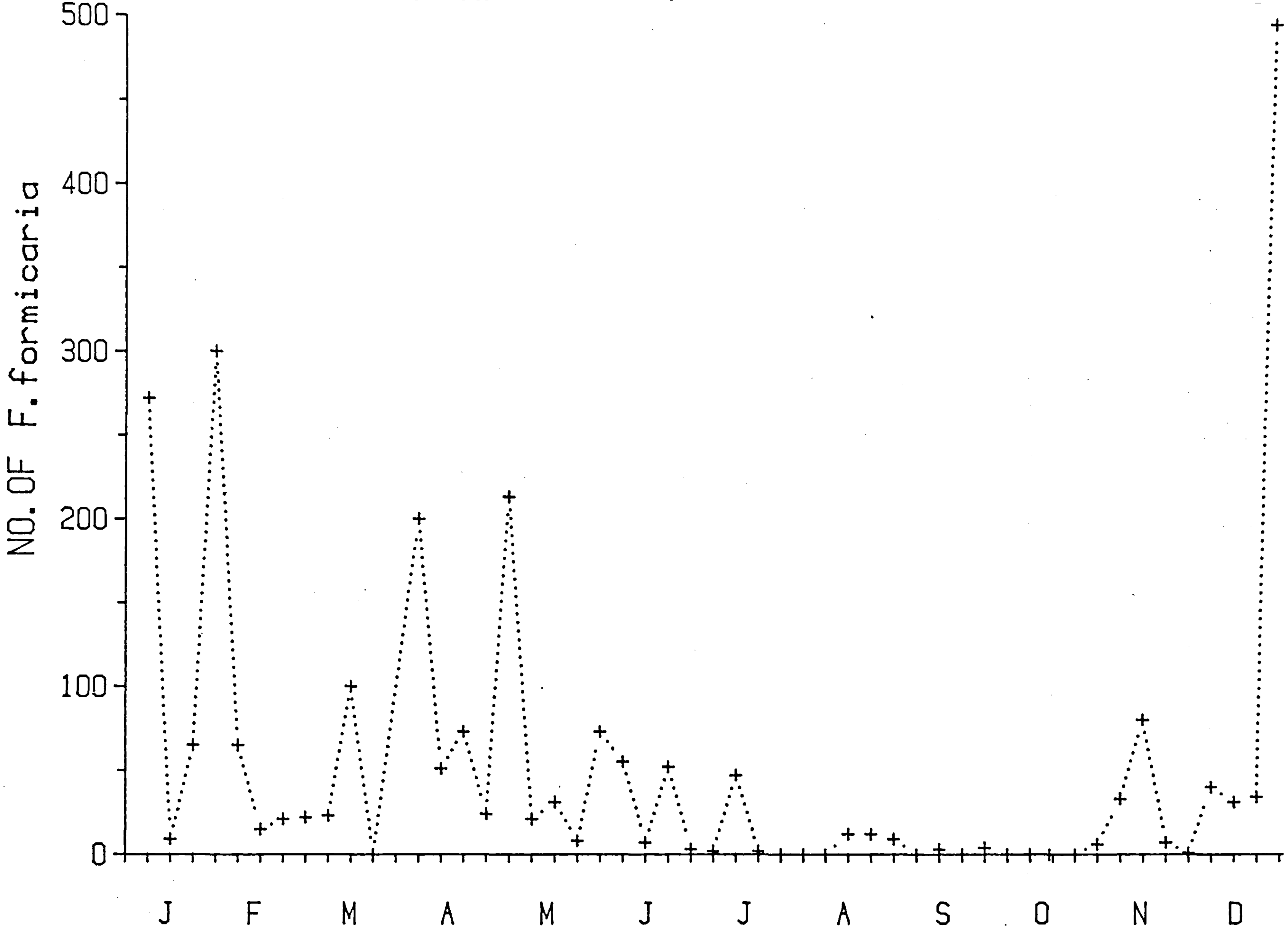
Figure 2. The relative abundance of aphid species.



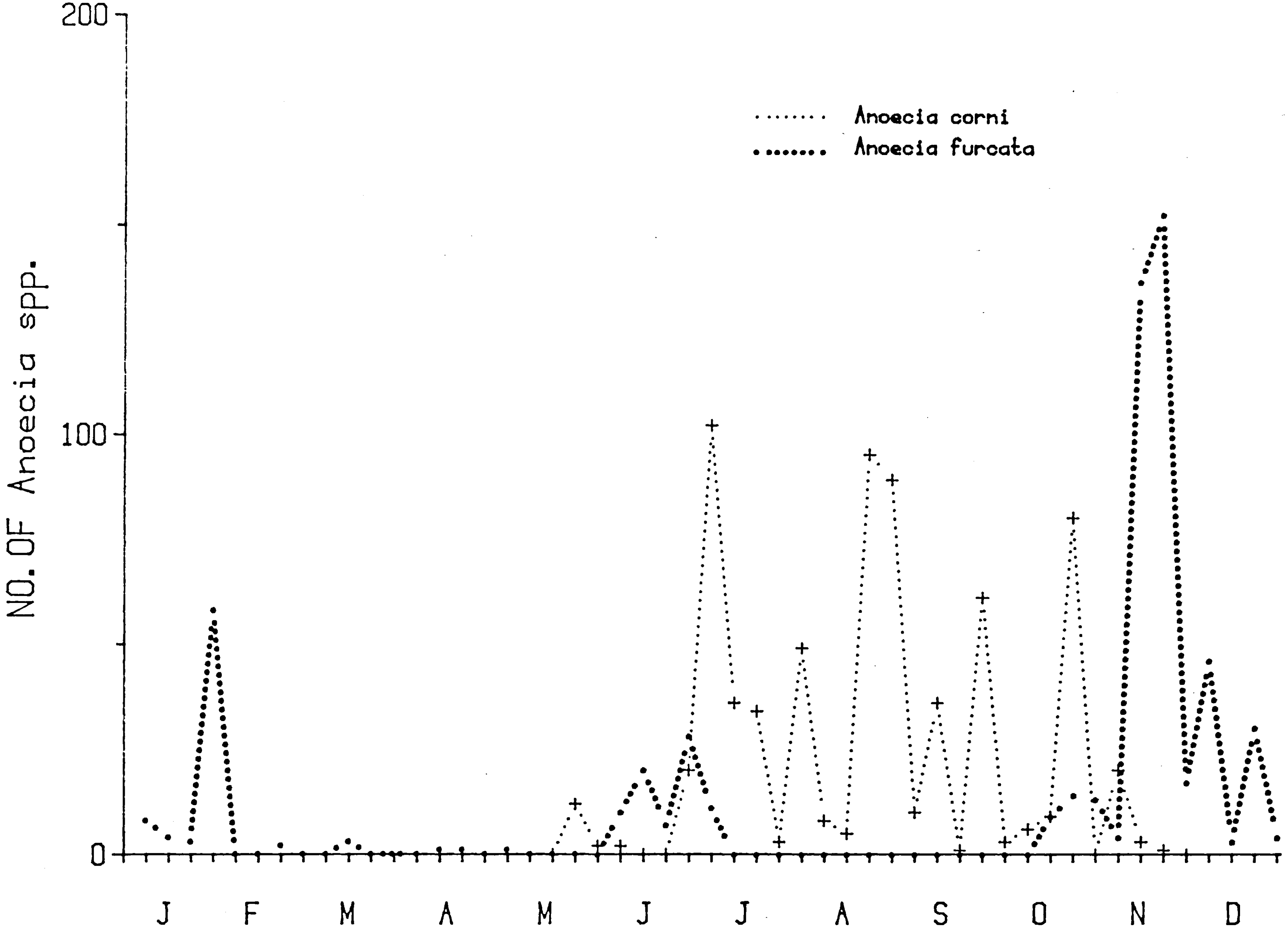
Graph 13. The abundance of _Tetraneura ulmi_ throughout 1983.



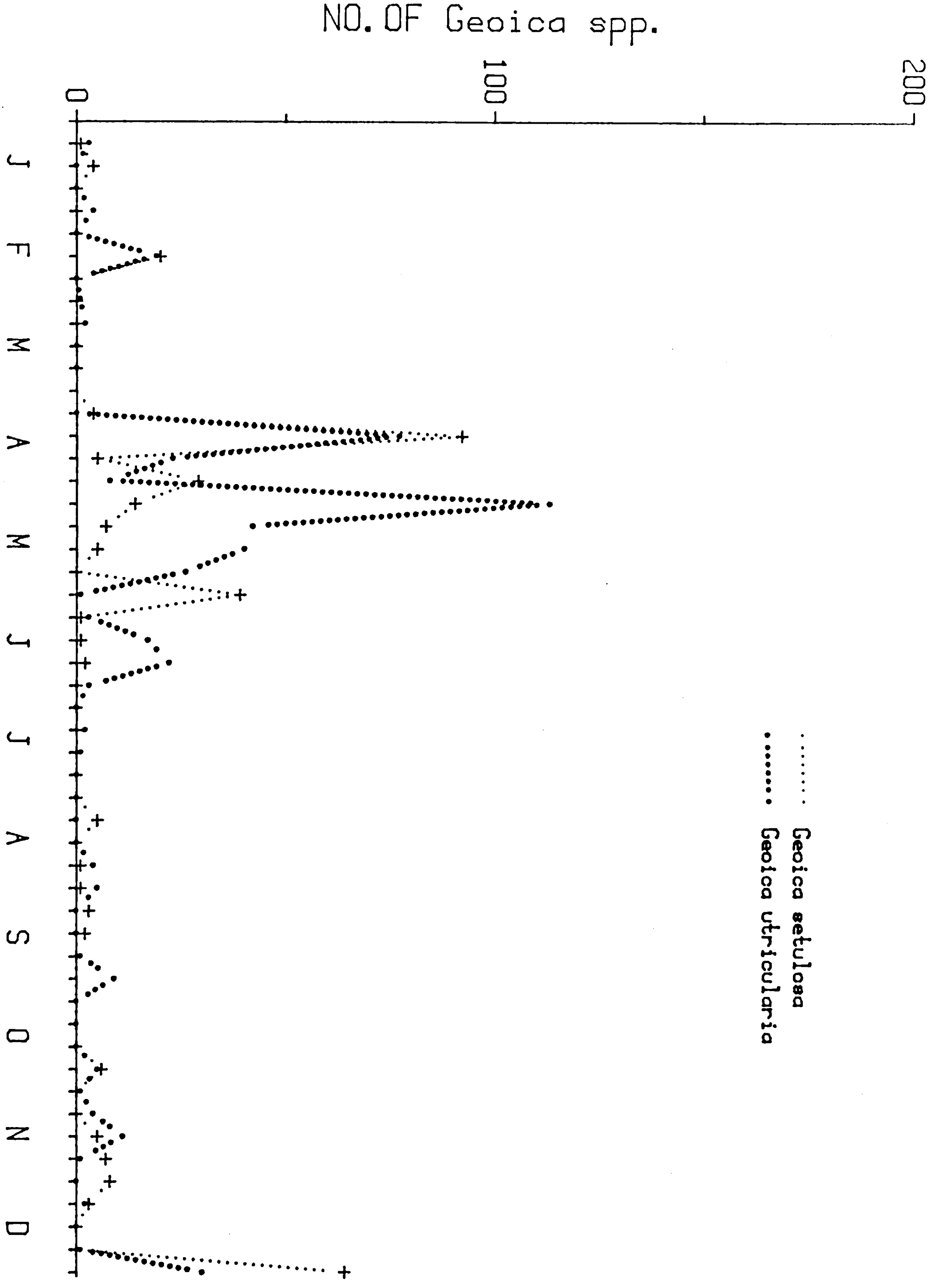
Graph 14. The abundance of *Baizongia pistaciae* throughout 1983.



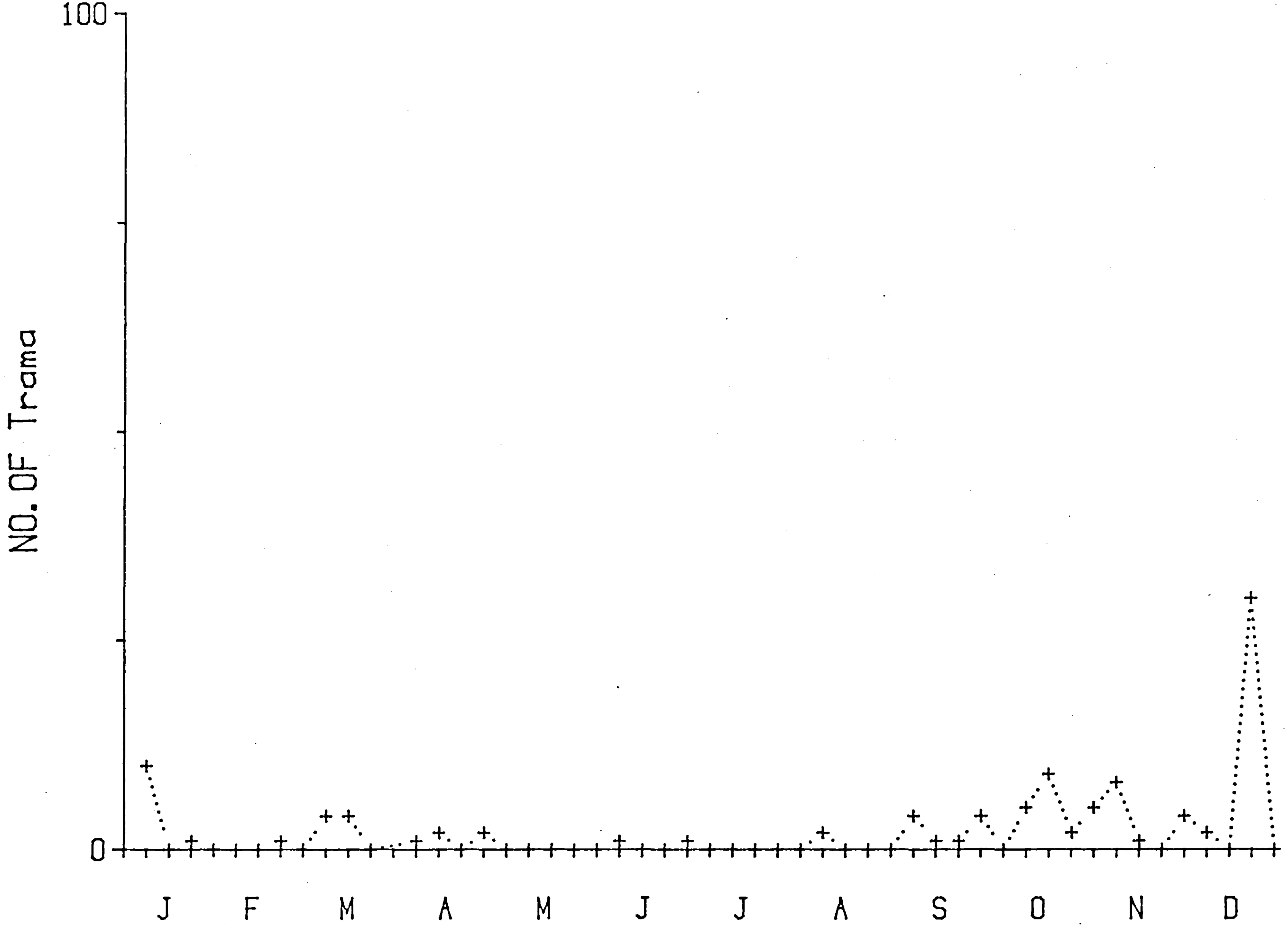
Graph 15. The abundance of <u>Forda formicaria</u> throughout 1983.



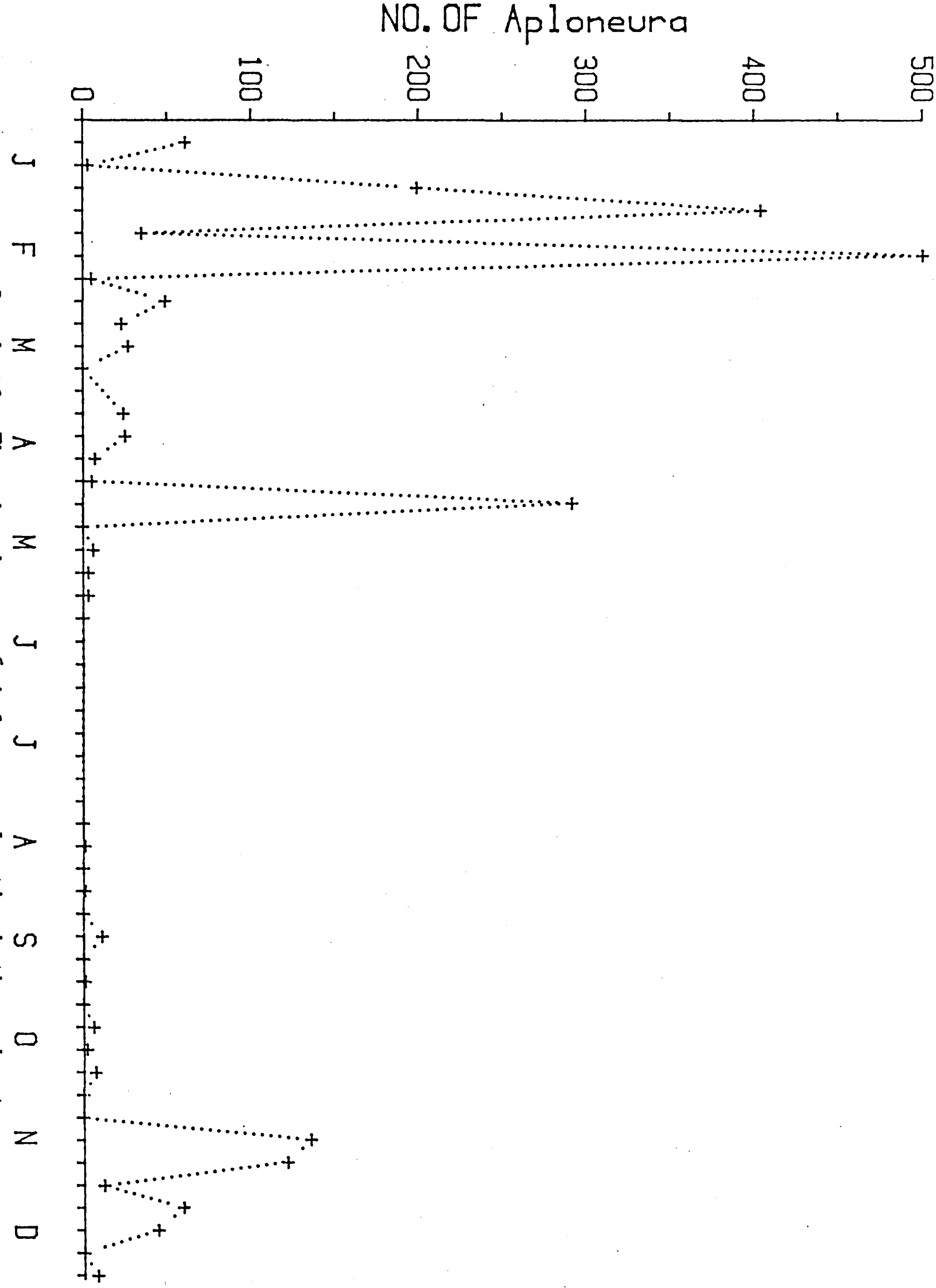
Graph 16. The abundance of Anoecia corni and Anoecia furcata throughout 1983.



Graph 17. The abundance of Geoica setulosa and Geoica utricularia throughout 1983.



Graph 18. The abundance of *Trama troglodytes* throughout 1983.



Graph 19. The abundance of Aploneura lentisci throughout 1983.

to December.

For 1983 these sections are:

I 12/1 to 20/4
II 29/4 to 22/7
III 29/7 to 19/10
IV 26/10 to 29/12

It is further interesting to compare these sections to the seven sections used to describe ant activity (Table 8, section 3.4), even at this stage a relationship between ant activity and aphid numbers seems apparent. The levels of aphid abundance are similar for 1984 and 1985, but many more were found in 1983 signifying that a larger standing crop of aphids can be maintained in ant nests in damper locations.

Figure 2., shows the relative abundance of the aphid species for 1983. From this it can be seen that some species contribute more to the aphid totals than others, therefore the weekly totals for individual species were plotted in graphs 13-19 (1984 and 1985 totals are in appendix E1, graphs 74-87). For the most abundant species of aphids; Tetraneura ulmi, Forda formicaria, Aploneura lentisci and to a lesser extent Baizongia pistaciae the trends hold true. Similarly for Geoica spp., Anoecia furcata and Trama troglodytes, despite low numbers, when all three years are considered. Anoecia corni has a different yearly distribution. It is not found in Lasius flavus nests until mid May, it then quickly increases, and then declines, reaching low values in July in common with other aphids. It recovers very rapidly, then disappears from the nest in late November to early December. Anoecia corni has an obligate host alternation between Cornus sanguinea and various grasses (including Agrostis, Holcus and Dactylis),and when

not in the ant nests is overwintering on Cornus. In Autumn all nymphs become alate sexuparae and fly to their primary host plant. Anholocyclic overwintering on grass roots does not take place in this species. Some other aphid species also have alternative host plants (see section 1.2), but this does not seem to be obligatory. Of all aphids A.corni recovers most rapidly after the July crash in numbers. The next fastest recolonizer of the ant nest was T.ulmi, another aphid which seems to breed better away from the nest mound. F.formicaria, B.pistaciae, Geoica spp. and T.troglodytes recolonize the nest later; A.furcata only reaches large numbers in November to December when A.corni has left the nest, likewise for Aploneura lentisci. Anoecia corni and A.furcata were plotted on the same graph to see if there was any interaction between these two similar species. In both 1983 and 1985 (no A.furcata were found in 1984) there is a strong negative association, each species only reaching high density in the absence of the other, therefore there may well be some degree of interspecific displacement (see section 5.4). This process was repeated for G.setulosa and G.utricularia, but in this case there appears to be no displacement although there could still be interspecific competition.

To discover whether these observed differences in aphid number at different times of year were real, or due to chance, U-tests were carried out for total aphids in 1983, (see Table 16a); and t-tests for the most common species in 1983 (see Table 16b). This suggests that the differences between aphid population levels in late Winter and early Spring could have been caused by chance, whereas there is some support for the July crash in aphid populations and likewise a difference in the population level observed during the recovery phase and early Winter levels. The species results by and large reflect this, except in cases where low numbers were present throughout the year i.e. A.corni, Geoica spp., T.troglodytes. Tetraneura ulmi alone shows a strong hint of a difference between late Winter and Spring population levels, which is linked to when T.ulmi breeds (see later), otherwise no difference is observed. The population crash was observed in the most abundant species, but the subsequent rise to Winter levels goes unnoticed. In species which did not show a population crash in July because of low numbers in previous months, there is evidence of an increase in numbers in early Winter.

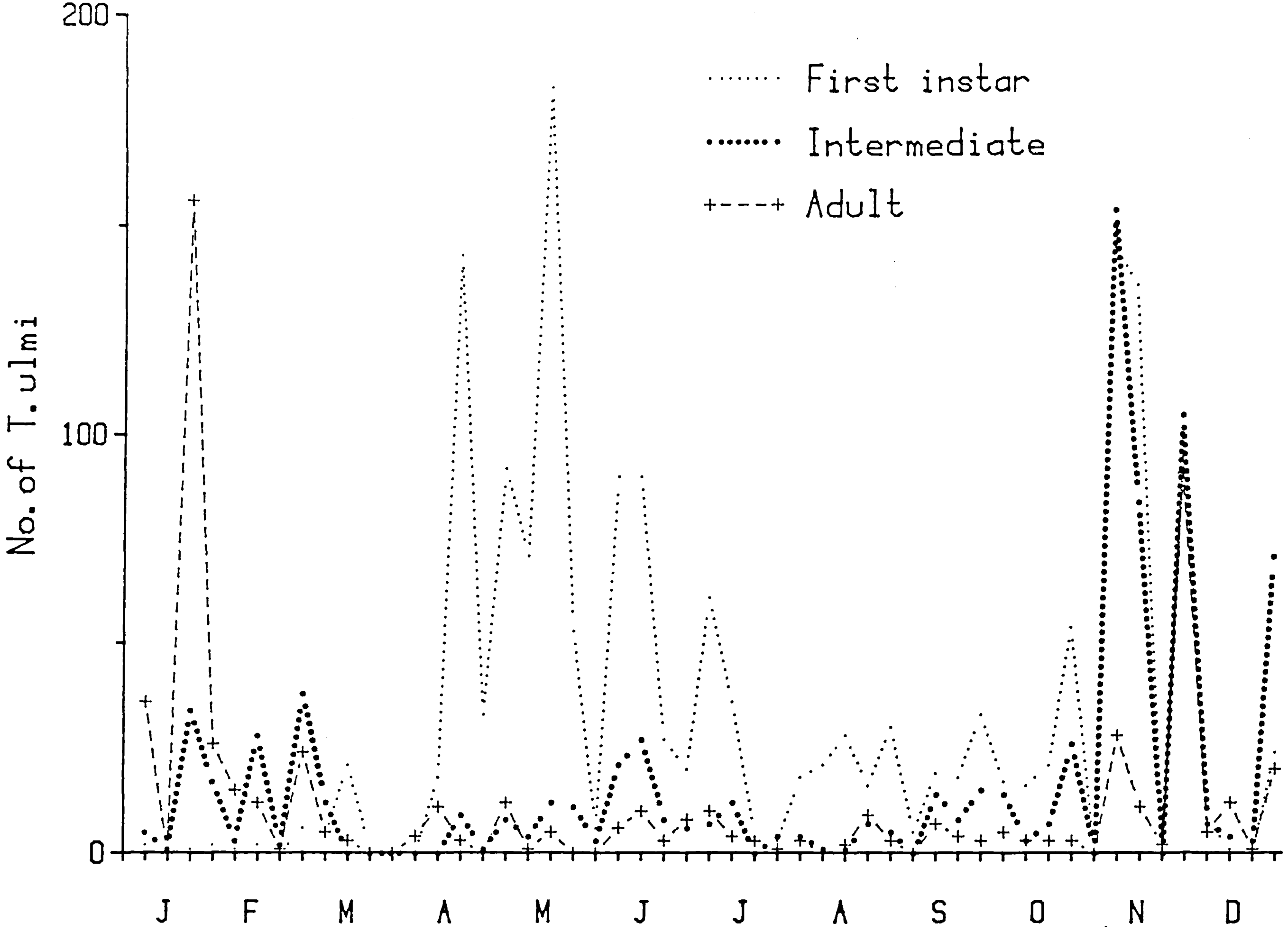
In a further attempt to understand the seasonal trends observed in aphid abundance, plots of the age distribution of the most common aphid species were made against time (graphs 20-25). For Tetraneura ulmi the Winter peak is made up of adult and intermediate stages, as first instar nymphs are not found in large numbers until March. The ensuing Spring rise is due to large numbers of first instar larvae, and the subsequent decline occurs when less first instar nymphs are found. During this period the numbers of adults and intermediates remains constantly low, far lower than the Winter levels. Despite the large number of first instar nymphs, very few are surviving to become intermediate or adult. After the population crash, it is the increase in first instar nymphs which is responsible for the recovery in numbers. As Autumn begins, increasing numbers of first instar nymphs mature to become intermediate and then adult.

	SECTIONS I - II		SECTIONS II - III		SECTIONS III - IV	
	U value	Significance	U value	Significance	U value	Significance
1983	75	N/S	26.5	0.001>p>0.01	19.5	0.001>p>0.01

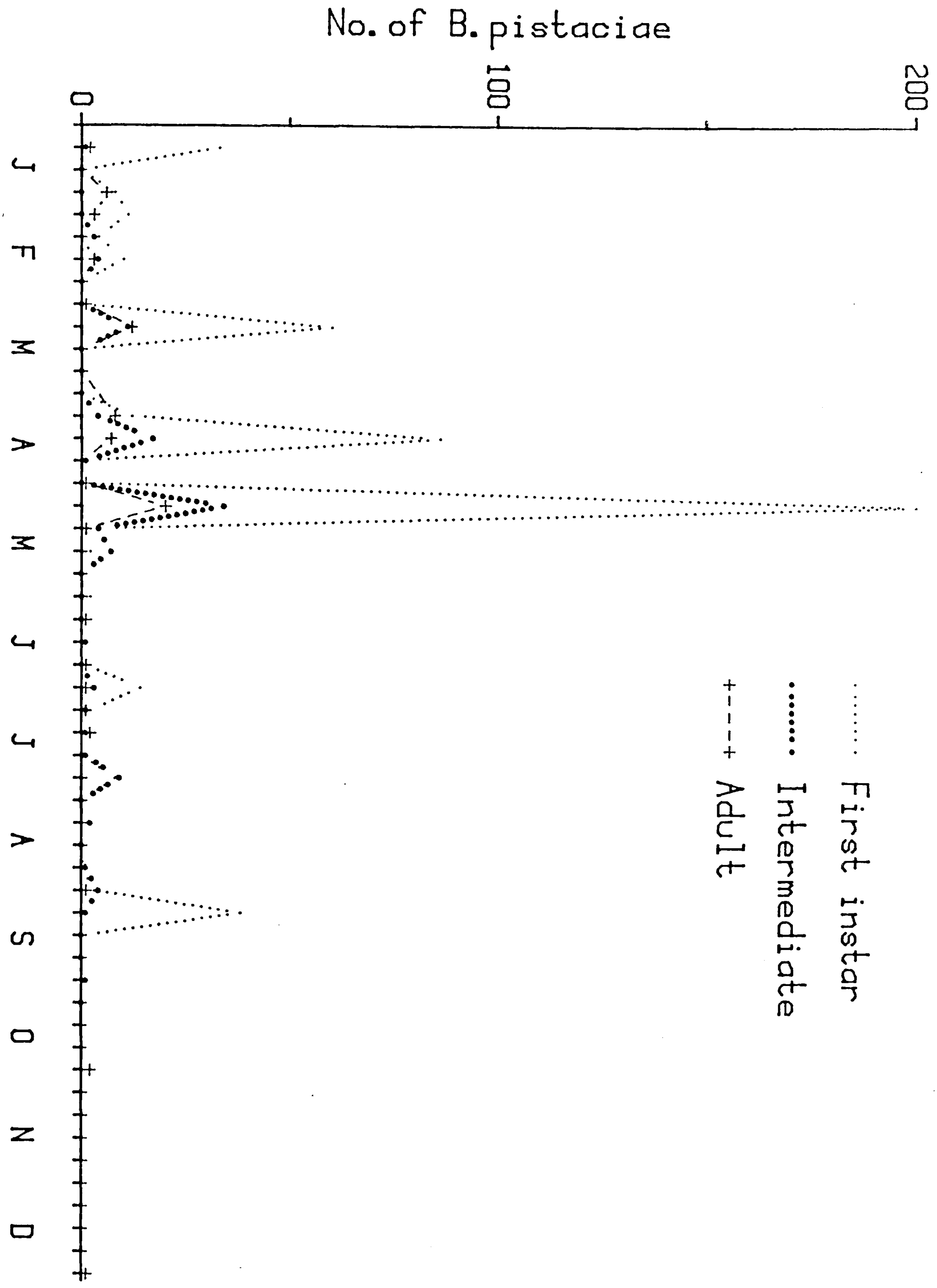
Table 16a. The fluctuation in total aphid abundance between different sections of the year.

	t value	Significance	t value	Significance	t value	Significance
T.ulmi	-3.00	0.001>p>0.01	2.12	p>0.05	-0.09	N/S
Forda formicaria	-0.78	N/S	4.02	p>0.001	-1.84	N/S
B. pistaciae	0	N/S	2.73	0.01>p>0.05	1.1	N/S
Anoecia furcata	-0.22	N/S	1.71	N/S	-5.61	p>0.001
Anoecia corni			-0.86	N/S	1.55	N/S
Aploneura lentisci	2.05	N/S	0.55	N/S	2.14	p>0.05

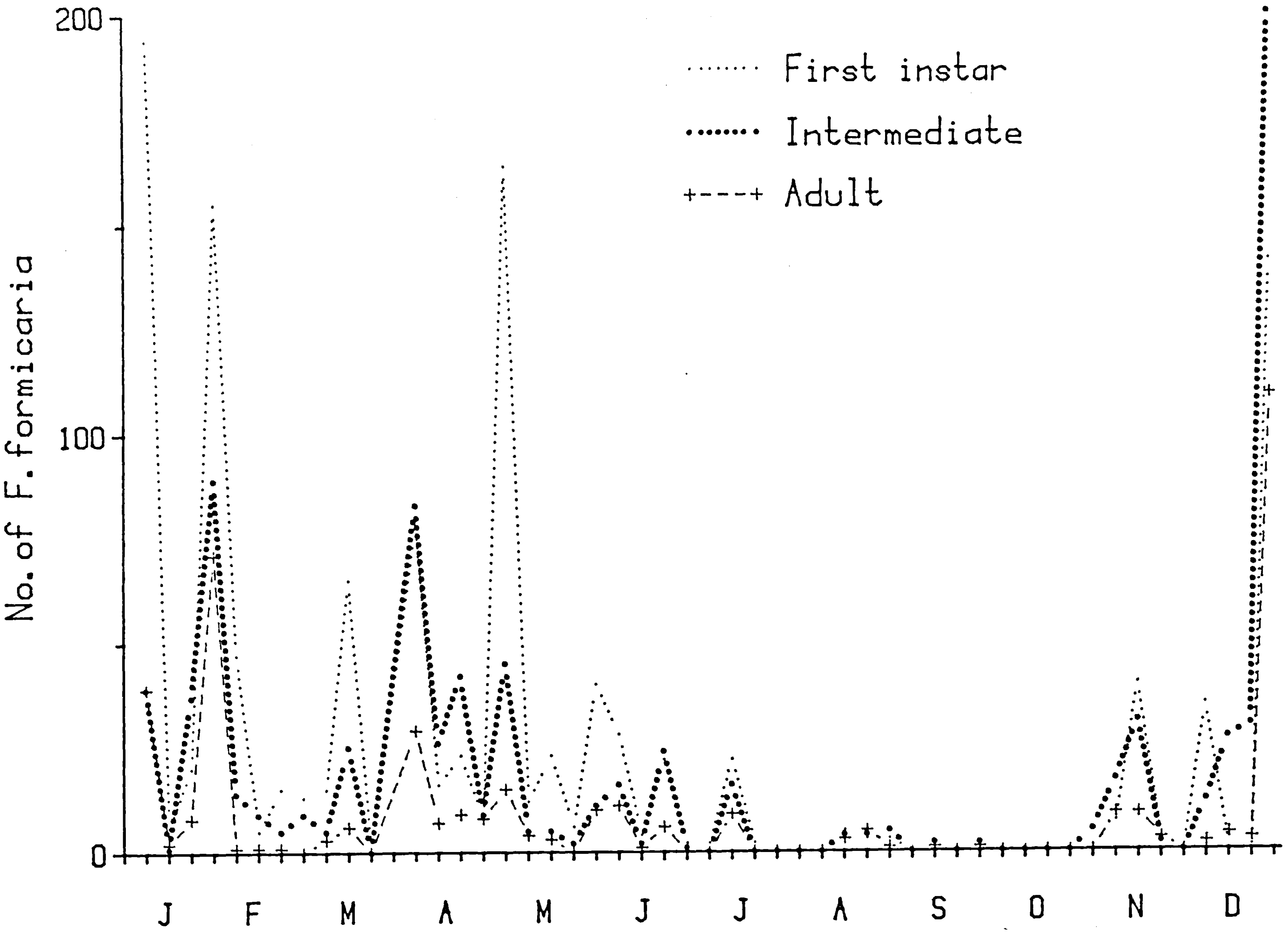
Table 16b. The fluctuation in species abundance between different sections of the year.



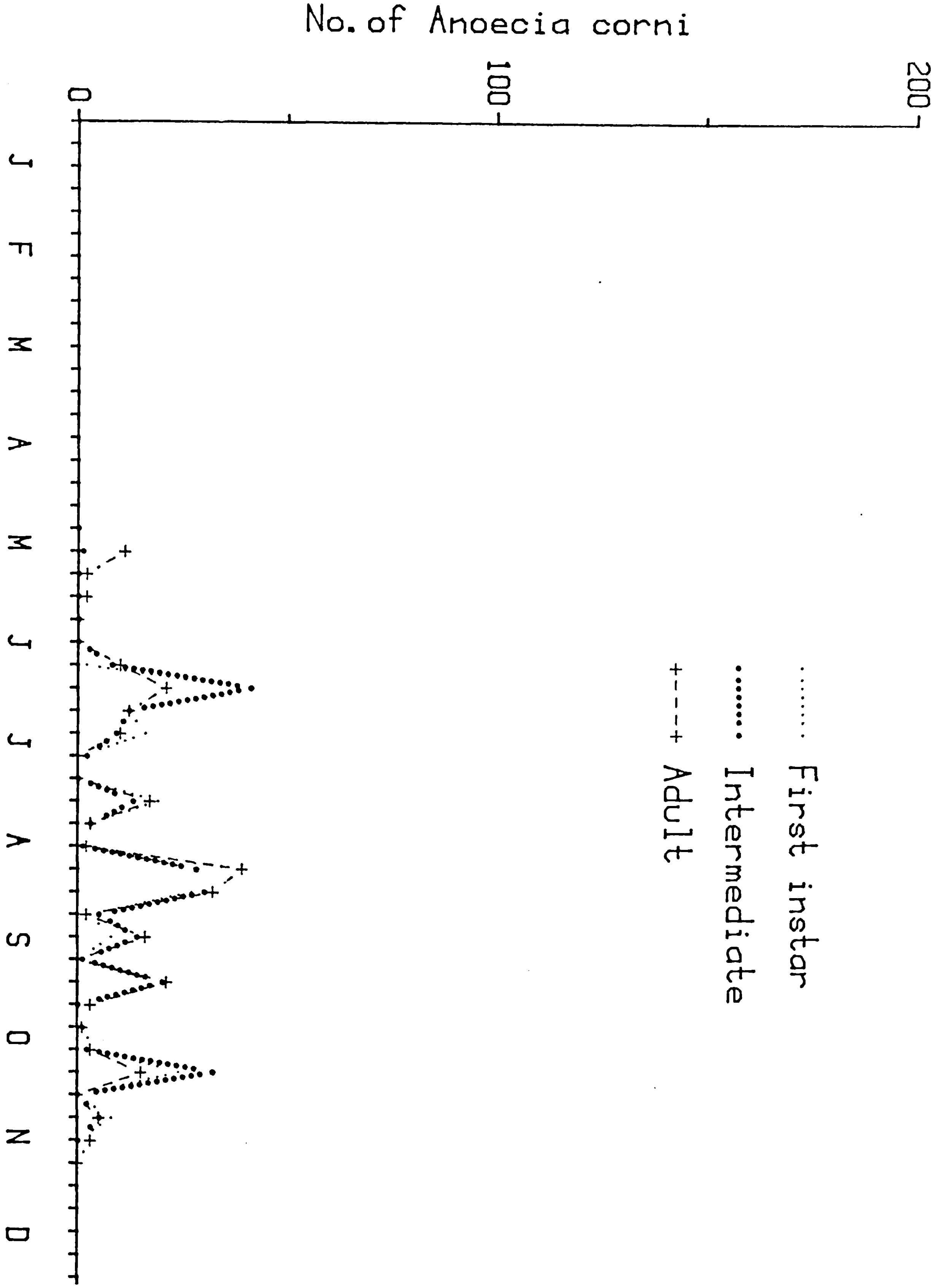
Graph 20. The age distribution of Tetraneura ulmi 1983.



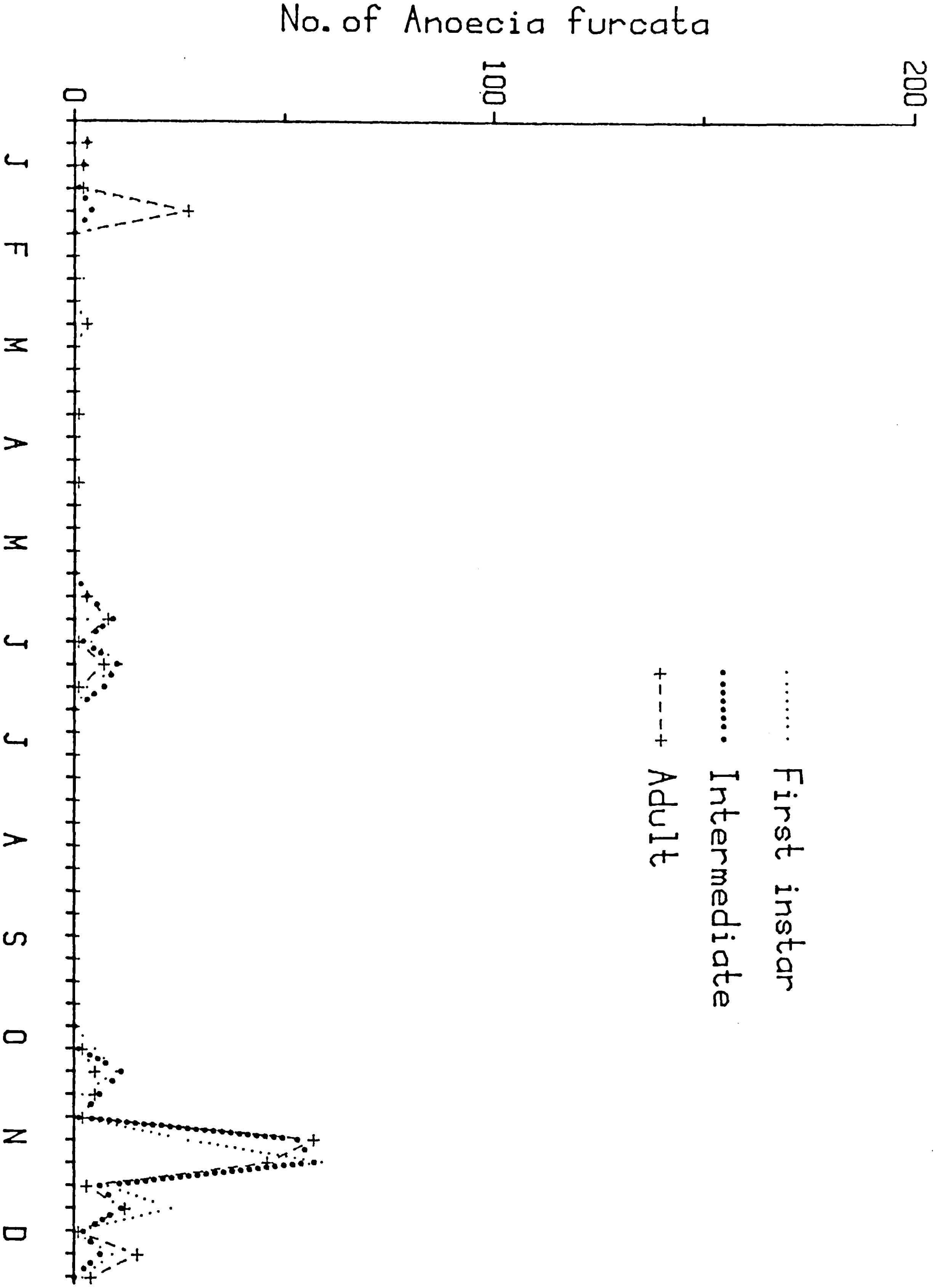
Graph 21. The age distribution of <u>Baizongia pistaciae</u> 1983.



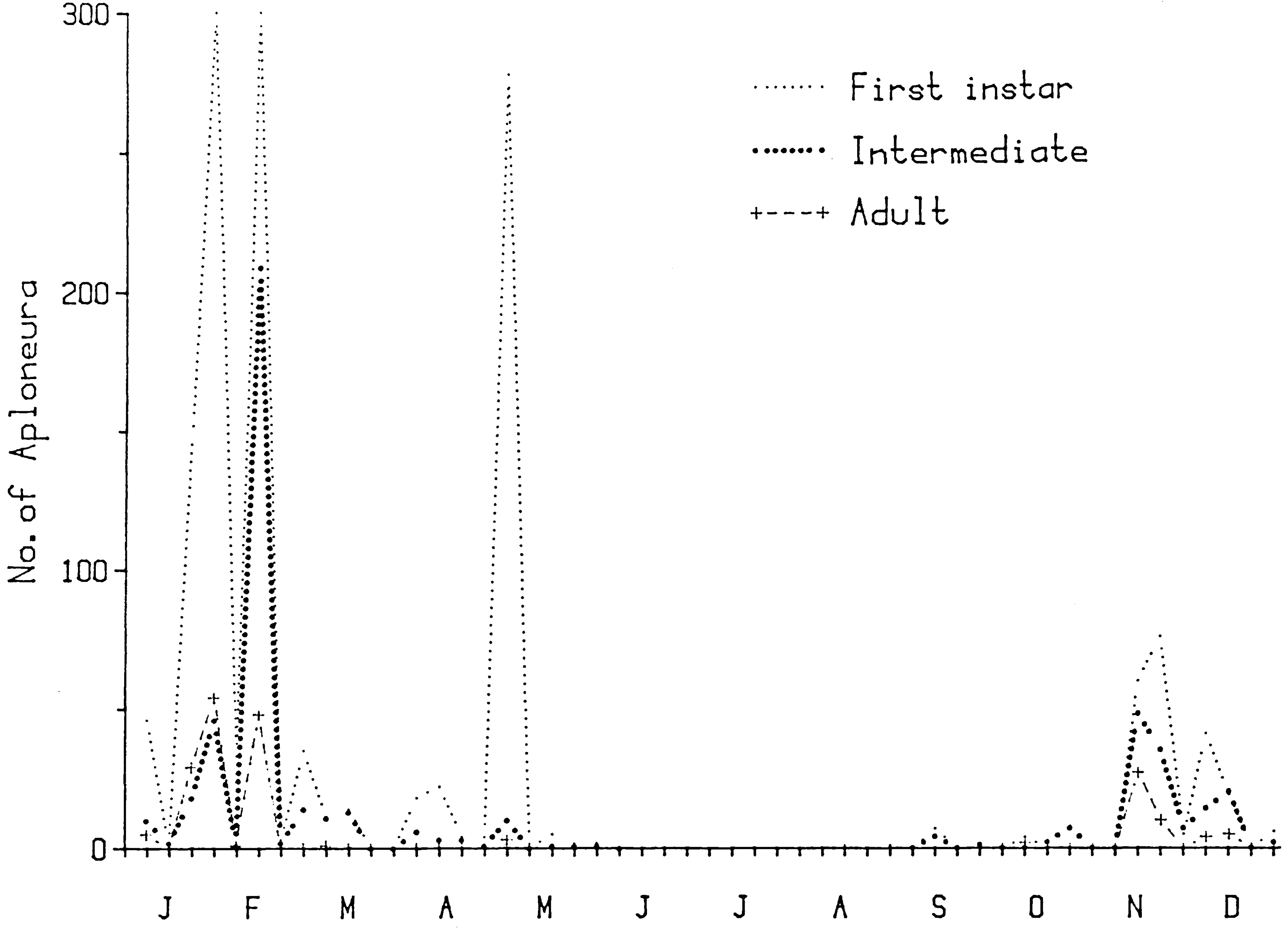
Graph 22. The age distribution of Forda formicaria 1983.



Graph 23. The age distribution of Anoecia corni 1983.



Graph 24. The age distribution of *Anoecia furcata* 1983.



Graph 25. The age distribution of Aploneura lentisci 1983.

In November to December, the majority of the first instar aphids are becoming adult, and these are producing further first instar nymphs and hence the peak occurs. By late December the production of nymphs has stopped, and intermediate nymphs become the dominant age class.

Forda formicaria continues to breed throughout the Winter, with the majority of first instars becoming intermediate and many of these becoming adult. In early Spring fewer adults are found, but these are producing more first instar nymphs, so overall aphid abundance remains high. As Spring progresses fewer first instar nymphs are found, and less of these are surviving to become intermediate. By the July crash, all age classes disappear, and it is only the intermediate and adult aphids surviving near the edge of the ant mound which reestablish the aphid population. From November to December, numbers of all age classes increase, the majority of first instar aphids becoming adult. The reproductive rate remains high, hence providing the December peak.

Although overall numbers are much lower for B.pistaciae, it does show that in January to February, few first instar aphids are produced, and the majority of these survive to adulthood. From March to May, large numbers of first instar nymphs are produced, but few survive and there is little overall increase in adult numbers since Winter. In early Summer first instar nymphs become less common, and by July very few are present. The age class which survives the July crash best are the intermediates. A slight recovery in numbers occurs in

September.

With Anoecia furcata and A.corni, different patterns of age classes occur; wherever there are peaks, equal numbers of first instar, intermediate and adult aphids occur, which implies either that there is little first instar mortality, the majority of them becoming adults, or that mortality of first instars is almost complete, which is unlikely. If the former is true, it also implies that there is a relatively low reproductive rate otherwise the peaks would be much larger, or possibly the adults remain in the nest for a very short time, and tend to breed elsewhere. Indeed A.corni produces alates throughout its stay in the ant nest (but many more in late Autumn), and these could be used to colonize other ant nests, rather than remain in the same one.

Aploneura lentisci resumes the previous pattern of rapid reproduction in late Winter, followed by a decline in the number of first instar nymphs in late Spring. Again the lack of intermediate and adult aphids suggests some form of first instar mortality.

The pattern of peak aphid occurrence in Spring and late Winter is also common amongst epigeic aphids. It reflects the new plant growth in Spring and the senescence of plants in Winter, when more nutrients are present in plant sap. It is unlikely that this can account for the trends observed here because these are grass aphids, and the grass being grazed, is growing continuously throughout most of the year. Furthermore many aphids are breeding as rapidly in Spring as they are in late Winter when the grasses are dormant. In addition, this periodic plant activity cannot account for the mortality apparent in the aphids.

4.3 The distribution of trophobionts within the ant nest

4.31 Measures of Clumping.

Table 17. shows values of Taylors coefficient b +/- 95% Confidence Intervals. All trophobionts have a consistently clumped distribution. The exceptions to this e.g.*Aploneura lentisci* 1985, occur when there are few records of the animal. There seem to be no overall differences in clumping behaviour in aphids from the 1983 and 1984-5 site on Staines Moor.

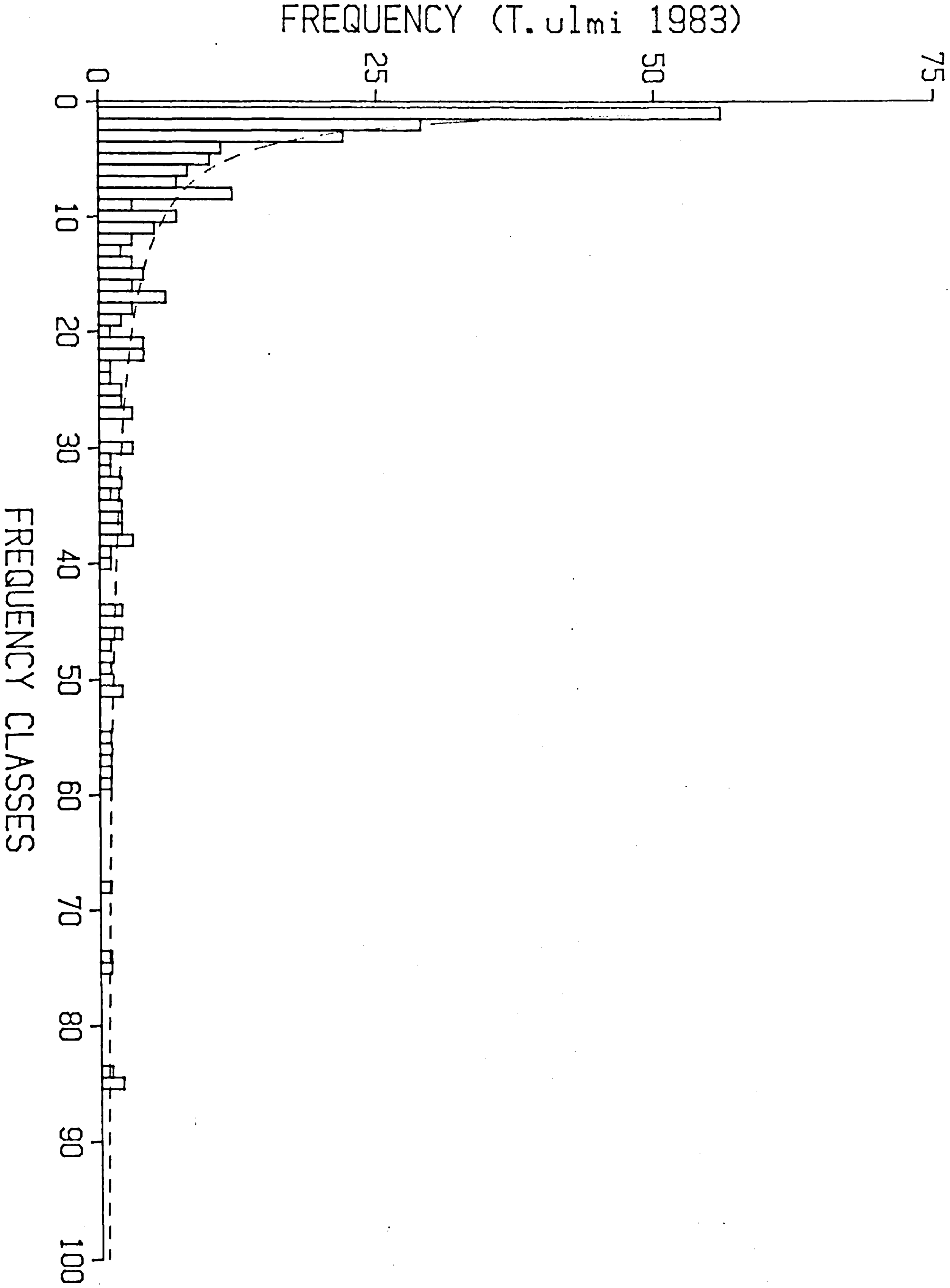
An alternative method of assessing the degree of clumping is to revert to the original frequency distribution of each aphid, (graphs 26-35, and 88-96 in appendix E2). Again these show an extremely clumped distribution, far more so than can be accounted for by fitting any Poisson or compound Poisson distribution e.g. negative binomial, Neyman type A. Reciprocal curves have been fitted to the frequency distribution which show very little deviation from the original results ($0.995>p>0.5$). Although the fact that a distribution fits empirical data quite well, is no justification of the assumption, but the closeness of fit to all aphids in the years 1983-1985 as well as *Lasius flavus*, suggests that it might have some meaning.

	b values +/- 95% Confidence Intervals		
	1983	1984	1985
Tetraneura ulmi	2.32 +/- 0.18	2.76 +/- 0.12	2.90 +/- 0.15
Forda formicaria	2.39 +/- 0.14	2.33 +/- 0.09	2.19 +/- 0.15
Baizongia pistaciae	2.64 +/- 0.08	2.41 +/- 0.14	2.80 +/- 0.13
Anoecia corni	2.65 +/- 0.12	2.57 +/- 0.16	2.35 +/- 0.13
Anoecia furcata	2.37 +/- 0.12		2.67 +/- 0.07
Geoica setulosa	2.56 +/- 0.06	2.61 +/- 0.08	2.12 +/- 0.08
Geoica utricularia	2.20 +/- 0.08	2.41 +/- 0.10	1.88 +/- 0.06
Trama troglodytes	2.53 +/- 0.06	2.53 +/- 0.07	1.75 +/- 0.03
Aploneura lentisci	2.54 +/- 0.12	2.51 +/- 0.13	3.87 +/- 0.02
Coccids	2.65 +/- 0.13	2.27 +/- 0.05	1.87 +/- 0.30

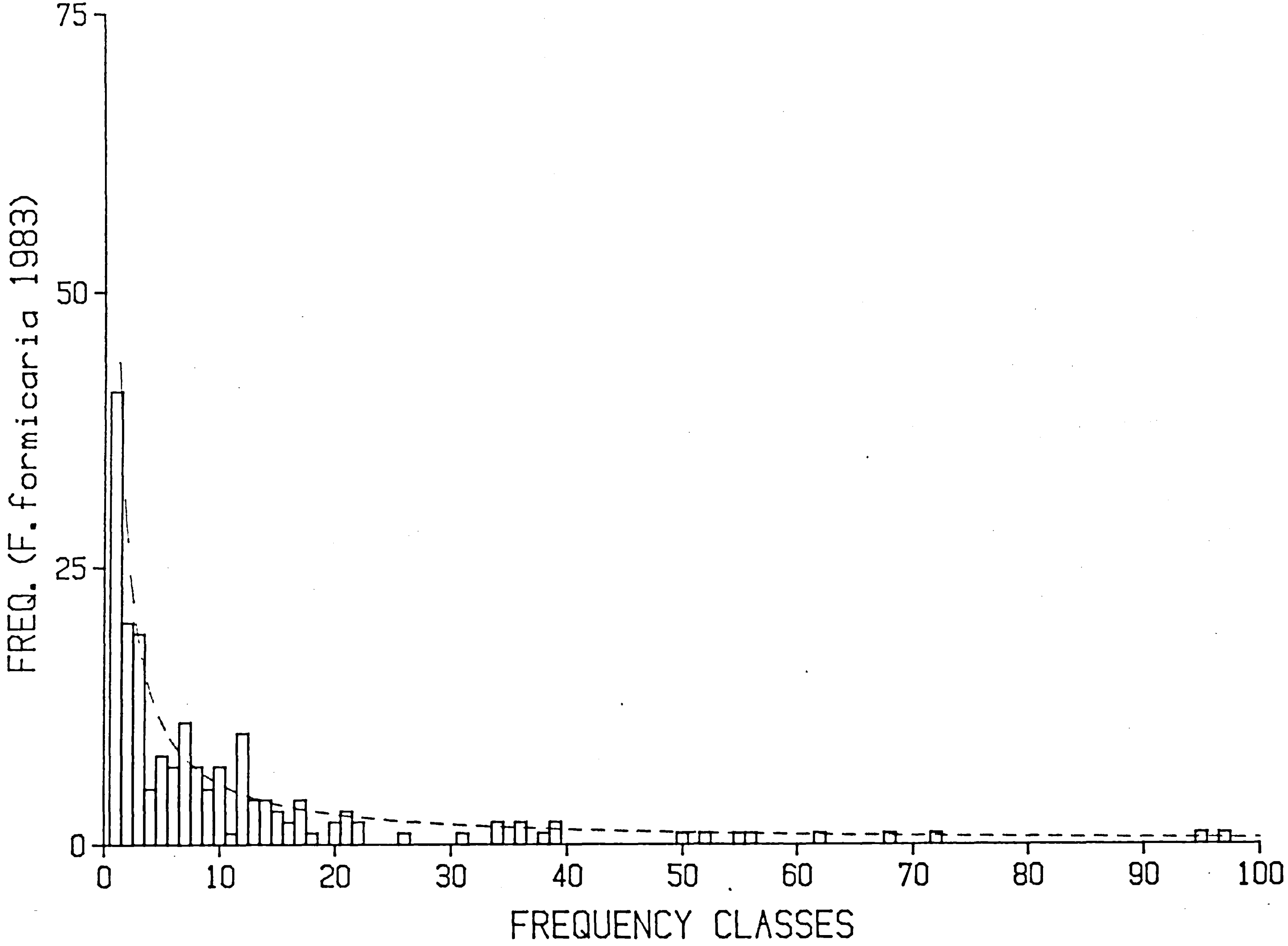
Table 17. Values of Taylors coefficient b for trophobionts.

	Mean clump size (cm^2)	Mean density of clump	Mean density per core	N/k value
Tetraneura ulmi	236	81	27	24
Forda formicaria	236	208	42	41
Baizongia pistaciae	393	141	28	21
Anoecia corni	393	111	22	21
Anoecia furcata	550	38	5	9
Geoica setulosa	393	118	39	20
Geoica utricularia	236	79	26	22
Trama troglodytes	157,393	6,15	3	9
Aploneura lentisci	550	13	2	9

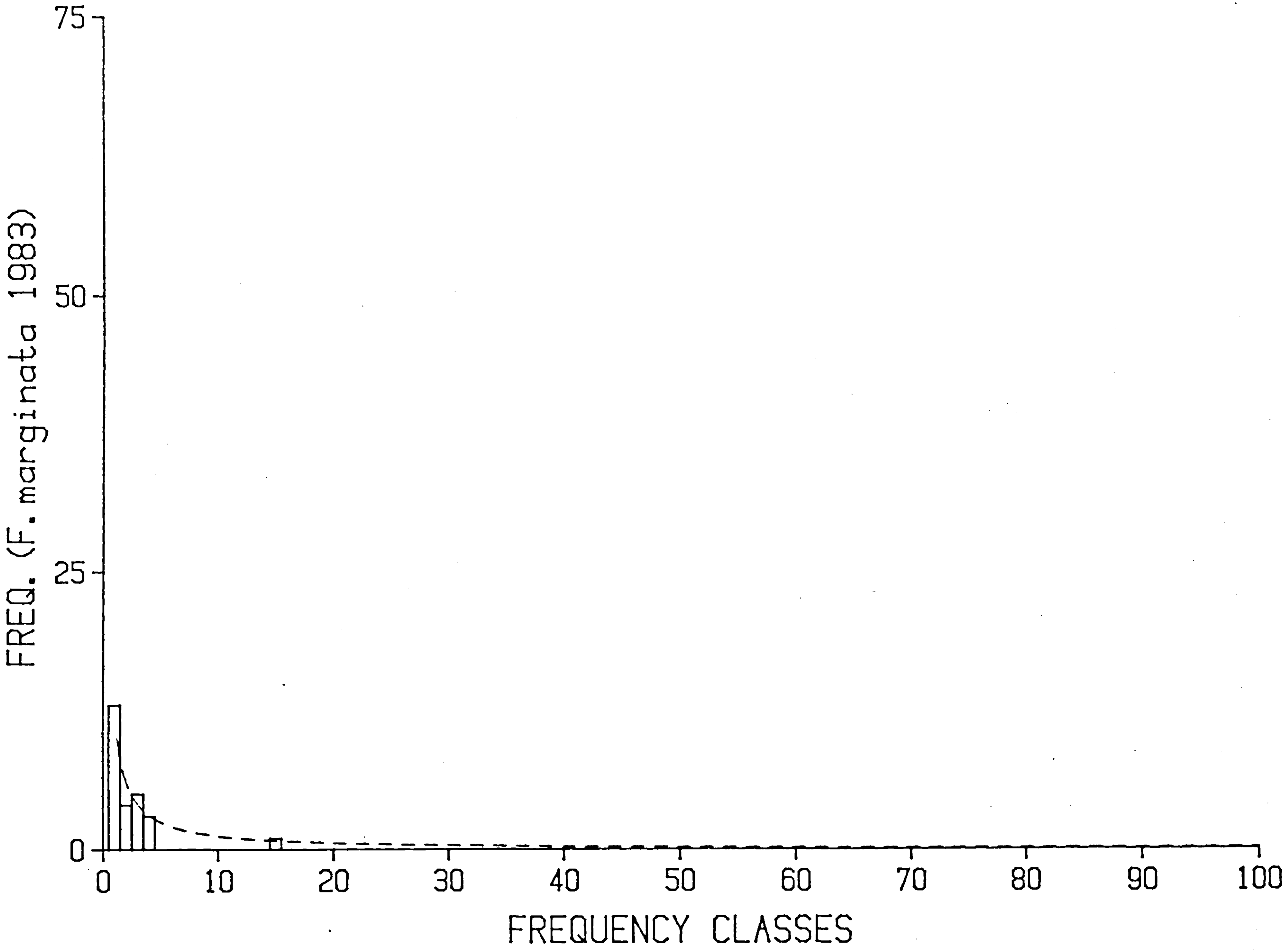
Table 18. Measurements of aphid clump size



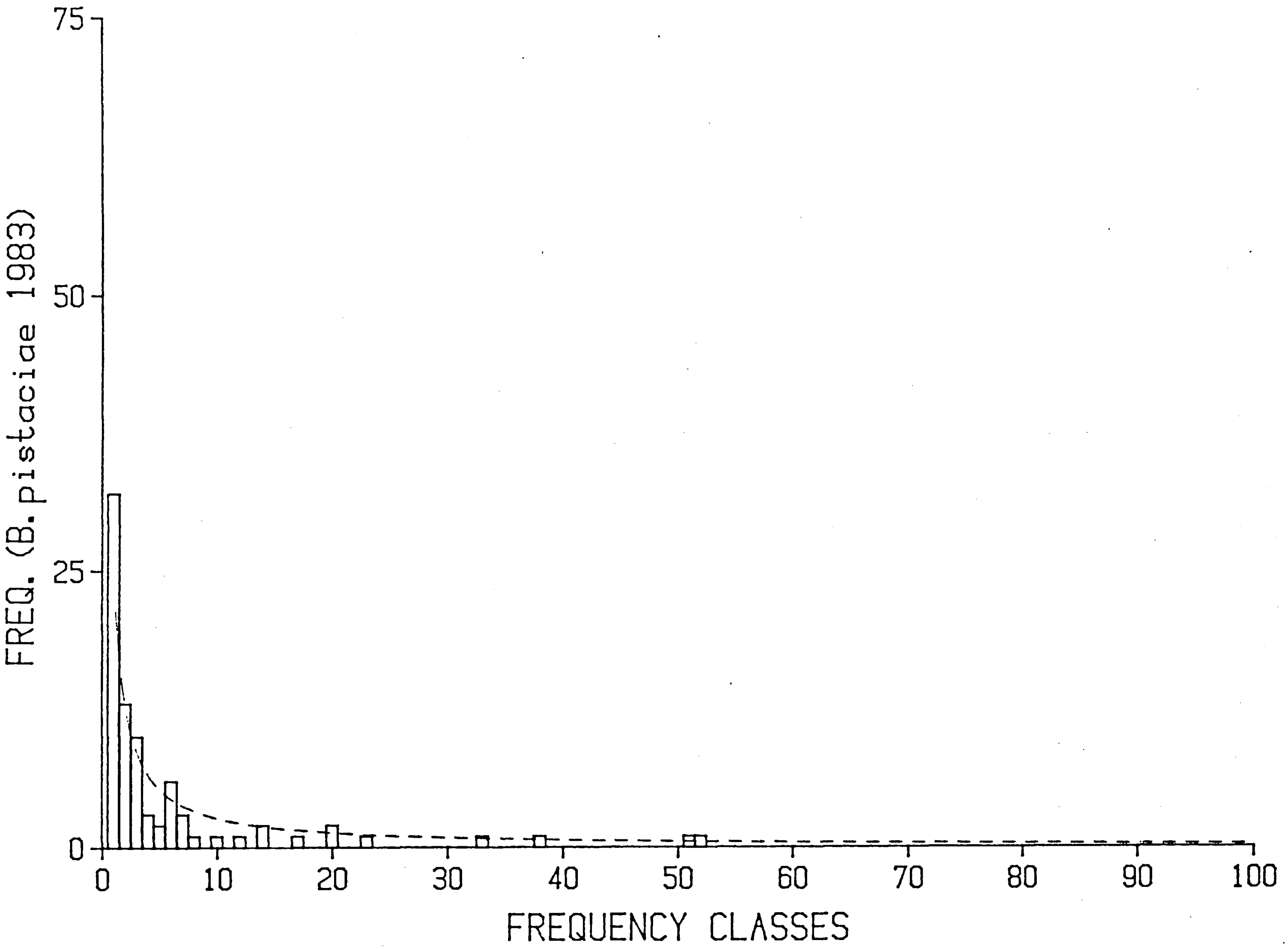
Graph 26. The frequency distribution of *Tetraneura ulmi* 1983.



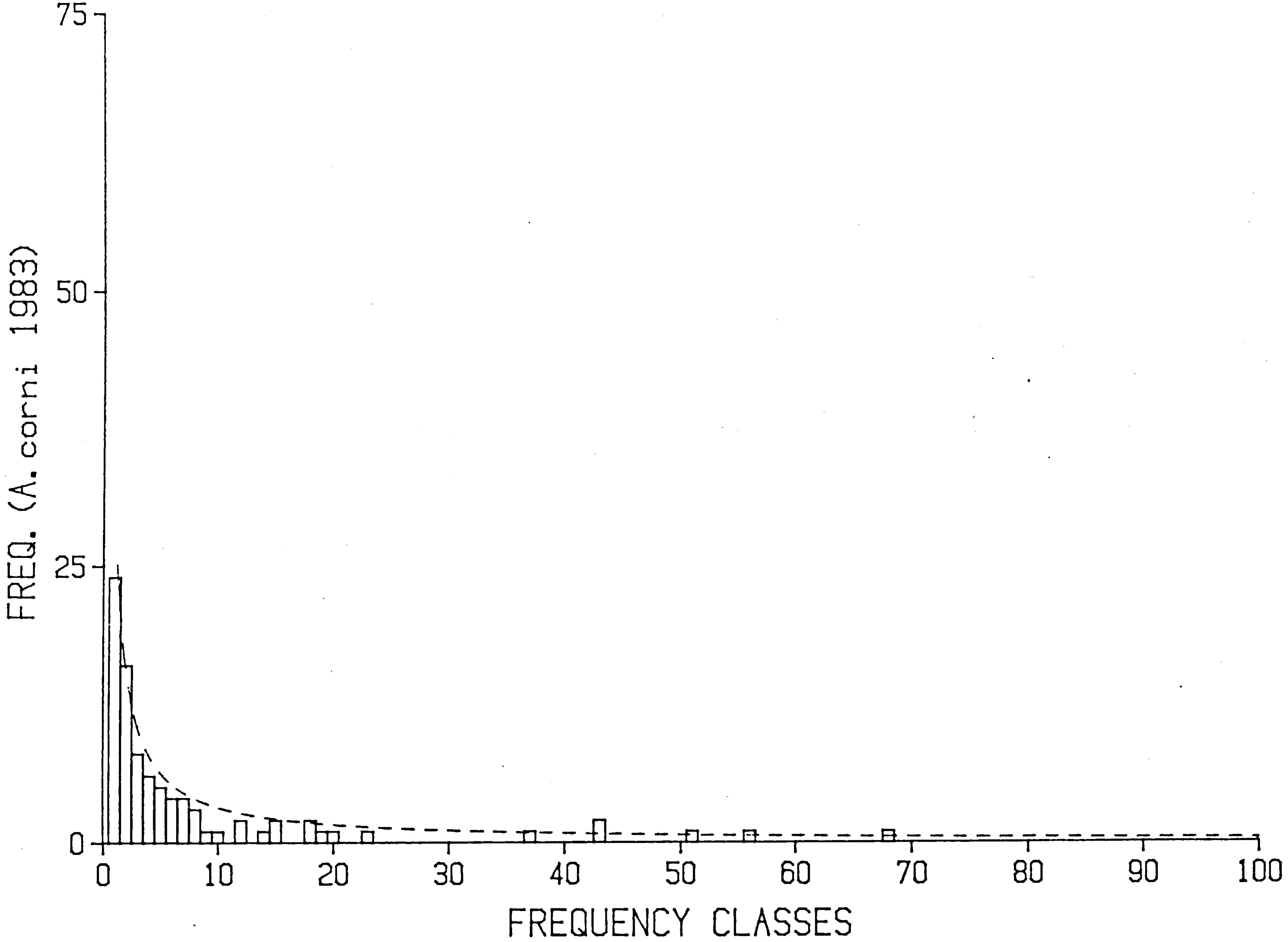
Graph 27. The frequency distribution of Forda formicaria 1983.



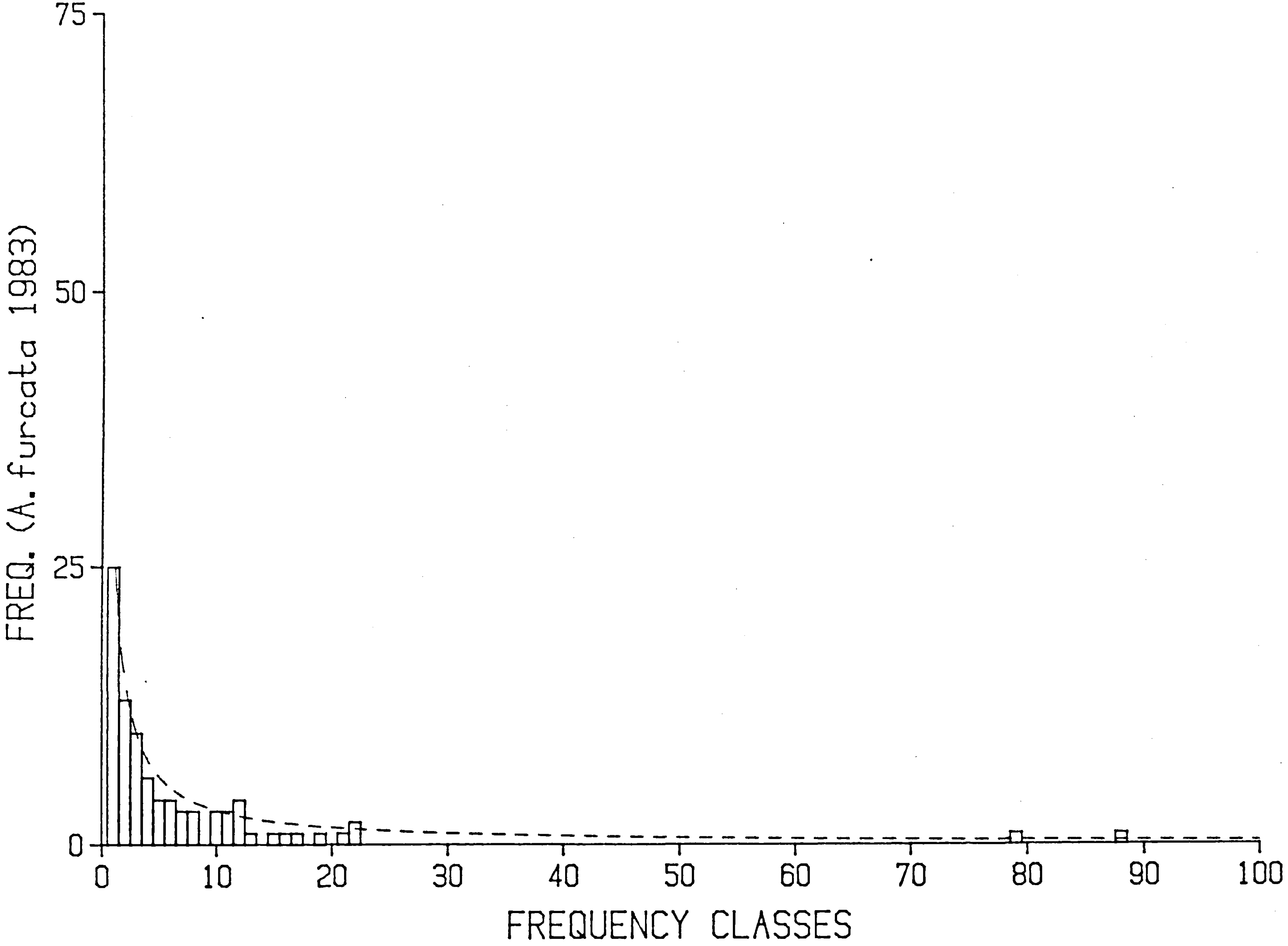
Graph 28. The frequency distribution of _Forda marginata_ 1983.



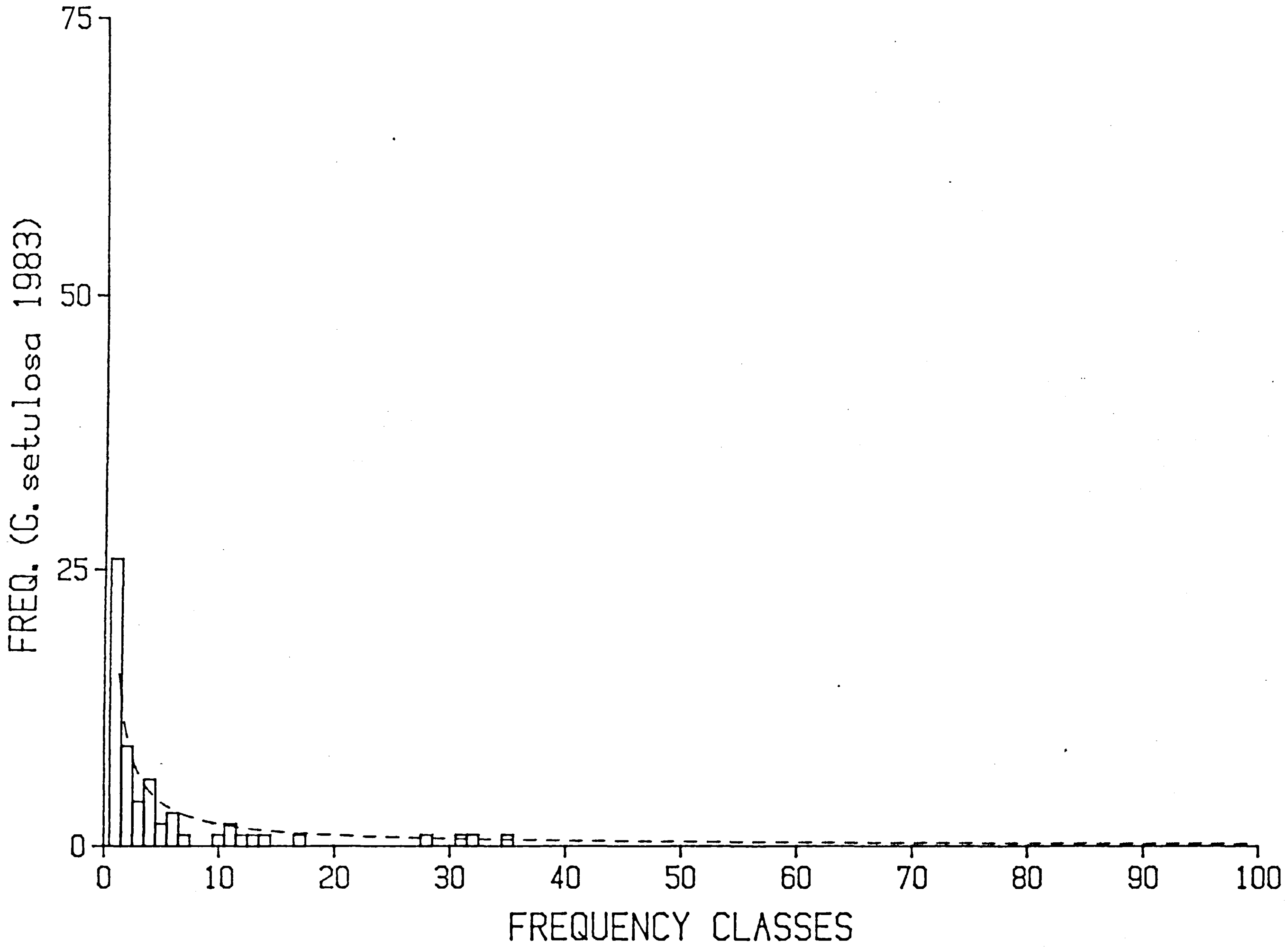
Graph 29. The frequency distribution of _Baizongia pistaciae_ 1983.



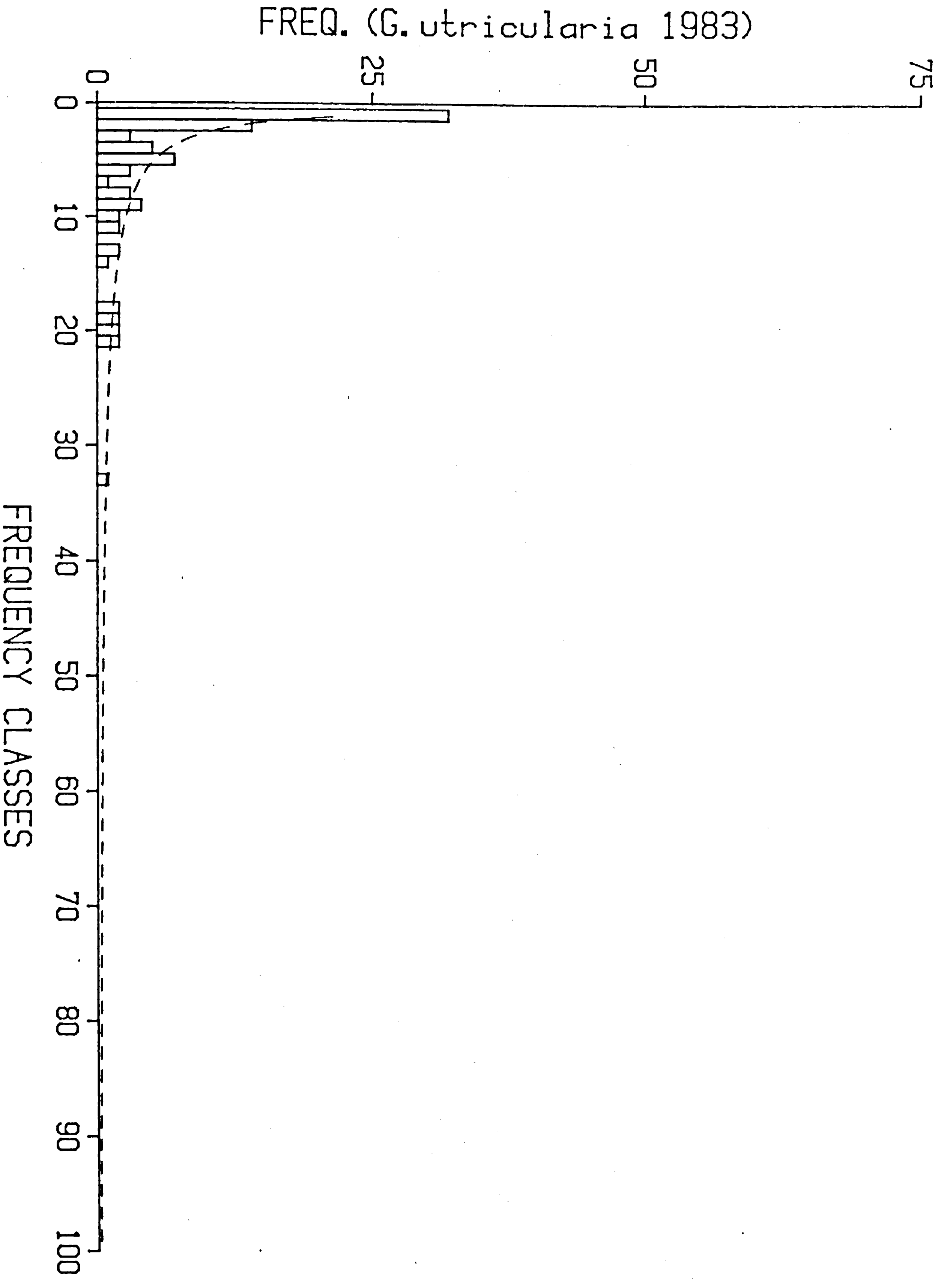
Graph 30. The frequency distribution of <u>Anoecia corni</u> 1983.



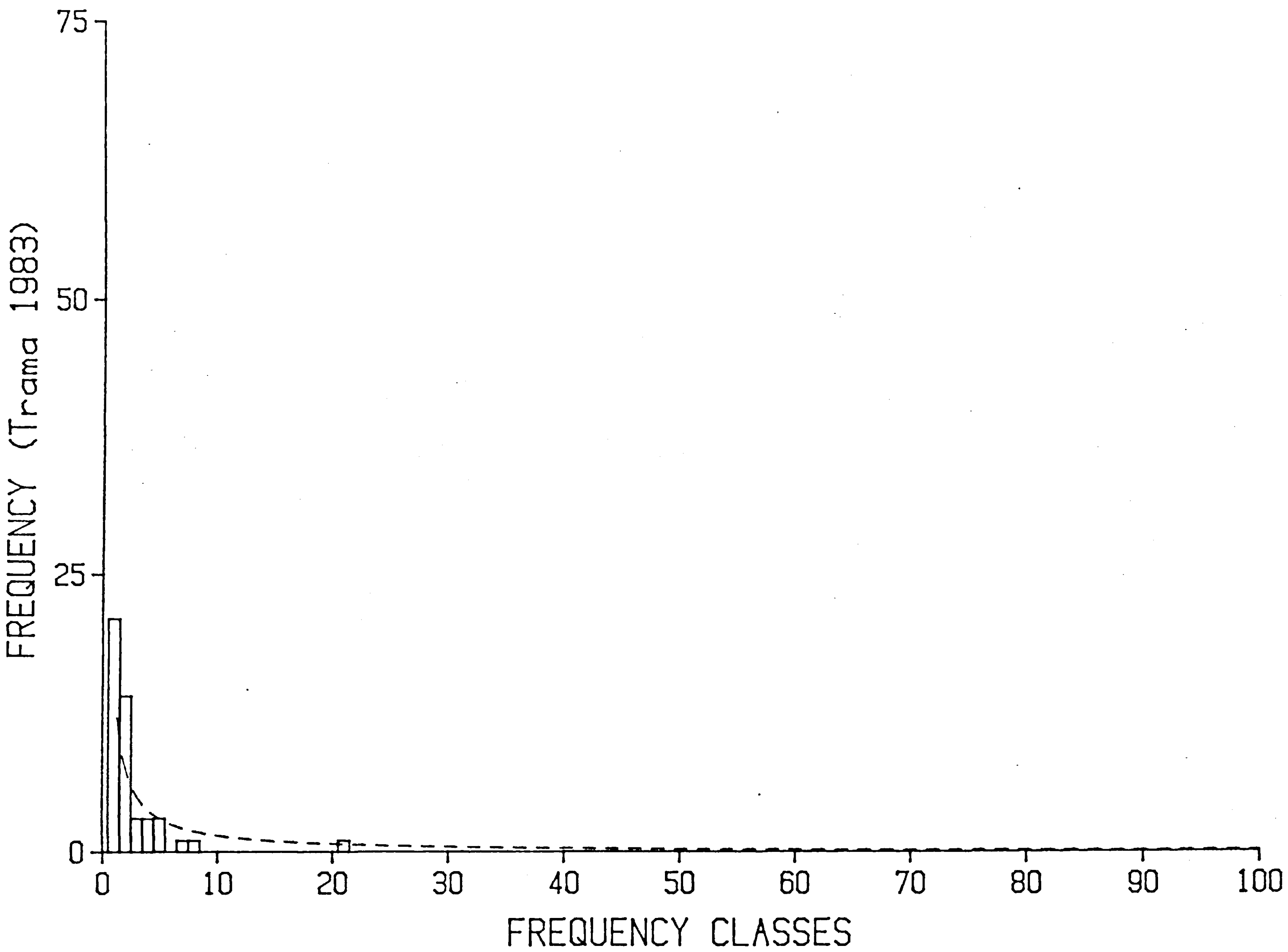
Graph 31. The frequency distribution of Anoecia furcata 1983.



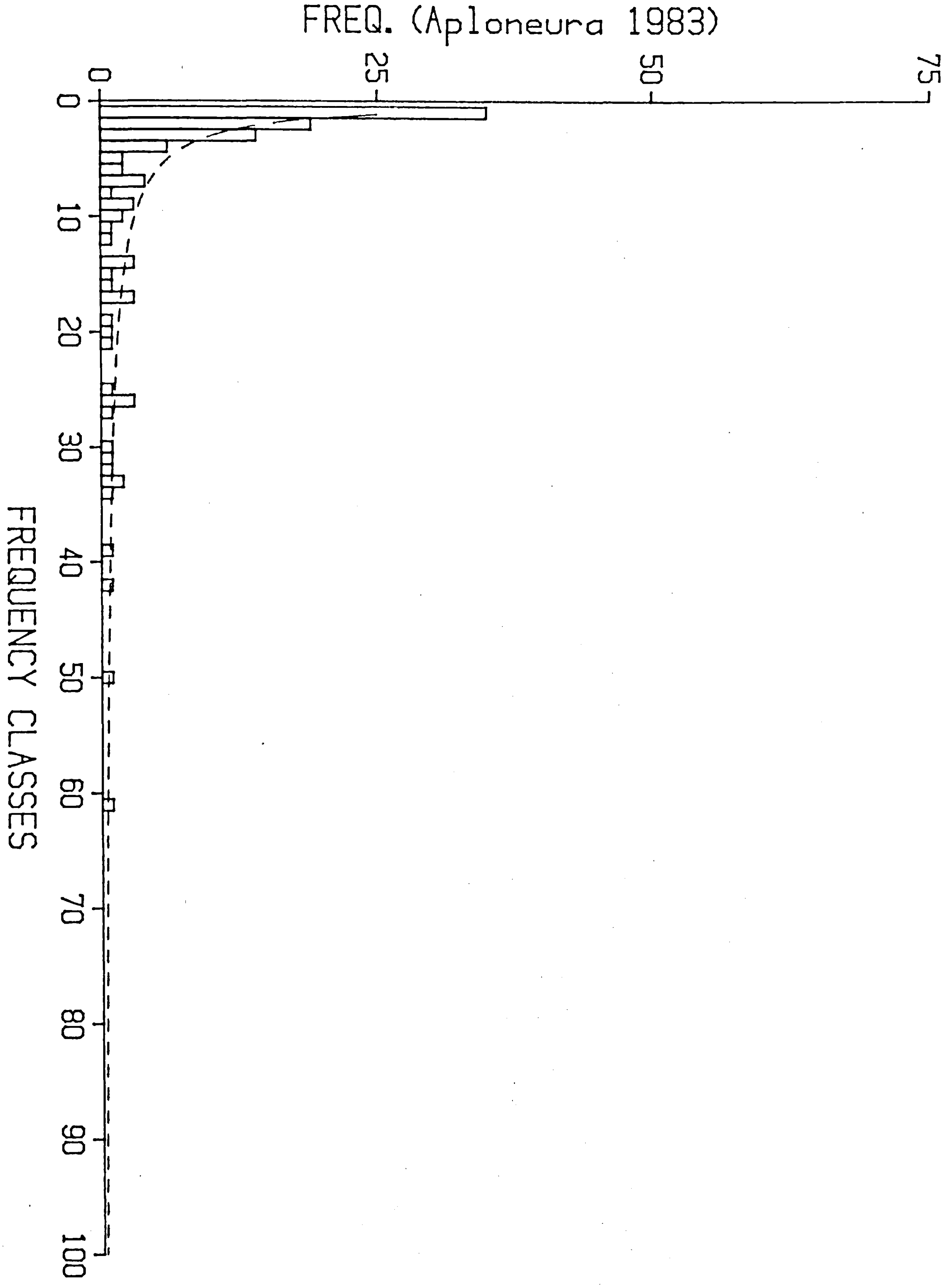
Graph 32. The frequency distribution of _Geoica setulosa_ 1983.



Graph 33. The frequency distribution of Geoica utricularia 1983.



Graph 34. The frequency distribution of *Trama troglodytes* 1983.



Graph 35. The frequency distribution of _Aploneura lentisci_ 1983.

Moreover the parameters which describe the reciprocal frequency equation:

$$y = N/kx$$

do have some biological significance;

N = the total number of aphids recorded

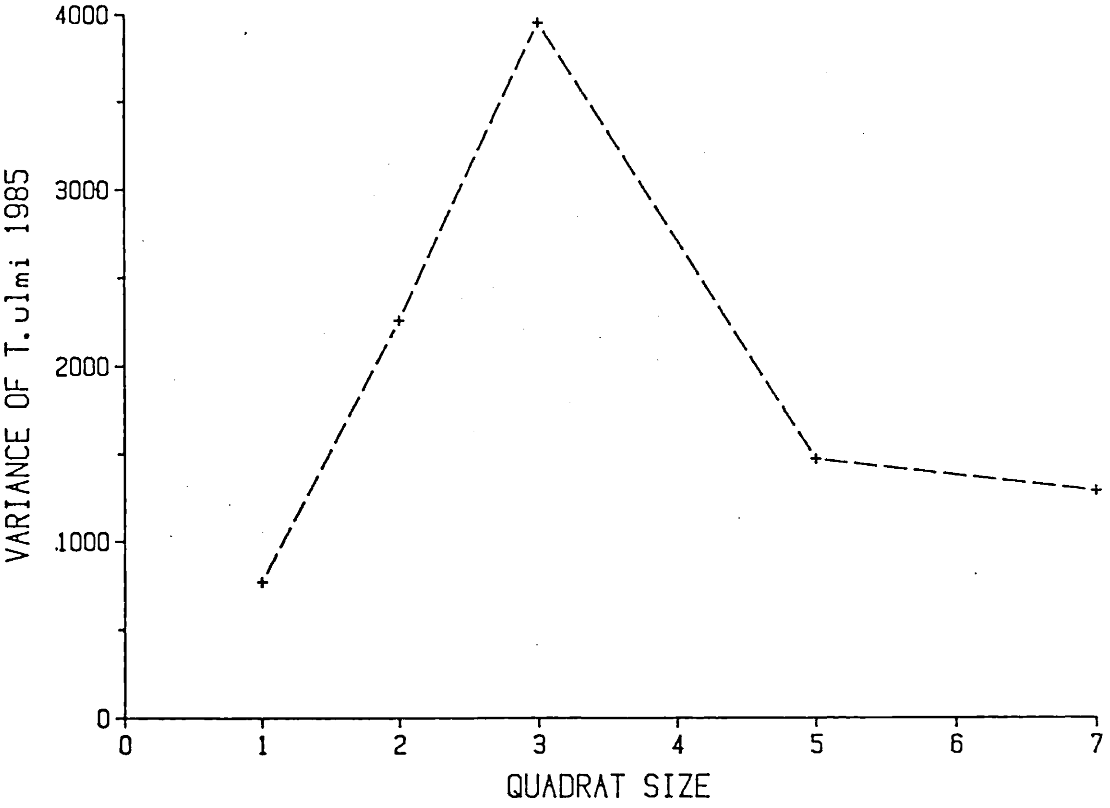
k = some measure of clumping as defined by

N/k = the mean number of aphids in a core (see Table 18).

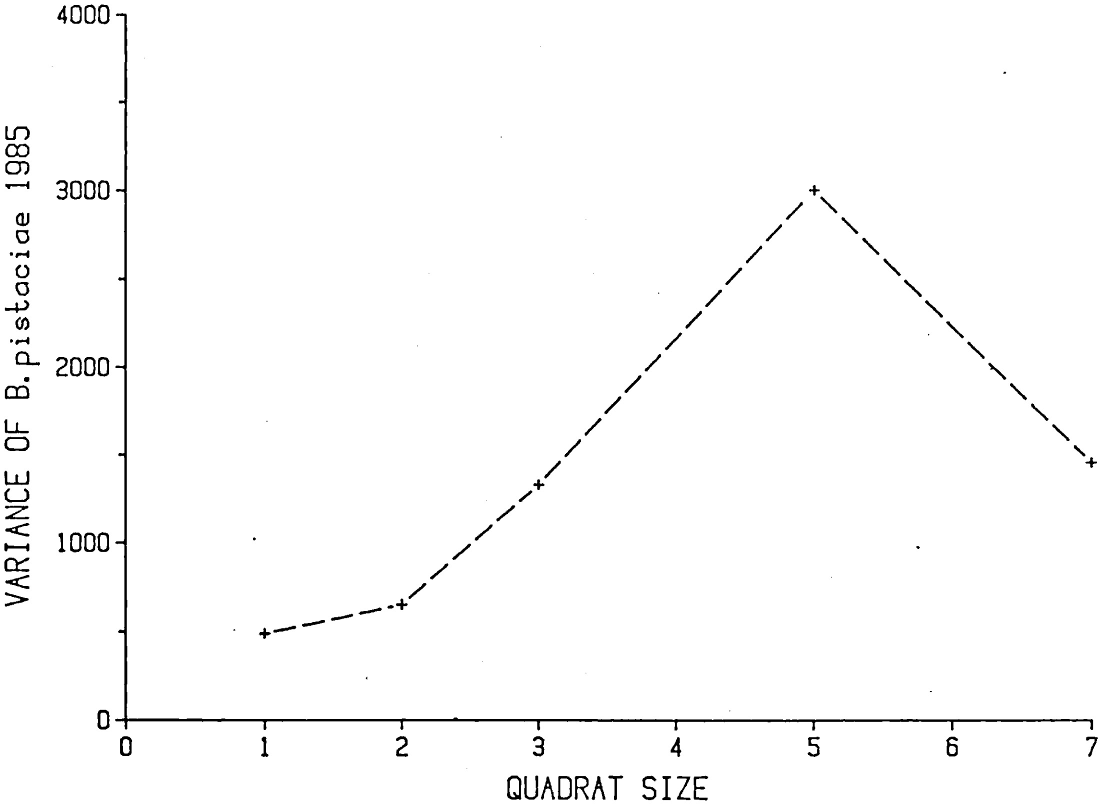
Further discussion of this model is restricted to appendix C.

Estimates of clump size can be obtained by using different size quadrats, or as in this case, by adding neighbouring contiguous quadrats to increase quadrat size, following the method of Kershaw (1973). As quadrat size is steadily increased, the dispersion of a clumped population may appear random, contagious and finally regular with very large quadrat size. The variance of the population size also changes, reaching a peak when the quadrat size equals clump size, then declines as the clumps appear regularly distributed. When species are at low density, the smallest quadrat size may be larger than the smallest clump, and in this situation, the variance rises steadily. Graphs 36-38, show the relationship between aphid variance and quadrat size. Table 18 summarizes the clump size for the 1985 aphid results.

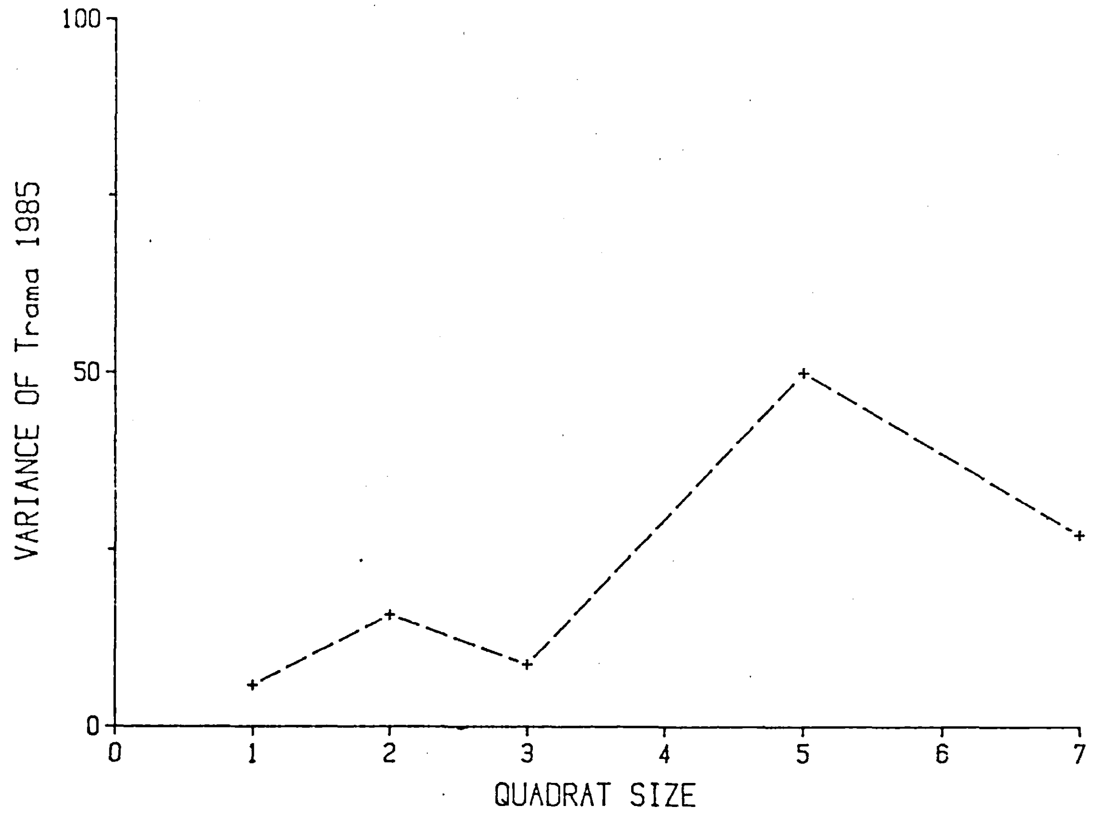
The first surprise is that the mean clump size for aphids is larger than the area of the corer. The clump size therefore does not represent the mean density of aphids per grass root, but perhaps the area covered by a 'family



Graph 36. The variance of Tetraneura ulmi with increasing quadrat size, 1985.



Graph 37. The variance of <u>Baizongia pistaciae</u> with increasing quadrat size, 1985.



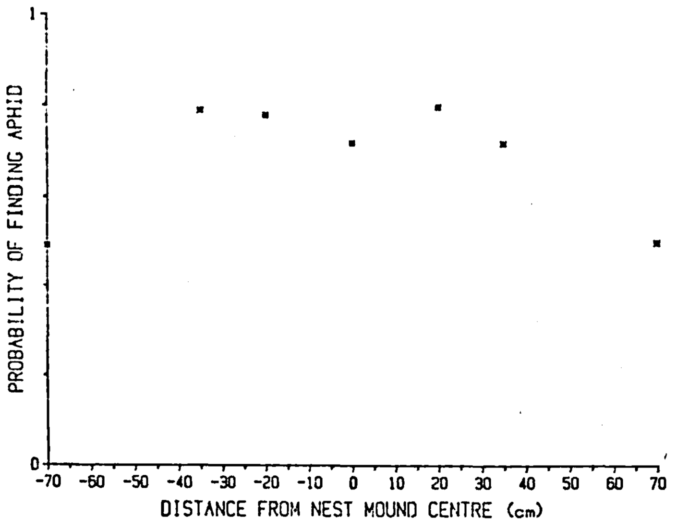
Graph 38. The variance of <u>Trama troglodytes</u> with increasing quadrat size, 1985.

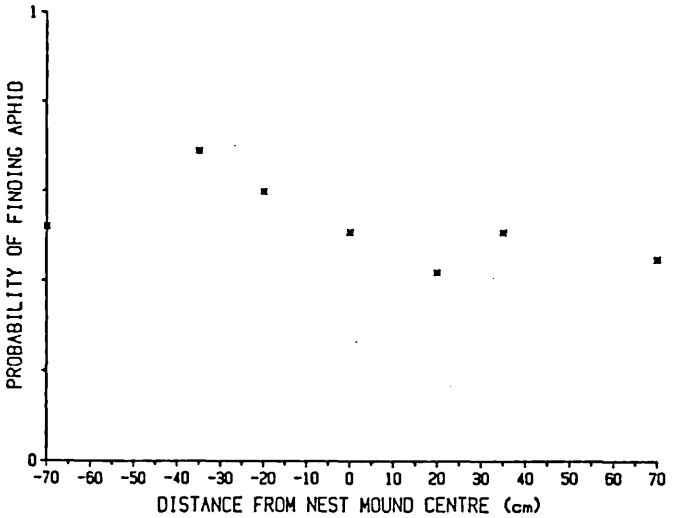
group'; those clones derived from a single female. The two clump sizes estimated for Trama troglodytes again do not reflect the number found per root, but may represent the different size 'family groups' supported by different size clumps of Compositae, a complication not found with gramnivorous aphids. The large clump sizes recorded for Anoecia furcata and Aploneura lentisci are due to low abundance in 1985. The mean density of clump shows that in general the Fordinae have larger clumps than the Eriosomatinae and Anoeciinae, which are larger than the Traminae.

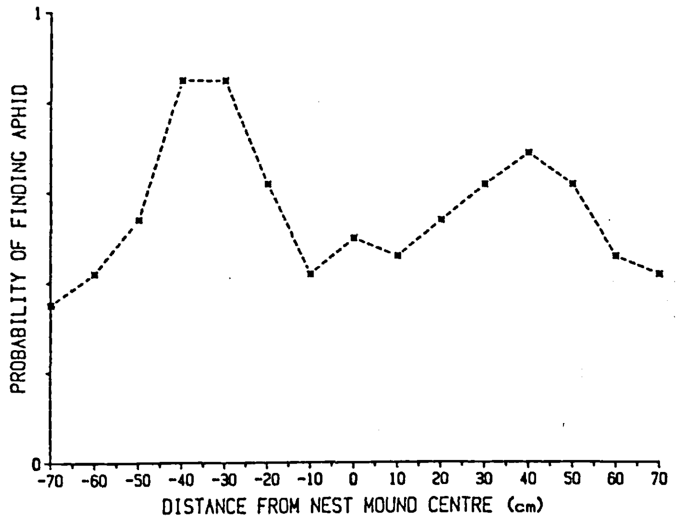
The mean density of aphids per core, calculated from the clump size and the frequency distribution show a fair agreement. The exception to this, Geoica setulosa is probably a failing of the variance method, as the N/k value is approximately the same for 1983,4 and 5. The mean density per core value depends upon the inferred clump size, and the scale for this is very coarse, thus providing a possible reason for the disagreement between the two measures. Pontin (1978), working on the same area of Staines Moor suggested that the clones produced by aphids may spread up to 0.5m before becoming unrecognizable.

4.32 The spatial separation of trophobionts in the nest mound.

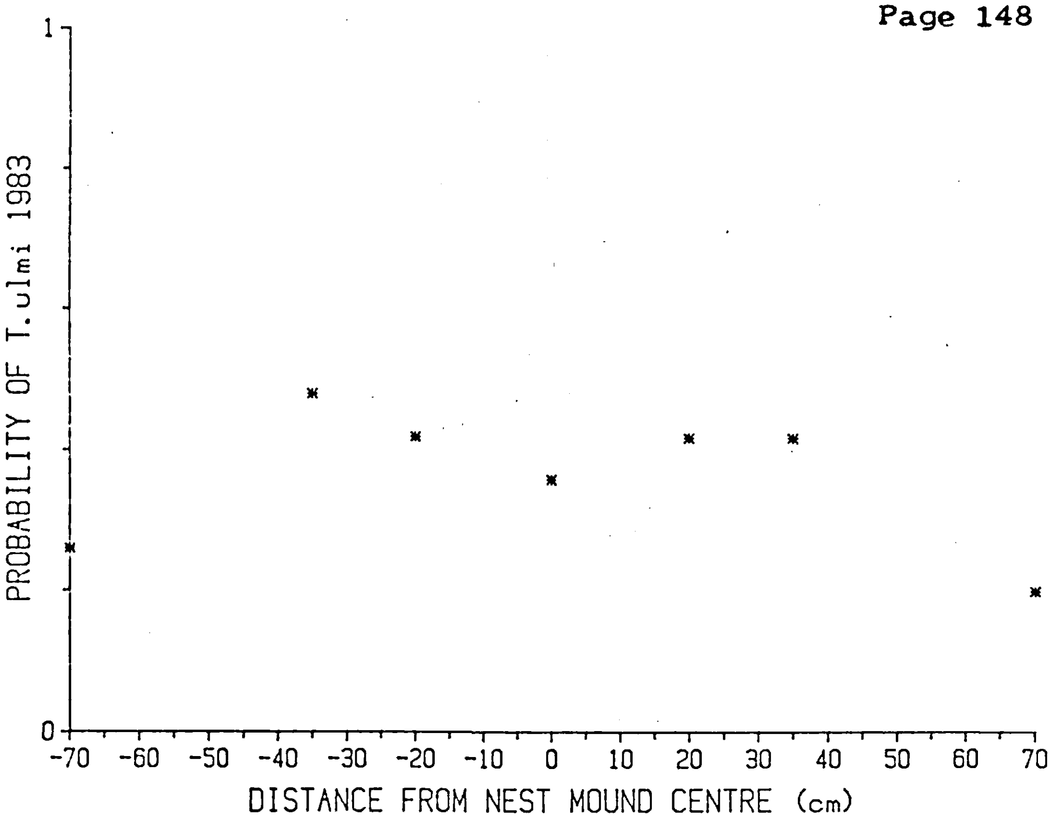
Ever since the Pilot study in 1982, there had been indications that certain aphids were more abundant at certain locations in the nest, and the sampling patterns were designed with this in mind. Graphs 39-41 describe the probability of one or more aphids occurring at a set distance from the centre of the nest mound (negative prefixes indicate Westerly directions, positive prefixes indicate Easterly directions), irrespective of species, per year. The graphs show that aphids are more common in the nest mound than in the surrounding territory. Within the nest mound the probability of finding an aphid is highest near the edge and lowest near the centre. Graphs 42-50 show the same trends per species in 1983, and present some noteworthy exceptions; both _Trama troglodytes_ and _Forda formicaria_ show fewer aphids at 70cm than would be expected from the combined 1983 data, and _Anoecia corni_ shows precisely the opposite distribution to the norm, with more aphids found in the nest territory than in the nest mound. The same information for 1985 is plotted in graphs 97-105 (see appendix E3). Again the same trends are present, but the reverse distribution of _A.corni_ is not so marked in 1985 because of the smaller number of aphids captured. Using the 1983 data, Chi-squared tests were carried out to find whether these observed differences in distribution could be attributed to chance.



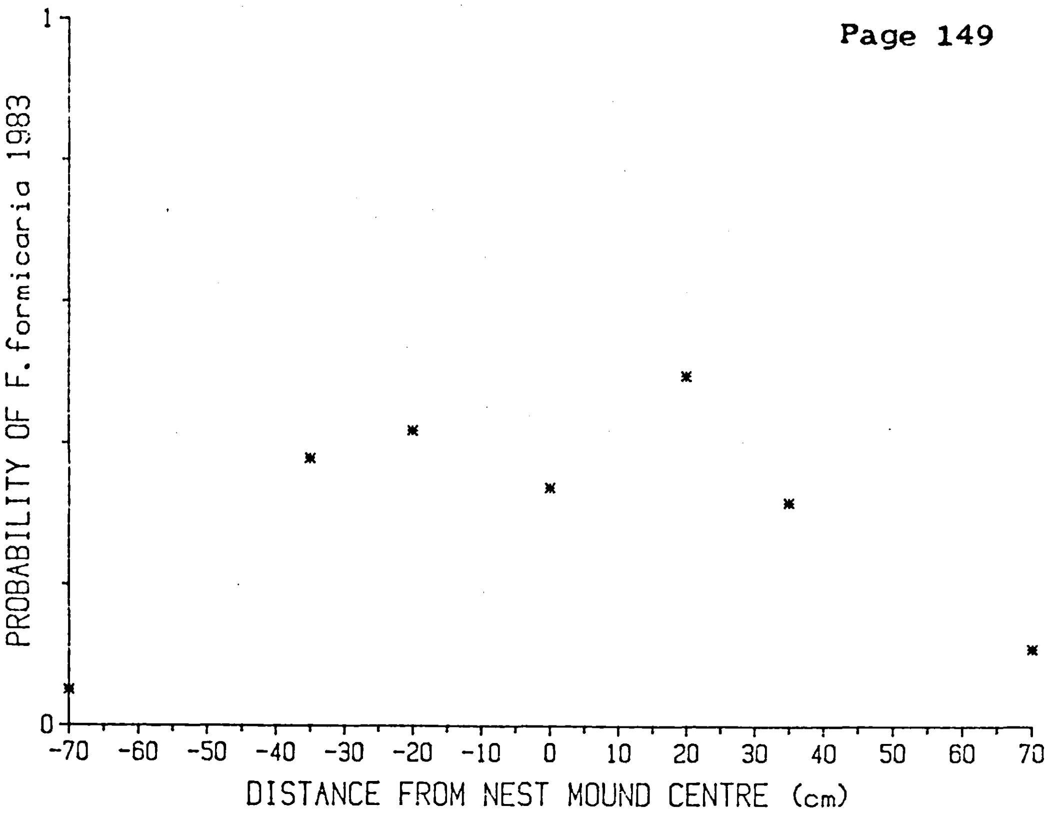




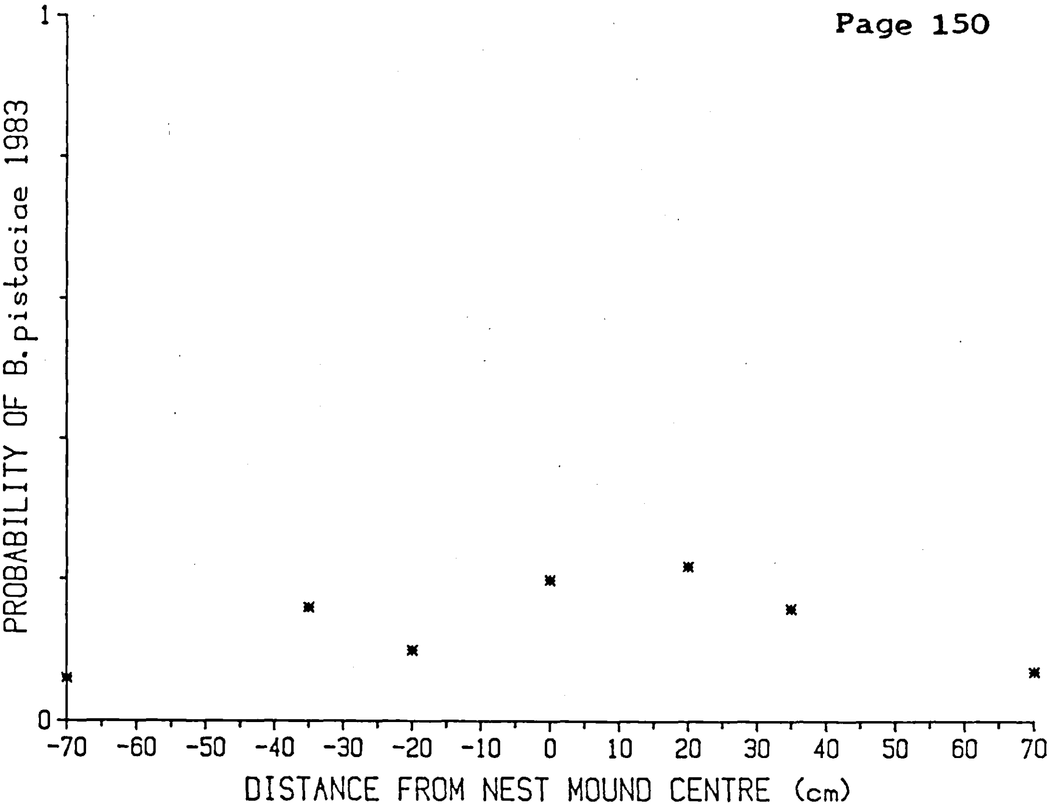
Graphs 39-41. The probability of finding one or more aphids at set distances from the centre of the nest mound, 1983, 1984, 1985 results.



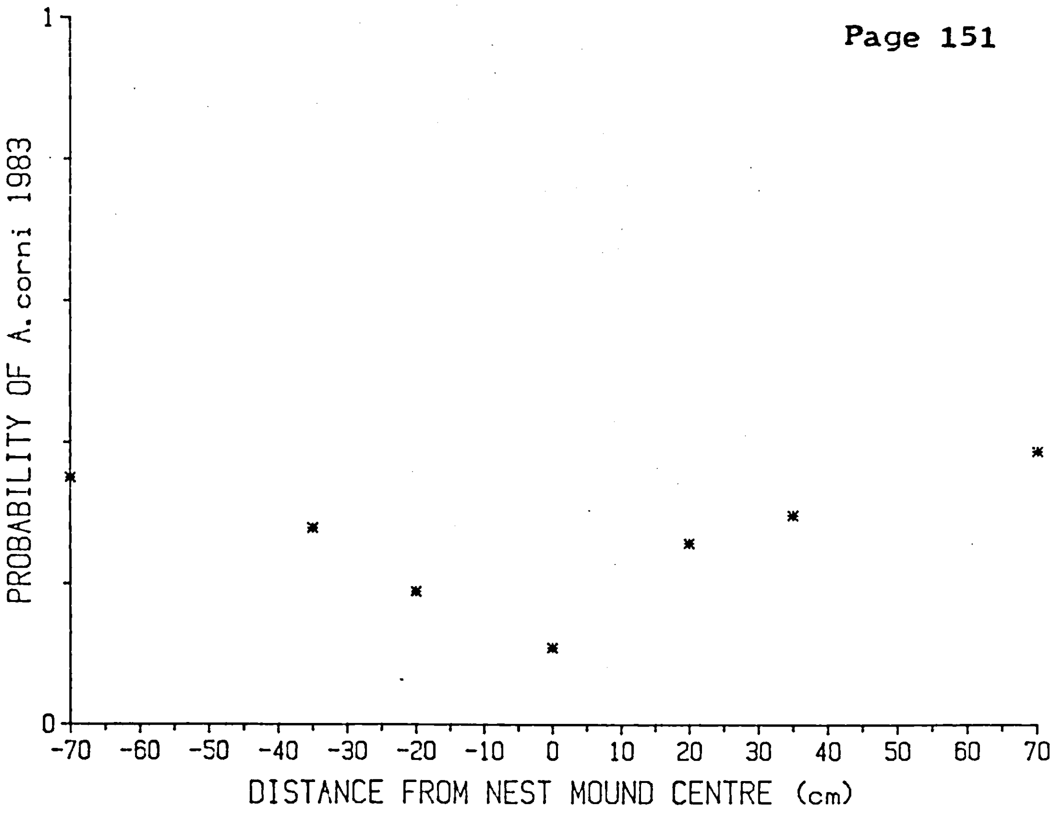
Graph 42. The probability of one or more *Tetraneura ulmi* per nest location.



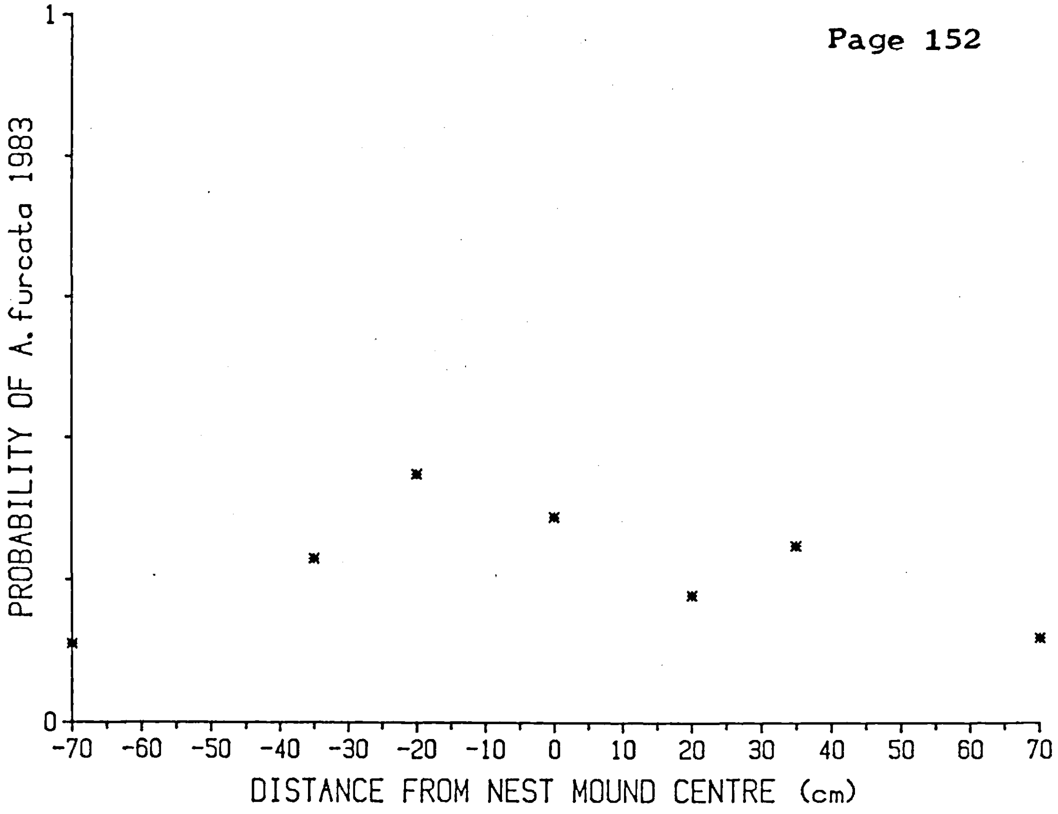
Graph 43. The probability of one or more <u>Forda formicaria</u> per nest location.



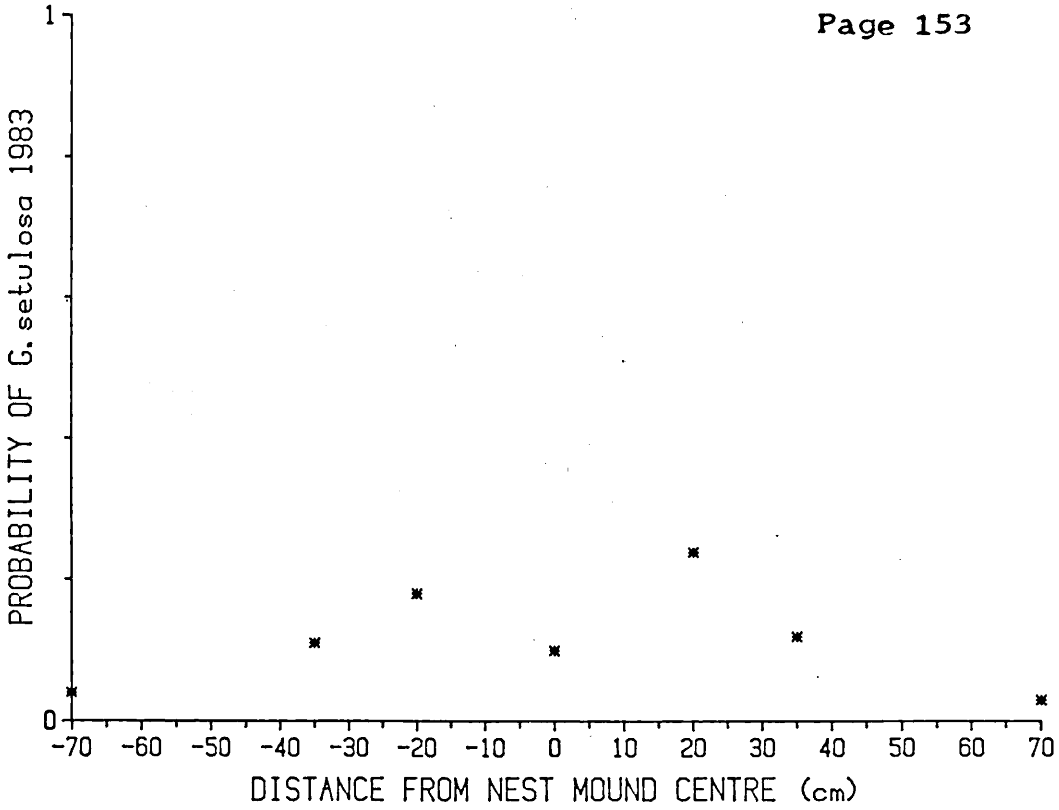
Graph 44. The probability of one or more *Baizongia pistaciae* per nest location.



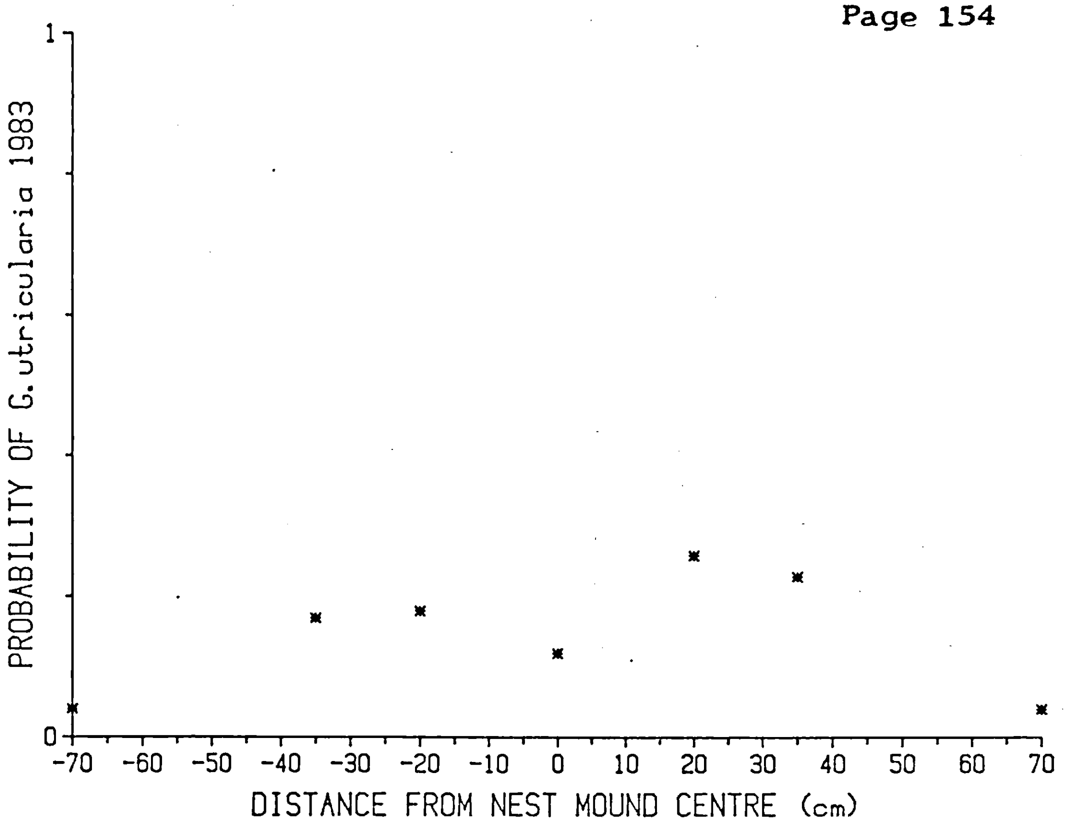
Graph 45. The probability of one or more *Anoecia corni* per nest location.



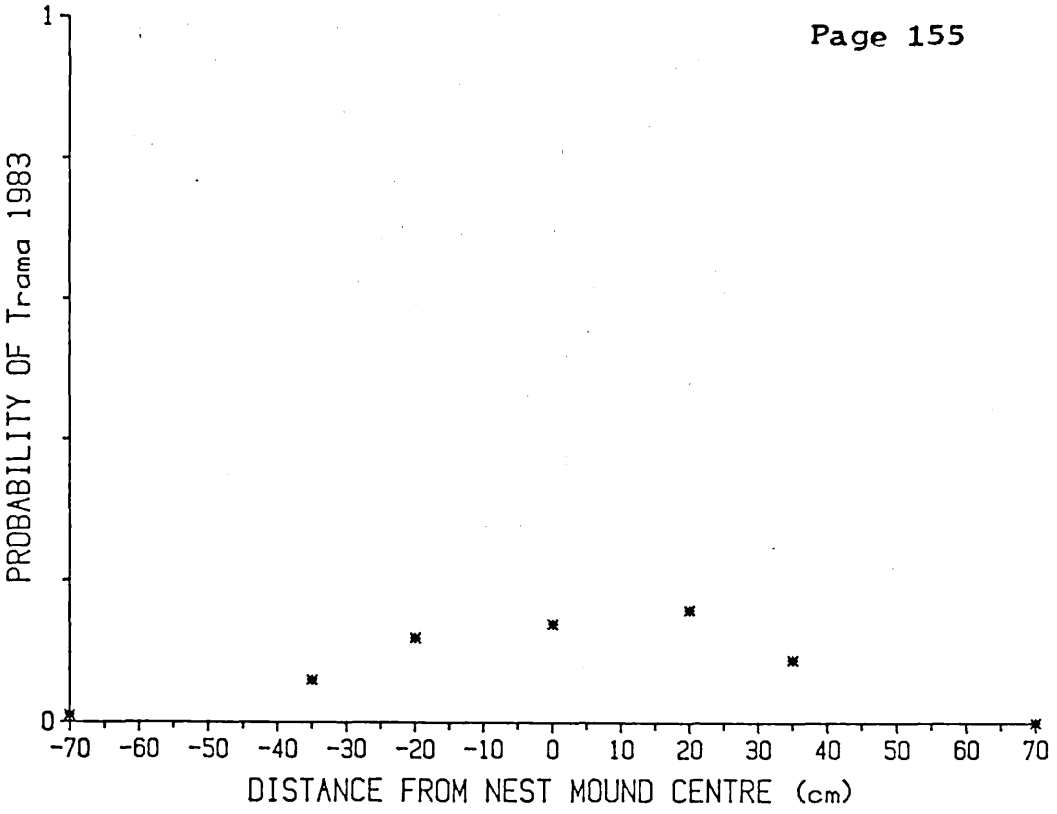
Graph 46. The probability of one or more *Anoecia furcata* per nest location.



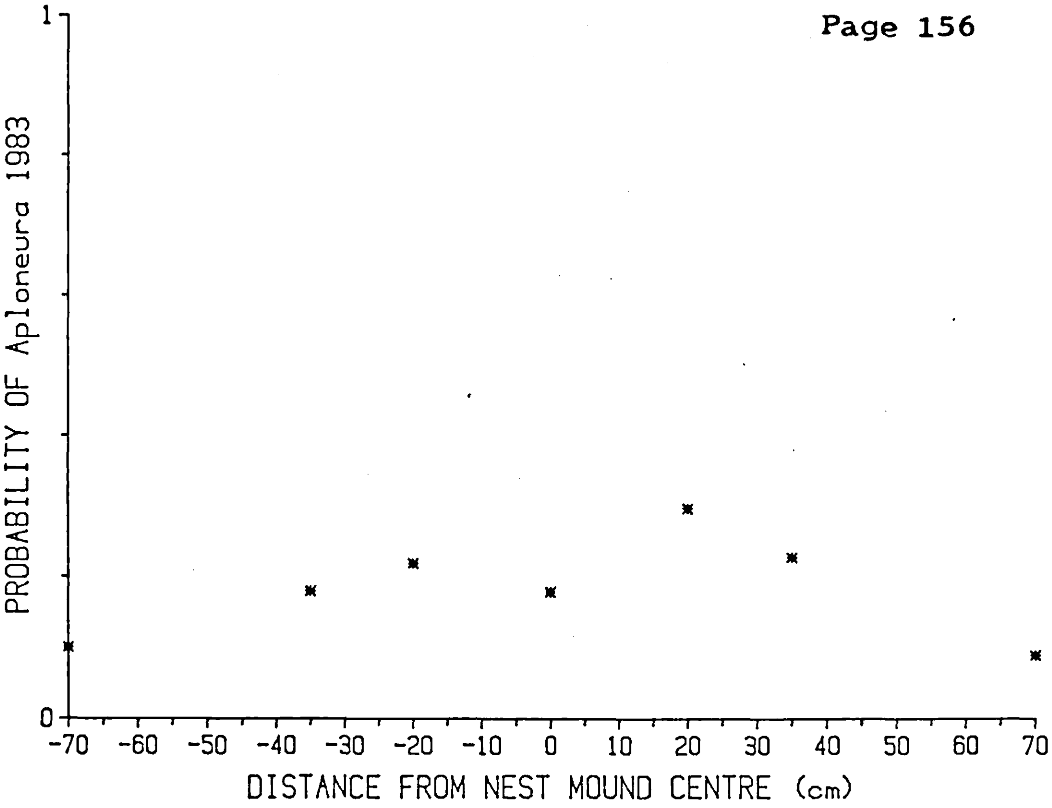
Graph 47. The probability of one or more _Geoica setulosa_ per nest location.



Graph 48. The probability of one or more *Geoica utricularia* per nest location.



Graph 49. The probability of one or more *Trama troglodytes* per nest location.



Graph 50. The probability of one or more _Aploneura lentisci_ per nest location.

	Distance from nest mound centre (cm)				Chi-squared value
	0	20	35	70	
Expected frequency	0.19	0.23	0.21	0.09	
Tetraneura ulmi	0.18	0.21	0.22	0.11	0.062
Forda formicaria	0.20	0.27	0.20	0.05	0.233
Baizongia pistaciae	0.24	0.20	0.19	0.08	0.108
Anoecia corni	0.08	0.13	0.22	0.28	5.970
Anoecia furcata	0.23	0.21	0.19	0.09	0.610
Geoica setulosa	0.16	0.29	0.20	0.07	1.440
Geoica utricularia	0.15	0.28	0.24	0.05	1.128
Trama troglodytes	0.28	0.26	0.16	0.01	1.088
Aploneura lentisci	0.18	0.25	0.19	0.1	0.032

Table 19. The probability of encountering a root aphid at a set distance from the nest mound centre, 1983.

Chi-squared, 3 D.F. (0.05) = 7.185

	January-March			November-December		
	Chi squared	p	Preferred location	Chi squared	p	Preferred location
Anoecia corni				3.45	N/S	
Anoecia furcata	1.25	N/S		0.09	N/S	
Baizongia pistaciae	1.08	N/S		9.32	0.05	not apparent
Forda formicaria	0.28	N/S		1.82	N/S	
Geoica setulosa	12.90	0.01	35cm	1.20	N/S	
Geoica utricularia	7.15	N/S		0.22	N/S	
Tetraneura ulmi	0.11	N/S		0.29	N/S	
Trama troglodytes	1.45	N/S		1.41	N/S	
Aploneura lentisci	0.58	N/S		1.02	N/S	

Table 20. Analysis of aphid nest position using probability of occurrence data (1983).

	January-March			November-December		
	Chi squared	p	Preferred location	Chi squared	p	Preferred location
Anoecia corni				18.51	0.001	70cm
Anoecia furcata	4.80	N/S		0.79	N/S	
Baizongia pistaciae	11.83	0.01	20cm	5.75	N/S	
Forda formicaria	6.69	0.1	35cm	1.64	N/S	
Geoica setulosa	29.36	0.001	35+70cm	2.91	N/S	
Geoica utricularia	2.13	N/S		2.94	N/S	
Tetraneura ulmi	16.48	0.001	70cm	0.26	N/S	
Trama troglodytes	4.97	N/S		1.33	N/S	
Aploneura lentisci	1.63	N/S		1.82	N/S	

Table 21. Analysis of aphid nest position using mean density data (1983).

	January-March			November-December		
	K	p	Preferred location	K	p	Preferred location
Anoecia corni				1.06	N/S	
Anoecia furcata	1.30	N/S		8.09	0.05	
Baizongia pistaciae	10.53	0.05		0.02	N/S	
Forda formicaria	9.78	0.05		2.51	N/S	
Geoica setulosa	0.38	N/S		2.70	N/S	
Geoica utricularia	1.67	N/S		2.36	N/S	
Tetraneura ulmi	19.15	0.001		15.24	0.01	
Trama troglodytes	2.89	N/S		2.57	N/S	
Aploneura lentisci	2.06	N/S		2.65	N/S	

Table 22. Analysis of aphid nest position using Kruskal-Wallis one way analysis by ranks.

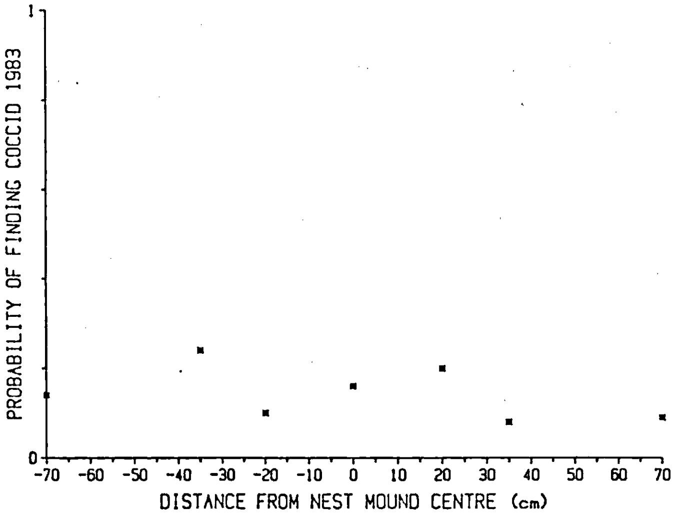
The 'expected' value was derived from the mean probability of an aphid per location. These values are shown in Table 19. As a whole over the year, aphids have a certain distribution (0=20<35>70). Individual species do not depart from this distribution (0.99>p>0.25) and any difference observed in the field can in part be attributed to the relative abundance of the aphids.

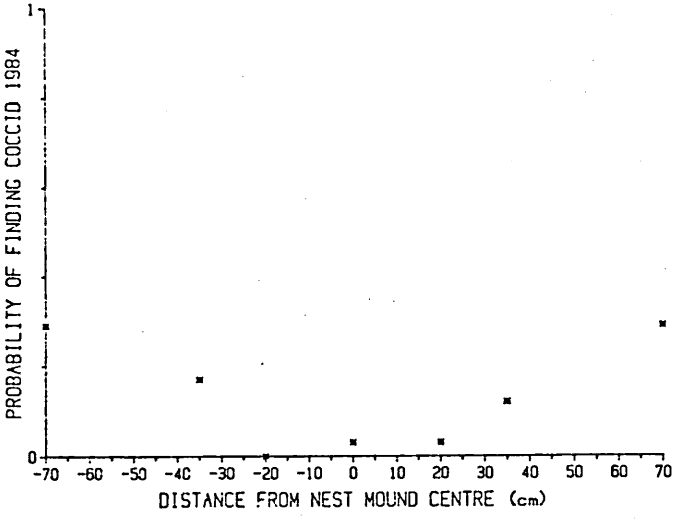
It is known that aphids are more abundant in early Spring and late Autumn (see section 4.2), therefore if a difference in aphid nest locations did exist, it was reasoned that it would be most apparent at these times of year, and furthermore real numbers should be analysed as well as probabilities of aphid occurrence. Therefore 1983 records were analysed from January to March and from November to December (see Tables 20-21). Kruskal-Wallis one way analysis of ranks was also applied to the 1983 results. It was expected that this test would provide levels of significance intermediate between those found with the other two tests, because although it does not deal with actual values of abundance, it does at least rank them, rather than just considering the aphid species as being present or absent, (see table 22). In general there is no interspecific difference in nest location when probabilities of aphid occurrence were considered. The exceptions to this are Baizongia pistaciae in November to December, when there was a hint that they occur more often 20cm from the nest, and Geoica setulosa which was more frequent at 70cm from the nest centre in January to March (p<0.01), but the trend was not observed in the November to December records.

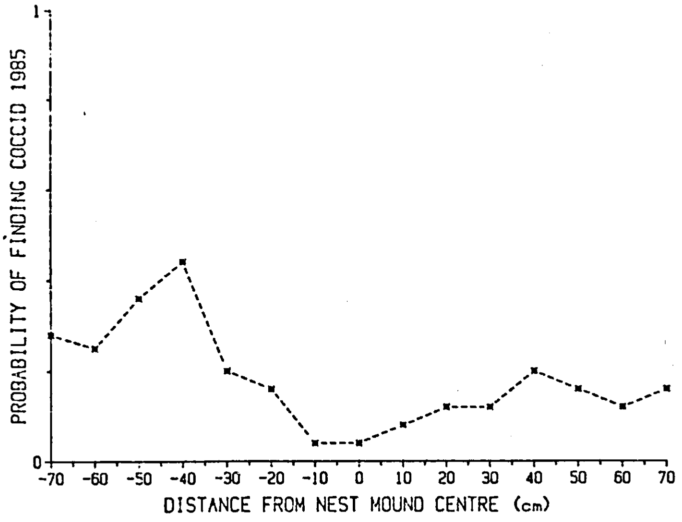
When mean density is considered instead of mean occurrence, strong differences appear between some aphids. *Tetraneura ulmi* although being most abundant at 20cm, also shows a peak at 70cm, which is far greater than can be explained away by chance ($p<0.001$). What provides even stronger support for this trend, is that during January to March, first instar nymphs are uncommon and therefore heat extraction errors are unlikely to be responsible for this. *Geoica setulosa* is far more abundant at both 35cm and 70cm than expected ($p<0.001$). There is also a fairly strong suggestion that *Baizongia pistaciae* is more abundant in the centre of the nest mound than expected during January to March ($p<0.01$). In November and December, aphid numbers are generally lower than in early Spring. The exception to this is *Anoecia corni* which was more abundant at 70cm than expected ($p<0.001$). Again *T.ulmi* is the most abundant aphid at 70cm, and *G.setulosa* is most abundant at 35cm, but no statistical difference is found. The Kruskal-Wallis test backs up these findings to some extent. It attaches greater importance to the distribution of *Forda formicaria*, *Tetraneura ulmi* and *Anoecia furcata*, but fails to find any spatial difference in the distributions of *Geoica setulosa* or *Anoecia corni*, in the latter case due to lack of results.

Baizongia pistaciae, *Tetraneura ulmi* and *Forda formicaria* were found to have different distributions in the nest mound at times of high aphid abundance (and therefore high interspecific competition). There are also suggestions that the same may be true for *Anoecia corni*, *Anoecia furcata* and *Geoica setulosa*. These findings are in agreement with the trends found in the Pilot Study.

The other trophobionts in the ant nest are coccids. Like aphids they also show clumped distributions, and are found throughout the nest. Graphs 51-53 show the probability of their occurrence for 1983,4,5. The trends are not in perfect agreement, but in general coccids are most common away from the nest mound, and least common in the centre of the nest. Estimates of clump size cannot be determined which implies that the clump size for coccids is smaller than the smallest core, which is a realistic suggestion as coccids are far more sedentary than aphids, and have different life history and dispersal behaviour.







Graphs 51-53. The probability of finding one or more coccids at set distances from the centre of the nest mound, 1983, 1984, 1985 results.

4.4 The association between trophobionts

With eight species of aphid and one species of coccid all feeding on the same range of grasses within the ant nest, some form of interaction is to be expected. These interactions can take the form of positive, negative and null associations. A null association implies no interaction between species. A negative association implies that one aphid is reducing the vigour of the other species from the levels they would obtain independently; where vigour includes fecundity, density etc. The common causes of this are competition, when each species has the same environmental requirement which is in short supply; production of substances by one organism which are inhibitory to the other one; and interference of one species with another, which reaches its extreme with predation. The term 'competition' has been avoided subsequently, because this aspect of negative associations can only be shown under controlled conditions. There were too many possible causes of negative association in the field, and my laboratory experiments were not conclusive. Equally positive associations can occur; if species do not share all environmental requirements; if one species in exploiting the environment, modifies it in such a way to allow the establishment of another.

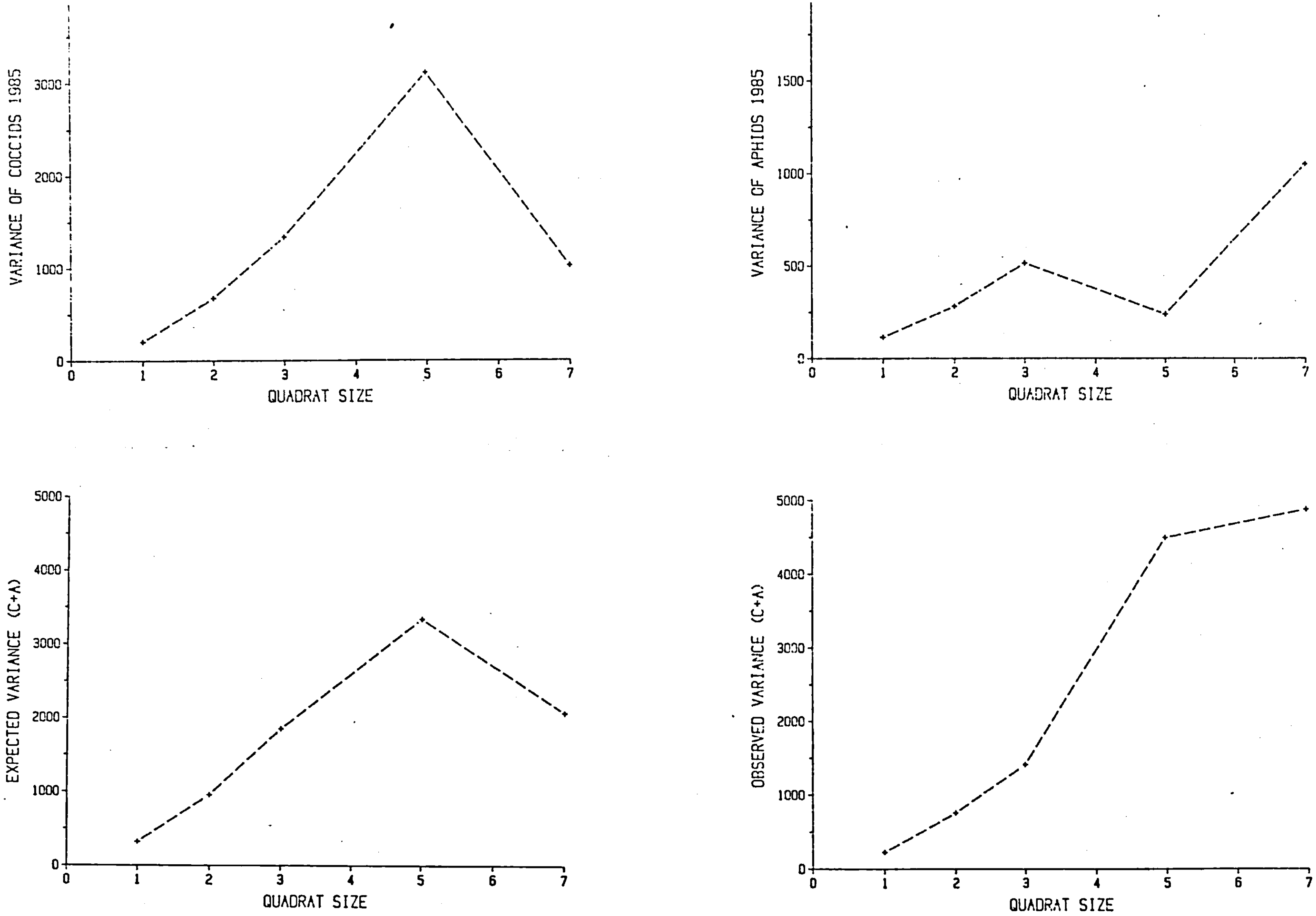
Many statistical tests can be used to determine association between variables. Regression and correlation analyses are mathematically quite similar, both sharing many of the computational steps. Regression describes the dependance of a variable Y on an independent variable X, which one can control experimentally. Whilst correlation is used when one is concerned whether two variables vary together or not. Such covariance is expressed as a value, not as a function one of another. Correlation is the correct method to use when one wishes to establish the intensity of association between pairs of variables in a population sample. It is essentially a descriptive technique, a statistically marked correlation does not imply causation.

Alternatively Contingency Tables can be used as a test of independence between variables, but this requires a proportion of ant nests which contain neither species under consideration.

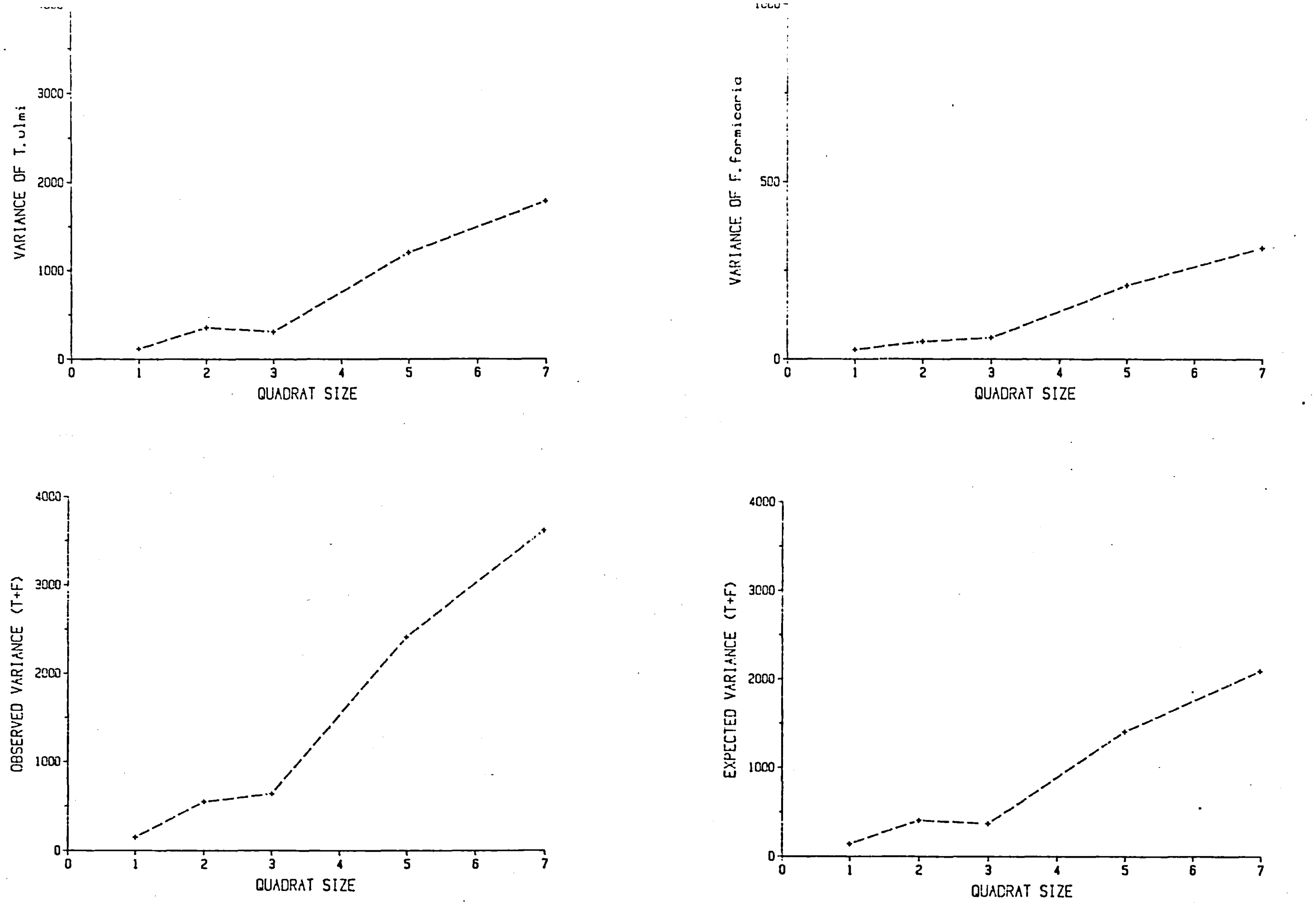
The method for determining clump size, outlined in section 4.31, can also be adapted to determine the degree of association. The covariance of two variables depends on their relatedness, i.e. if

Variance A + Variance B = Variance (A+B)

then there is no association between variables. Conversely if they are associated in some way, the observed covariance will be different from this expected value, higher in the case of positive association, lower in the case of negative association. This is demonstrated in graphs 54-55, and further explained in Kershaw (1973, p.142 et seq). Graphs 54a and b show the variance of aphids and coccids in 1985 respectively. Graph 54c shows the expected variance (variance of aphids + variance of coccids). Graph 54d shows the observed variance of aphids and coccids, derived from calculating their variance together. This shows an increase in variance above that expected from theoretical considerations, hence there is a positive association (but not statistically marked). Similarly for graphs 55a-d.



Graph 54. The association between aphids and coccids as determined by the graphical variance method.



Graph 55. The association between *Tetraneura ulmi* and *Forda formicaria* as determined by the graphical variance method.

	Coccids	Tetraneura ulmi	Forda formicaria	Baizongia pistaciae	Anoecia corni	Anoecia furcata	Geoica setulosa	Geoica utricularia	Trama troglodytes	Aploneura lentisci
Coccids	-	-0.027	0.389	-0.028	-0.403	0.082	0.196	0.019	-0.162	0.269
Tetraneura ulmi		-	0.224	0.168	0.083	0.158	0.206	0.506	-0.100	0.141
Forda formicaria			-	0.292	-0.539	0.240	0.264	0.402	-0.086	0.531
Baizongia pistaciae				-	-0.103	-0.182	0.282	0.345	-0.116	0.157
Anoecia corni					-	-0.213	-0.243	-0.114	-0.007	-0.468
Anoecia furcata						-	0.091	0.139	0.264	0.206
Geoica setulosa							-	0.484	-0.079	0.091
Geoica utricularia								-	-0.139	0.100
Trama troglodytes									-	0.035
Aploneura lentisci										-

Table 23 Non-parametric correlations (RHO) for aphids 1983

	Coccids	Tetraneura ulmi	Forda formicaria	Baizongia pistaciae	Anoecia corni	Anoecia furcata	Geoica setulosa	Geoica utricularia	Trama troglodytes	Aploneura lentisci
Coccids	-	-0.004	-0.208	-0.222	-0.098		-0.143	-0.055	0.114	0.241
Tetraneura ulmi		-	0.519	0.338	0.053		0.493	0.527	-0.379	0.175
Forda formicaria			-	0.586	-0.118		0.456	0.584	-0.027	-0.08
Baizongia pistaciae				-	0.050		0.614	0.733	0.066	-0.195
Anoecia corni					-		-0.111	-0.234	0.221	0.12
Anoecia furcata						-				
Geoica setulosa							-	0.521	-0.206	-0.371
Geoica utricularia								-	-0.102	0.121
Trama troglodytes									-	-0.066
Aploneura lentisci										-

Table 24 Non-parametric correlations (RHO) for aphids 1984

	Coccids	Tetraneura ulmi	Forda formicaria	Baizongia pistaciae	Anoecia corni	Anoecia furcata	Geoica setulosa	Geoica utricularia	Trama troglodytes	Aploneura lentisci
Coccids	-	-0.092	0.277	0.224	-0.107	-0.061	0.008	-0.039	0.072	-0.044
Tetraneura ulmi		-	-0.079	0.187	-0.06	0.313	0.047	0.286	-0.134	0.326
Forda formicaria			-	0.336	-0.384	-0.064	0.301	0.347	0.438	0.105
Baizongia pistaciae				-	-0.376	0.346	0.165	0.391	0.225	0.222
Anoecia corni					-	-0.245	-0.513	-0.253	-0.143	-0.025
Anoecia furcata						-	0.180	0.357	0.217	0.045
Geoica setulosa							-	0.378	0.079	0.004
Geoica utricularia								-	0.132	-0.066
Trama troglodytes									-	-0.255
Aploneura lentisci										-

Table 25 Non-parametric correlations (RHO) for aphids 1985

The analysis of aphid and coccid associations were conducted at two levels of interaction; firstly temporal associations between species over the year, secondly spatial associations between species within the nest.

Non-parametric correlation coefficients (Spearmans RHO), for all combinations of aphids and coccids found together in ant nests for 1983, 1984, 1985 are given in tables 23-25. In general there are positive associations amongst the majority of aphids, and little association with coccids. Of the few statistically marked negative associations, all but one occur with facultatively ant tended aphids i.e. Anoecia corni (which shows negative associations with all aphids in 1983, 1985 and most in 1984) and Aploneura lentisci (which may not even be ant tended). The only trace of a negative association is between Trama troglodytes and Tetraneura ulmi in 1984, which is unlikely to be meaningful as they feed on different plants. Conversely some aphids showed strong hints of a positive association, especially between:

Geoica utricularia and G.setulosa
G.utricularia and Tetraneura ulmi
G.utricularia and Forda formicaria
G.utricularia and Baizongia pistaciae

Geoica setulosa is also positively associated with T.ulmi, F. formicaria and B.pistaciae in all years, but these results only become significant in 1984.

F.formicaria and B.pistaciae
F.formicaria and T.ulmi (but not in 1985).

Upon reconsideration of graphs 13-19, these trends are to be expected. It is surprising that Anoecia corni A.furcata did not show marked negative correlations, therefore A.corni, A.furcata, G.setulosa and G.utricularia (1983 results), were reanalysed using contingency tables (see Table 26). Because of the need for nests containing neither aphid, few species were suitable for this technique. Again G.setulosa and G.utricularia showed marked positive associations, and A.corni and A.furcata showed the strong negative association predicted.

When the aphid associations are considered in the light of their most abundant nest locations (section 4.22), the relationships become even more interesting. T.ulmi which is most common at 20cm from the centre of the nest mound, is not positively associated with B.pistaciae which also frequents this position. Both are positively associated with F.formicaria which is most abundant near the edge of the nest mound. G.setulosa is most abundant 35-70cm from the centre of the nest mound, and is most highly negatively associated with A.corni which is also common at 70cm. This suggests that certain aphids may coexist in the nest because they occupy different locations.

Spatial associations between aphids were calculated by analysing their pattern of occurrence in soil cores using the covariance method outlined previously. The results are presented in table 27. Contrary to temporal trends, when aphids occur together, there is little interaction between them, i.e. little interspecific competition or inhibitory affects. Strong positive associations only occur between aphids which are known to have different nest locations i.e. T.ulmi (most abundant at 20cm) and G.setulosa (most abundant at 35-70cm); A.furcata (most abundant at the nest centre) and *G.setulosa*.

		Anoecia corni		Total
		+	-	
Anoecia furcata	+	8	17	25
	-	16	9	25
	Total	24	26	50

Chi-squared = 5·13 $p<0.01$

		Geoica utricularia		
		+	-	Total
Geoica setulosa	+	19	6	25
	-	11	14	25
	Total	30	20	50

Chi-squared = 4.08 $p<0.05$

Table 26. Analysis of aphid association using contingency tables.

	Tetraneura ulmi	Forda formicaria	Baizongia pistaciae	Anoecia furcata	Geoica setulosa	Geoica utricularia	Trama troglodytes
Tetraneura ulmi	-	N/S	N/S	N/S	+ve (p<0.001)	N/S	N/S
Forda formicaria		-	N/S	N/S	N/S	N/S	N/S
Baizongia pistaciae			-	N/S	N/S	N/S	N/S
Anoecia furcata				-	+ve (p<0.001)	N/S	
Geoica setulosa					-	N/S	N/S
Geoica utricularia						-	N/S
Trama troglodytes							-

Table 27. The spatial association between aphids (1985) using covariance method.

	Maximum fecundity (1st instars/♀/day)	Maximum life span of adult (days)	Root feeding position
Tetraneura ulmi	5	15	stem bases, first instars all over roots
Forda formicaria	3	15	roots
Baizongia pistaciae	-	3	roots
Geoica utricularia	2	36	stem bases, first instars near root tips
Smynthnodes betae	-	2	internodes

Table 28. Estimates of fecundity, lifespan and feeding position of subterranean aphids.

The definitive laboratory experiment to assess intraspecific and interspecific competition between aphids, is to breed each species separately to gain some estimate of fecundity, then breed mixed cultures of pairs of aphids, assess the fecundity and construct replacement series using the method of Williamson (1971). Such an experiment was attempted, but there are serious problems involved in rearing aphids on plant roots, especially in the absence of ants, which are discussed in appendix A7. However, an estimate of fecundity was taken, along with life span and root feeding position (see table 28). The values are not those expected in the field, because aphid behaviour may change in laboratory, non ant tended cultures. But maximum fecundity may be fairly close to that level found in the field, because the aphids seem unable to restrict their nymph production when they are first taken into the lab, which is when these counts were recorded. Maximum lifespan is probably meaningless in the absence of ants, but it does show that aphids can live quite a long time. Geoica utricularia may have survived longest because it seems to resist desiccation better than other aphids. Both species of Geoica were certainly very common inthe dry spell of 1984. There consistently seem to be different root feeding positions in the aphids studied. First instar nymphs of T.ulmi and G.utricularia are more mobile than the adults, and may be the main dispersal stages. Pontin (1963) also noted that root aphids feed on different parts of the host plant, and this may provide a further way of reducing interaction between aphid species.

4.5 Conclusion

(i) The frequency distribution of all aphid species can be fitted by a curve of the form

$$Y = N/kX$$

where N/k is the mean number of aphids per core.

(ii) The clump size for all species of aphids is larger than the area of the corer. The clump size of the coccid is smaller than the area of the corer.

(iii) When considered in terms of presence or absence, individuals of each aphid species have the same probability of occurring at a set distance from the centre of the nest mound. What does change with species is the part of the nest in which the aphid is most abundant.

Baizongia pistaciae is more common near the centre of the nst mound.

Tetraneura ulmi although most common near the centre of the nest mound, is more abundant at 70cm from the nest mound than expected by chance.

Geoica setulosa is most abundant near the edge of the nest mound and in the outlying territory.

Anoecia corni is most abundant in the outlying territories.

(iv) The number of aphids in an ant nest varies over the year. Levels are high in late Winter to Spring, then decrease through Summer, reaching lowest values in late July. There is a gradual recovery in numbers from August to October, and high values are again found in November to December. The only exception to this pattern is Anoecia *corni* which is only found in *Lasius flavus* mounds from late May to November, at other times being on its alternative host *Cornus sanguinea*. The decline in aphid numbers can be explained by the increasing loss of first instar larvae.

(v) When aphid abundance is analysed temporally many aphid species are positively correlated. The exceptions to this are facultatively ant tended root aphids e.g. *Anoecia corni* and *Aploneura lentisci*, and aphids which occur at similar nest locations e.g. *Tetraneura ulmi* and *Baizongia pistaciae*.

(vi) When aphid abundance is analysed spatially, little association is found between species.

(vii) Aphids were found to feed at different positions on plant roots.

CHAPTER FIVE

THE RELATIONSHIP OF ANTS TO SOIL ORGANISMS

5.1 Introduction

Previous chapters have concentrated on the overall abundance of ants and trophobionts respectively. This chapter seeks to quantify the interactions between these species together with any association with abiotic factors. Whilst gathering information on ants and aphids, further results were collected on other soil organisms commonly found in the ant nest. This additional information is included because of its numerical importance, but it should be emphasised that this was a digression from the main study, and as such, the taxonomy of these animals is very general.

5.2 Ants and trophobionts

5.21 The association between ants and trophobionts.

It is known that *Lasius flavus* uses subterranean aphids both as a carbohydrate and protein source. Therefore different stages of the ant lifecycle were correlated against all species of trophobionts to ascertain the extent of this relationship, and whether there were any interspecific differences. Temperature, humidity and rainfall are also included, as a guide to which abiotic factors affect aphid numbers (see tables 29-31).

Worker activity is highly correlated with total brood biomass ($p<0.001$), far more so with larval brood biomass ($0.001<p<0.01$) than adult alate biomass, where the only marked relationship occurred in 1985. Numbers of workers, larval biomass and adult biomass all increase with increasing temperature, for reasons outlined in section 3.4.

The total number of aphids found seems independent of the abiotic factors considered, which is in keeping with their observed abundance throughout the year. In general there is a positive association between aphids and ant activity, which is especially marked with *Tetraneura ulmi*, *Baizongia pistaciae* and *Geoica* spp. A negative association was expected between aphids and ant larvae because of the reported depredations of workers, but in fact what was found was that the positive correlation still existed (but to a lesser degree), except for *Trama troglodytes* and *Aploneura lentisci* which showed marked negative associations. In general it seems that ants do not significantly damage aphid populations whilst feeding their larvae. High protein demand occurs at a time of year when the aphids are breeding most rapidly. In section 4.2 it was shown that although many first instar aphids are produced, few develop to become adults. It is suggested that these immature stages are taken by workers as food for the brood. *Aploneura lentisci* may be especially susceptible to these predation pressures, as it is not an ant tended aphid.

	Worker abundance	Total brood biomass	Larval biomass	Adult biomass	Tempe-rature	Humidity	Rain
Worker abundance		0.719	0.691	0.155	0.446	-0.373	0.164
Total brood biomass	0.719		0.866	0.352	0.594	-0.356	0.219
Larval biomass	0.691	0.866		0.077	0.405	-0.353	0.255
Adult biomass (alates)	0.155	0.352	0.077		0.432	-0.251	-0.118
Coccids	-0.087	-0.221	-0.159	-0.198	-0.354	0.001	0.003
Total aphids	0.173	-0.101	0.064	-0.384	-0.272	0.095	-0.155
Tetraneura ulmi	0.390	0.190	0.268	-0.119	0.155	-0.146	-0.242
Forda formicaria	0.077	-0.098	0.023	-0.337	-0.329	0.177	0.022
Baizongia pistaciae	0.443	0.263	0.346	-0.048	0.117	-0.235	-0.012
Anoecia corni	0.219	0.265	0.079	0.384	0.713	-0.165	-0.128
Anoecia furcata	-0.318	-0.218	-0.116	-0.372	-0.298	0.253	-0.084
Geoica setulosa	0.284	0.123	0.257	-0.196	-0.177	0.026	0.109
Geoica utricularia	0.447	0.271	0.342	-0.246	0.005	-0.042	-0.033
Trama troglodytes	-0.163	-0.386	-0.297	-0.090	-0.076	0.356	0.240
Aploneura lentisci	-0.217	-0.471	-0.328	-0.399	-0.651	0.243	0.068

Table 29. Product-moment correlations between Lasius flavus, subterranean aphids and environmental factors (1983).

	Worker abundance	Total brood biomass	Larval biomass	Adult biomass	Tempe-rature	Humidity	Rain
Worker abundance		0.755	0.729	0.312	0.333	-0.468	-0.471
Total brood biomass	0.755		0.455	0.714	0.558	-0.434	-0.327
Larval biomass	0.729	0.455		-0.130	0.144	-0.335	-0.173
Adult biomass (alates)	0.312	0.714	-0.130		0.454	-0.230	-0.291
Coccids	-0.336	-0.324	-0.212	-0.161	-0.152	0.275	0.235
Total aphids	0.445	0.073	0.586	-0.459	-0.033	0.200	-0.106
Tetraneura ulmi	0.473	0.260	0.488	-0.245	0.002	-0.298	0.041
Forda formicaria	0.389	0.178	0.599	-0.359	-0.090	0.233	-0.095
Baizongia pistaciae	0.489	0.192	0.503	-0.262	-0.081	-0.115	-0.234
Anoecia corni	0.158	0.053	0.003	0.159	0.307	0.003	-0.196
Anoecia furcata							
Geoica setulosa	0.579	0.172	0.648	-0.275	0.077	-0.315	-0.180
Geoica utricularia	0.409	0.245	0.393	-0.219	-0.192	0.130	0.002
Trama troglodytes	-0.336	-0.533	-0.400	-0.194	-0.271	0.331	-0.062
Aploneura lentisci	-0.284	-0.094	-0.276	-0.028	0.048	0.065	0.046

Table 30. Product-moment correlations between Lasius flavus, subterranean aphids and environmental factors (1984).

	Worker abundance	Total brood biomass	Larval biomass	Adult biomass	Tempe-rature	Humidity	Rain
Worker abundance		0.923	0.658	0.496			
Total brood biomass	0.923		0.686	0.606			
Larval biomass	0.658	0.686		-0.011			
Adult biomass (alates)	0.496	0.606	-0.011				
Coccids	0.044	-0.128	0.037	-0.182			
Total aphids	-0.146	-0.257	-0.255	-0.114			
Tetraneura ulmi	0.312	0.328	0.079	0.201			
Forda formicaria	-0.259	-0.469	-0.268	-0.443			
Baizongia pistaciae	-0.096	-0.234	-0.233	-0.132			
Anoecia corni	0.402	0.478	0.171	0.517			
Anoecia furcata	-0.017	0.061	-0.011	0.157			
Geoica setulosa	-0.101	-0.185	0.147	-0.311			
Geoica utricularia	0.229	0.171	0.241	-0.126			
Trama troglodytes	-0.222	-0.247	-0.234	-0.169			
Aploneura lentisci	0.038	0.070	0.122	-0.215			

Table 31. Product-moment correlations between Lasius flavus, subterranean aphids and environmental factors (1985).

Trama troglodytes despite its modifications for living with ants, also seems susceptible, perhaps because of its low reproductive rate at this time of year (maximum reproduction occurs in early Winter). Pontin (1978) suggested that as many as 3000 first instar aphids are lost per ant nest per day.

What does show high negative associations with aphid numbers is the hatch of winged ants. At this time of year, aphids practically disappear from the nest mound. It is interesting that the only aphid that is not negatively associated with this is Anoecia corni, presumably because it is most abundant at 70cm from the centre of the nest mound, and is away from the worst effects of predation. Other aphids which are commonly found at 70cm at this time of year (T.ulmi, G.setulosa), show no marked negative association. After hatching, the alate ants, especially the females, have to build up food reserves, not only to produce their first brood, but to survive until the first workers mature (Spring), without feeding. This accounts for the reduction in the number of aphids.

Coccids appear to be independent of both abiotic and biotic factors. They show no sign of being positively associated with ants, and in 1984 there is even a hint of a negative association. This could account for their observed distribution which is generally away from the nest mound.

5.22 An assessment of ant - root aphid mutualism

It is commonly stated that aphids thrive when attended by ants, because of: the protection afforded from natural enemies, improved hygiene by the removal of honeydew, and increased feeding rates, especially in this case, where ants may clear soil away from the roots to assist feeding. That root aphids are dependant upon ants is clear from their structural adaptations (see section 1.2), but these benefits are overstated. Most natural enemies of aphids e.g. Aphidius spp., some adult coccinellids (e.g. Coccinella divaricata), coccinellid and syrphid larvae are disregarded by Lasius niger, and ants have even been observed palpating parasites whilst they were ovipositing upon aphids! (Banks p.313 in Way 1963). Although there is a virtual absence of aphid predators and parasites in Lasius flavus mounds, this is presumably due to the lack of external openings (Pontin 1960). Nixon (1951) concluded that protection is not an active manifestation of the ant-aphid association, unrelated to their value as a food source, but a consequence of the reaction of ants to swift or erratic movements.

El Ziady and Kennedy (1956), showed that ant attendance caused increased rates of aphid feeding which resulted in a greater aphid biomass. The advantage to both ants and aphids seems obvious, but further experiments by Banks (1958) showed that increased aphid density was merely due to the delay in dispersal of the adults. So once again the 'symbiosis' seems to favour the ant.

Way (1963) regarded the main benefit to root aphids to be the shelter afforded by the ant nest, especially in overwintering species which are protected from extremes of temperature, excess moisture and fungal attack. Zwolfer (in Way 1963) believed that some species of root aphids can only survive the Winter in ant nests, indeed in this country the primary host of many of the Fordinae (*Pistacia lentiscus*) is not available. However, benefit can ultimately only be shown by the propagation of genes. Apterous individuals are an evolutionary dead end in themselves unless they can spread via ant dispersion, which is only possible when colonies have overlapping interconnecting territories which is not the case with *Lasius flavus* (Odum and Pontin 1963), or when colonies reproduce by budding e.g.*Formica* spp. If increased numbers of apterous aphids in the presence of ants produce more alates than in the absence of ants, then this alone is enough to show profit. But not only is the increased fecundity in doubt, but *Lasius flavus* mounds produce very few alates (see appendix D1) and workers have been observed biting off the wings of aphids and returning them to the nest (Mordvilko 1907 in Way 1963). From this it is obvious that the evolutionary bias of this symbiosis is in the favour of *Lasius flavus*, due to its successful exploitation of aphids. In *Lasius niger* colonies root aphid alates are far more common, and it is possible that these aid recolonization of *Lasius flavus* mounds in late Summer. As many root aphids follow parthenogenetic cycles, then there is little opportunity for them to mix genes to out-evolve the *Lasius flavus* exploitation system (Pontin 1978).

5.3 The relationship of ants to other soil organisms

5.31 Dispersion in the ant nest.

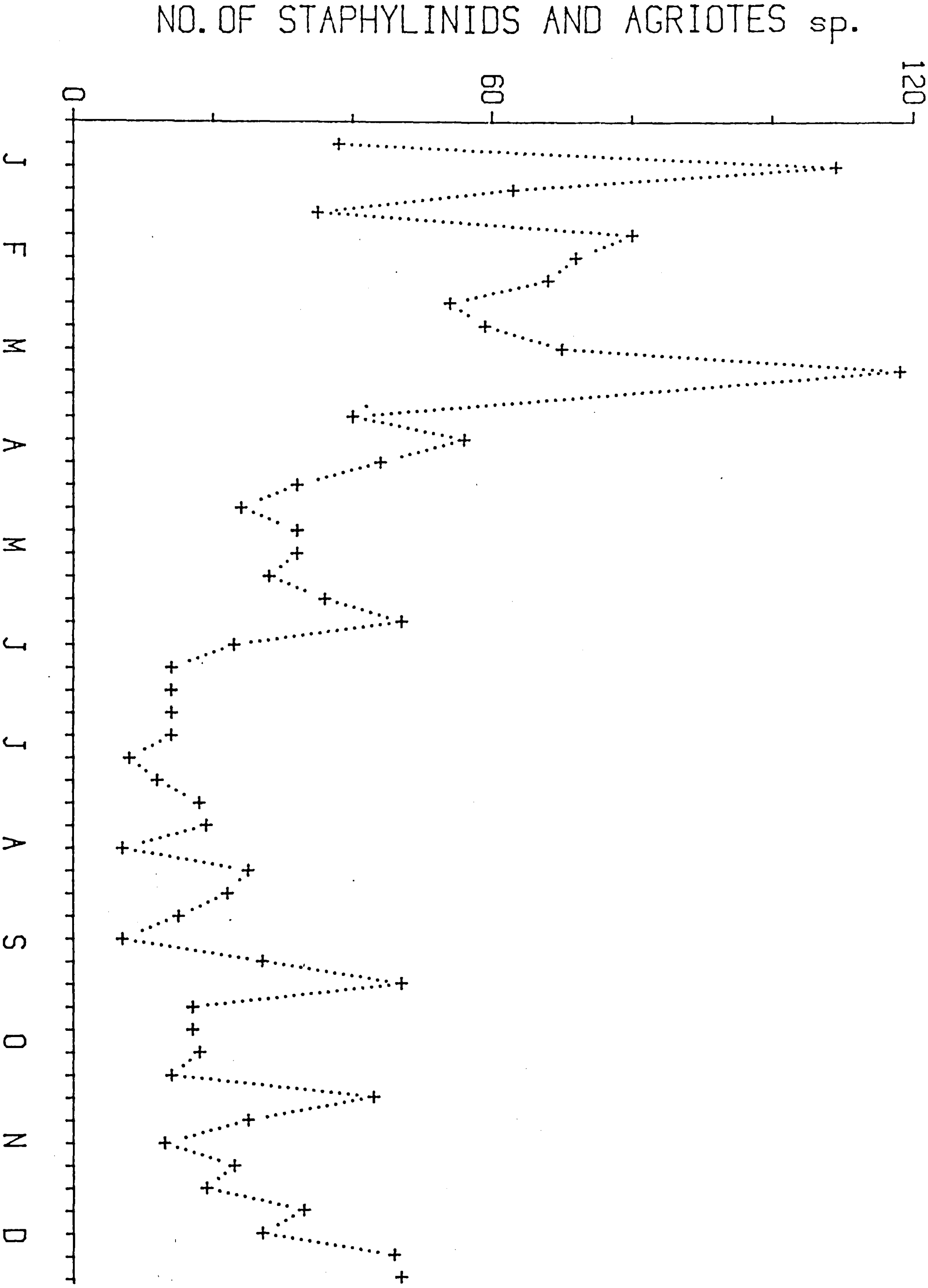
Many soil animals have been consistently found within *Lasius flavus* nests. Excluding ants and their trophobionts, these make up 30% of the animals found in the nest (1983 values), and hence form an important part of the ecosystem.

When taking soil cores, animals can be extracted which inhabit the surface vegetation. In the case of beetles, these surface forms (often weevils) were excluded from the counts. The majority of the remaining beetles (approximately 80%) were Staphylinids (c.f. 83%, Salt et al 1948), most commonly from the family Aleocharinae (e.g.*Dinarda*), but Tachyporinae (e.g. *Habrocerus*) and Staphylininae (e.g.*Quedius*) were also found. Wire worms (*Agriotes* sp.), were also included in these counts. Soil Collembola are considered as a group because of their similar lifestyles. No web spinning spiders were found in the samples, and crab spiders were only common during during early Summer. Therefore the majority of those found were wolf spiders. Mites were divided into predatory and phytophagus types, the former on account of their longer legs and larger size. Phytophagus mites were mainly Oribatid mites, but no further attempts at identification were made. Ectoparasitic mites e.g.*Antennophorus* were never found on *Lasius flavus*. The myriapods included in this analysis were Symphyla and Geophilomorph centipedes. Symphyla accounted for 60% of the soil myriapods, compared with the value of 86% found by Thompson 1924 (in Kevan 1955 p.152), and 86% from Salt et al (1948). Millipedes were rare, which is not surprising as they are essentially woodland creatures which unlike centipedes have not become adapted to moorland habitats (Blower, in Kevan 1955). Parasitic Hymenoptera are excluded from the analysis because of their low abundance.

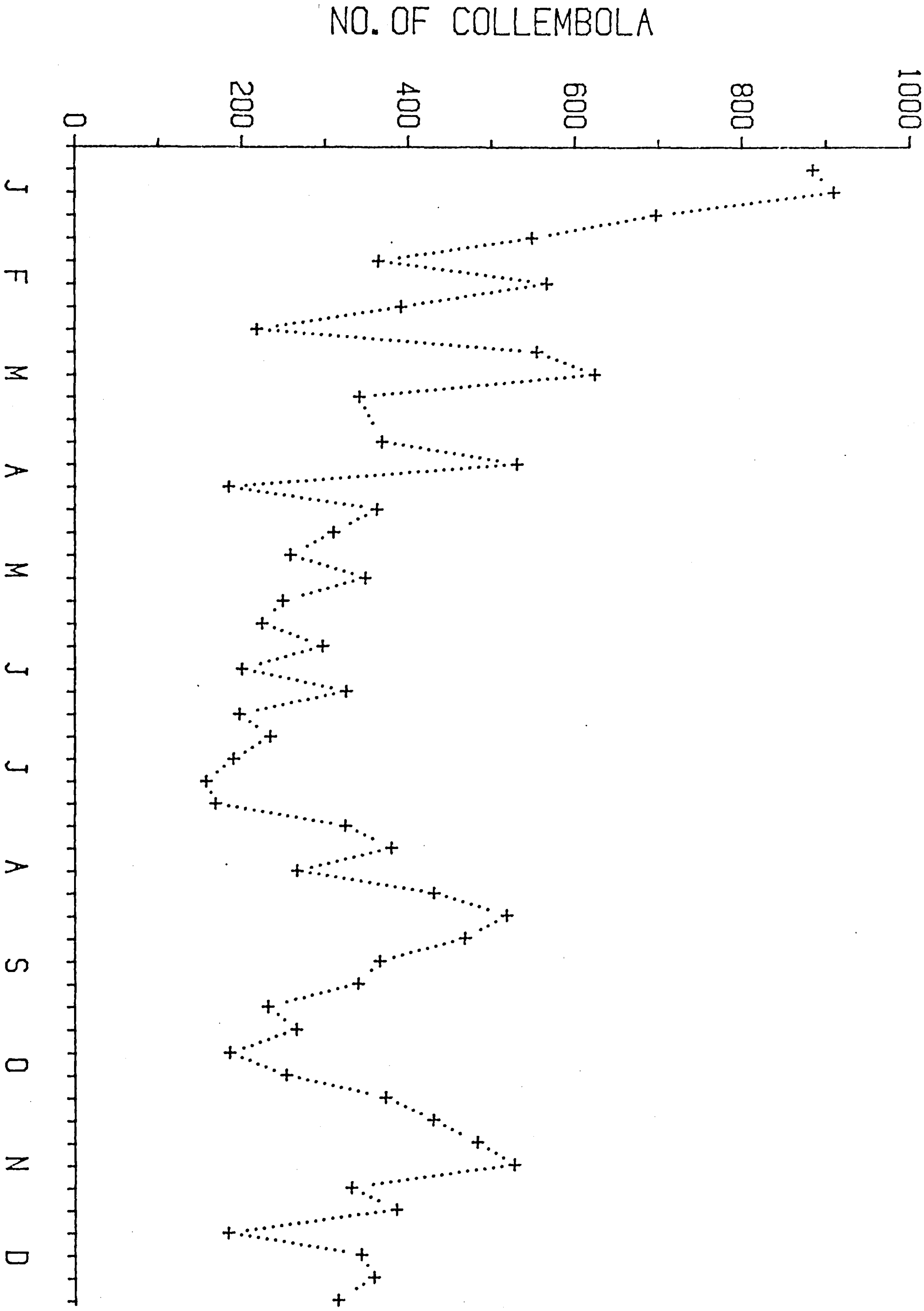
Values of Taylors coefficient b are given in table 32, for each of the major groups of organisms found in the samples. Overall these values are quite wide ranging, often because they are not for individual species, but for taxonomic groups, within which different species may have widely differing ecologies. In general staphylinids and spiders show a random distribution, which reflects their solitary, predatory nature. Collembola, predatory mites and symphilids show clumped distributions. Myrmica scabrinodis, phytophagus mites and Acalypta platychila (Tingidae), show highly clumped distributions. Such a distribution is found with phytophagus mites because large numbers of larvae were often found together. Clumped counts of Myrmica occur when they are in the process of taking over a Lasius flavus mound.

5.32 Seasonal trends between ants and soil organisms.

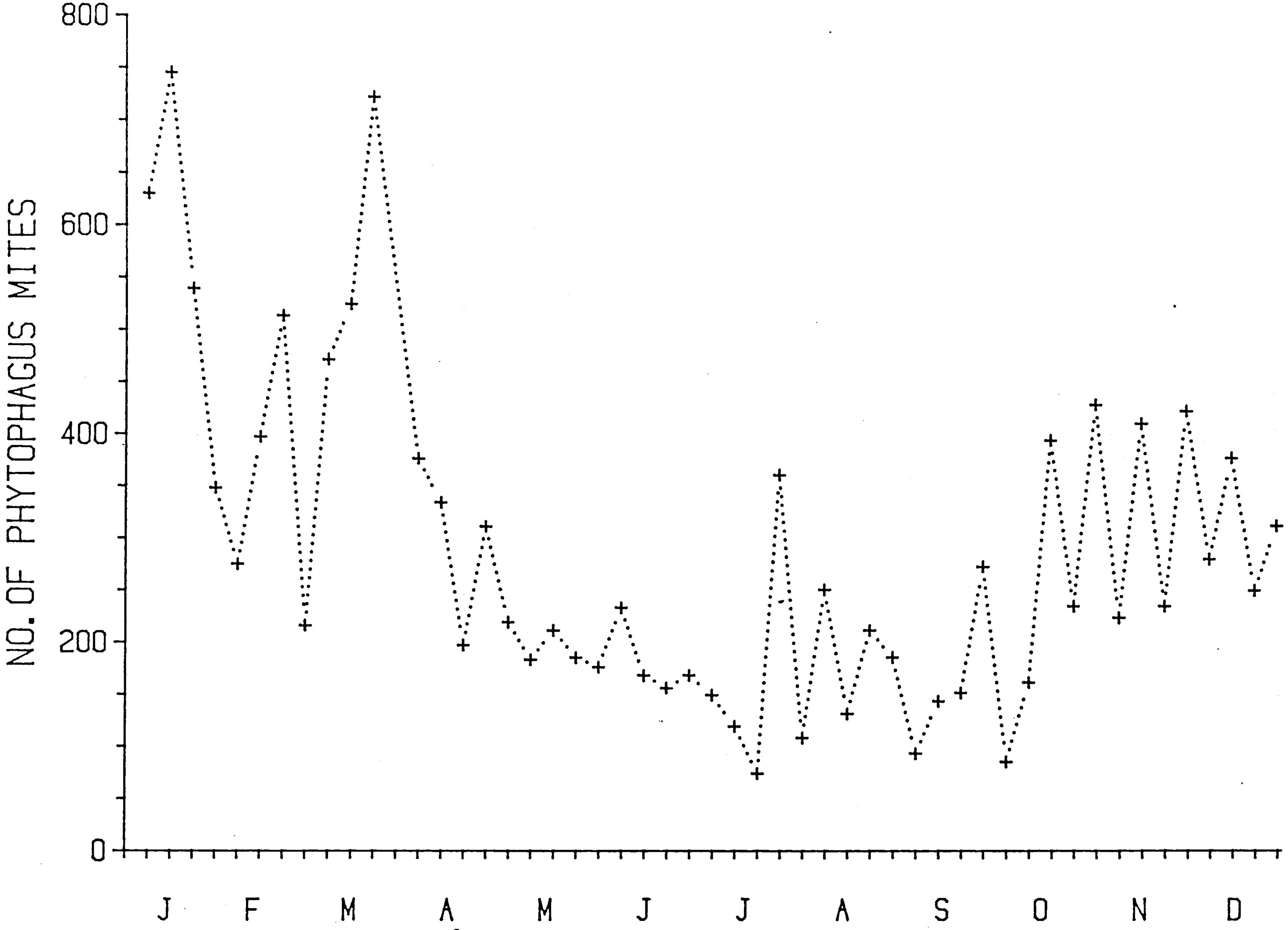
Graphs 56-63 (and 106-121 in appendix E4), show how the numbers of soil organisms varied over the year. The year was split into the same seven sections outlined in section 3.4, so that direct comparisons could be made with ant activity. Table 33 summarizes the differences between numbers in 1983, using Mann-Witney U-tests.



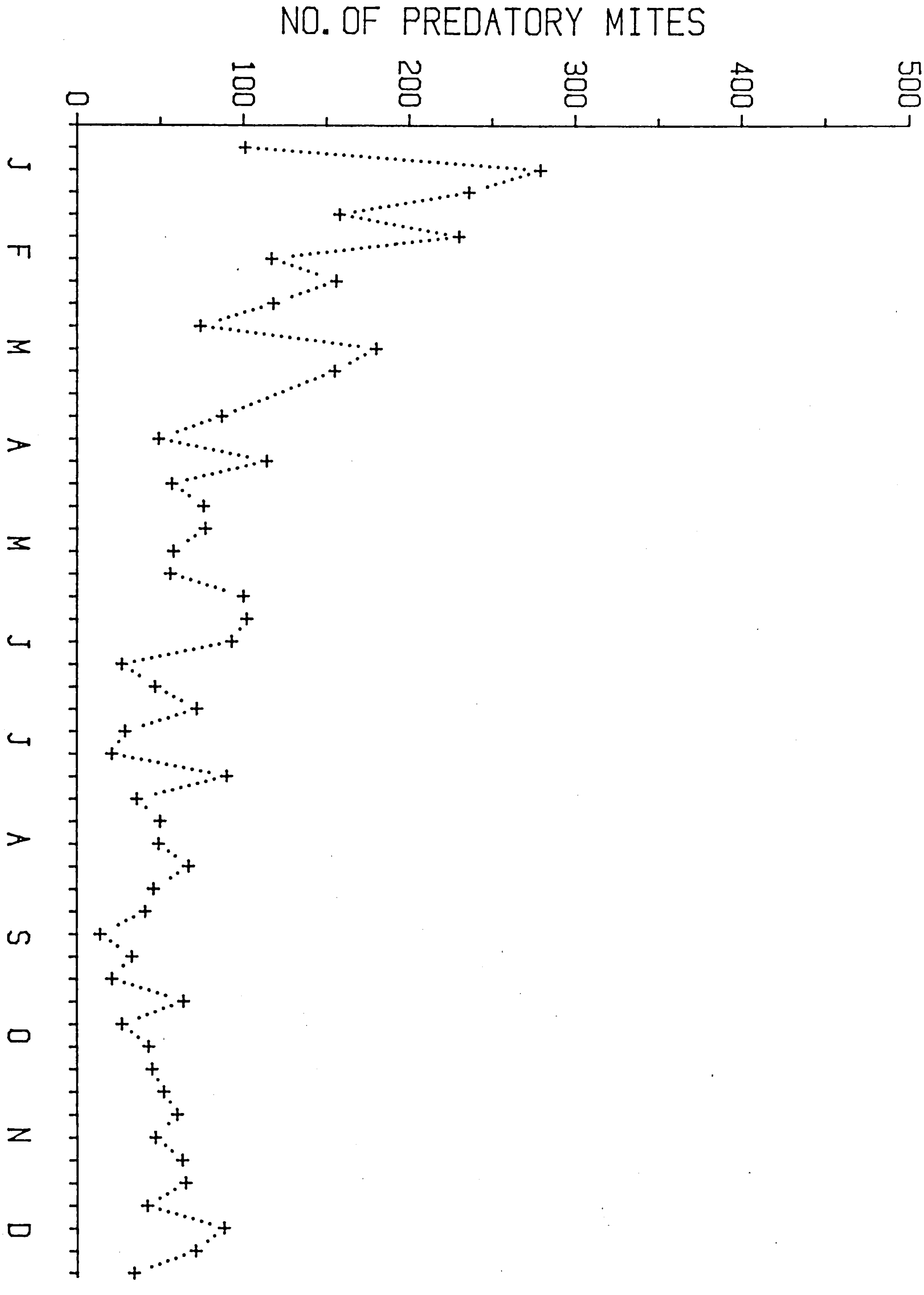
Graph 56. The abundance of staphylinids and *Agriotes* sp. in 1983.



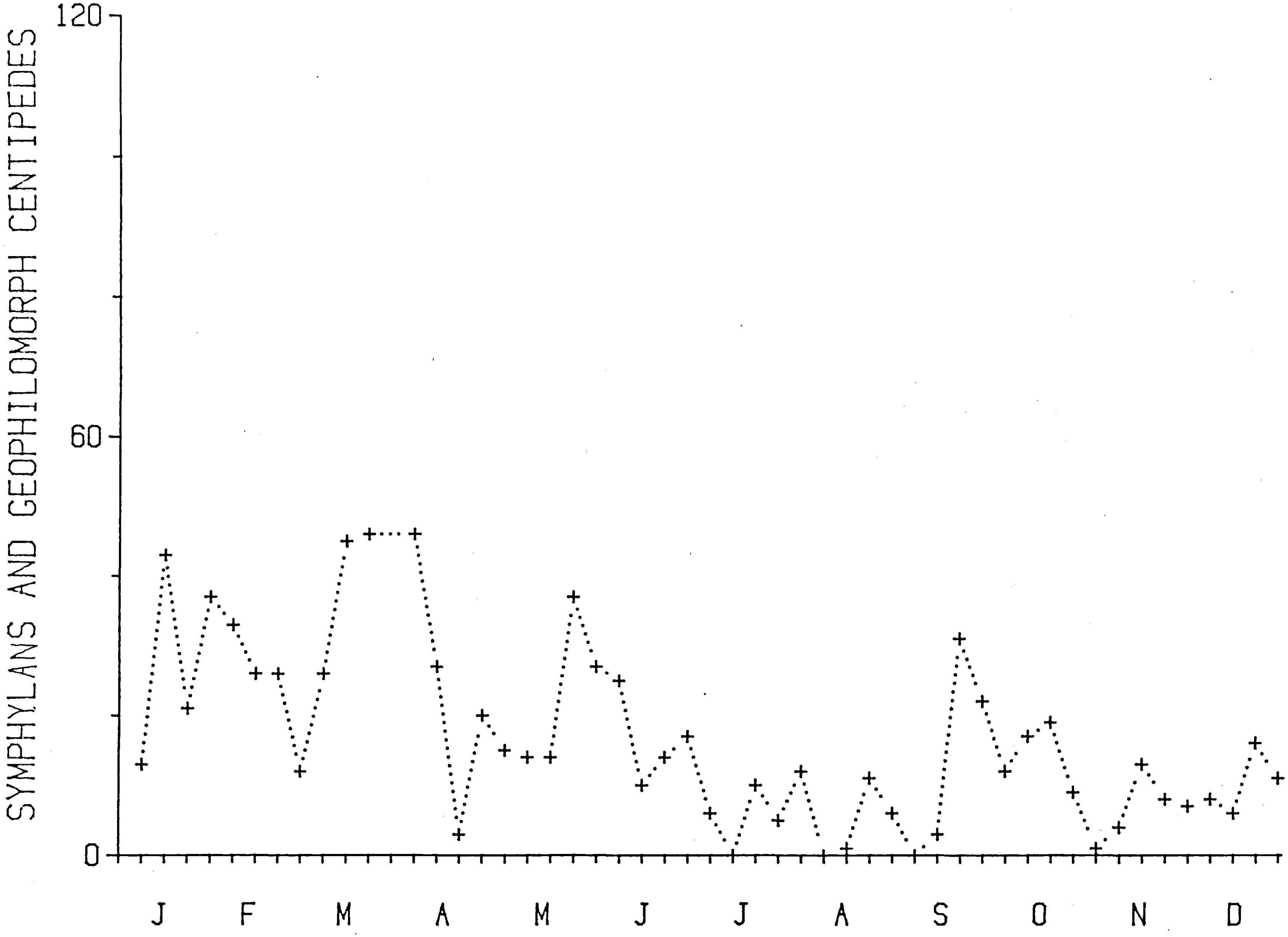
Graph 57. The abundance of soil collembola in 1983.



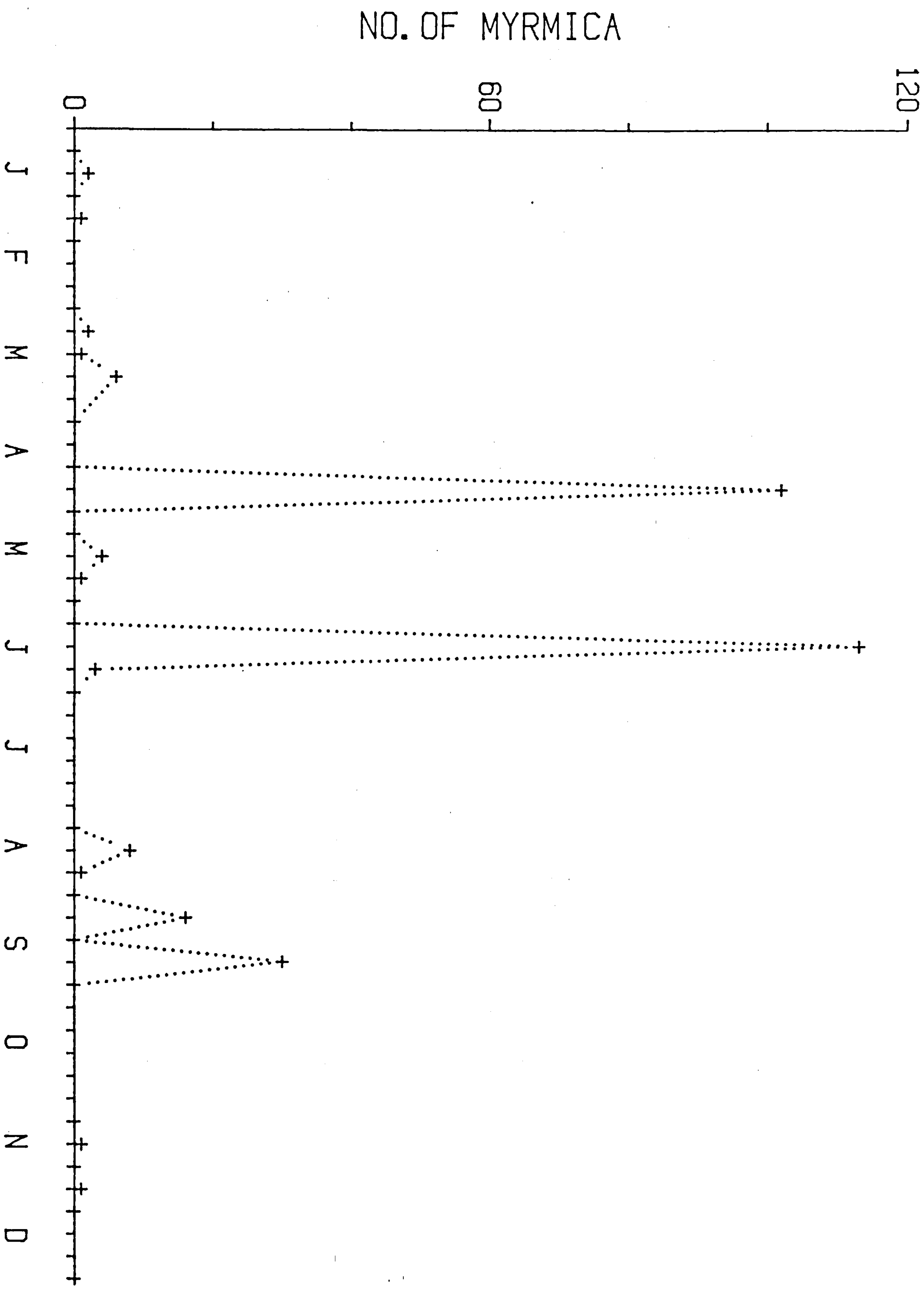
Graph 58. The abundance of phytophagus mites in 1983.



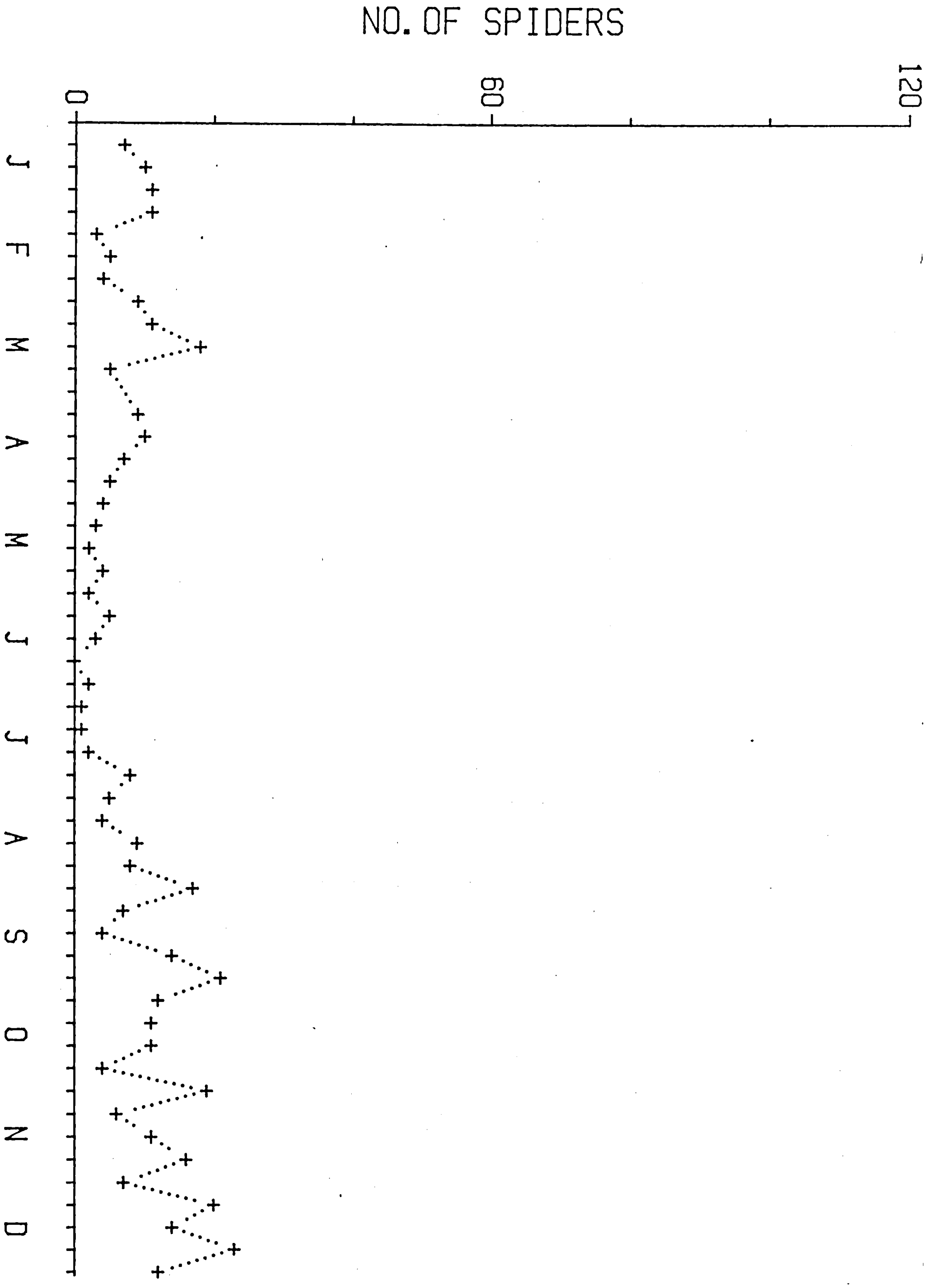
Graph 59. The abundance of predatory mites in 1983.



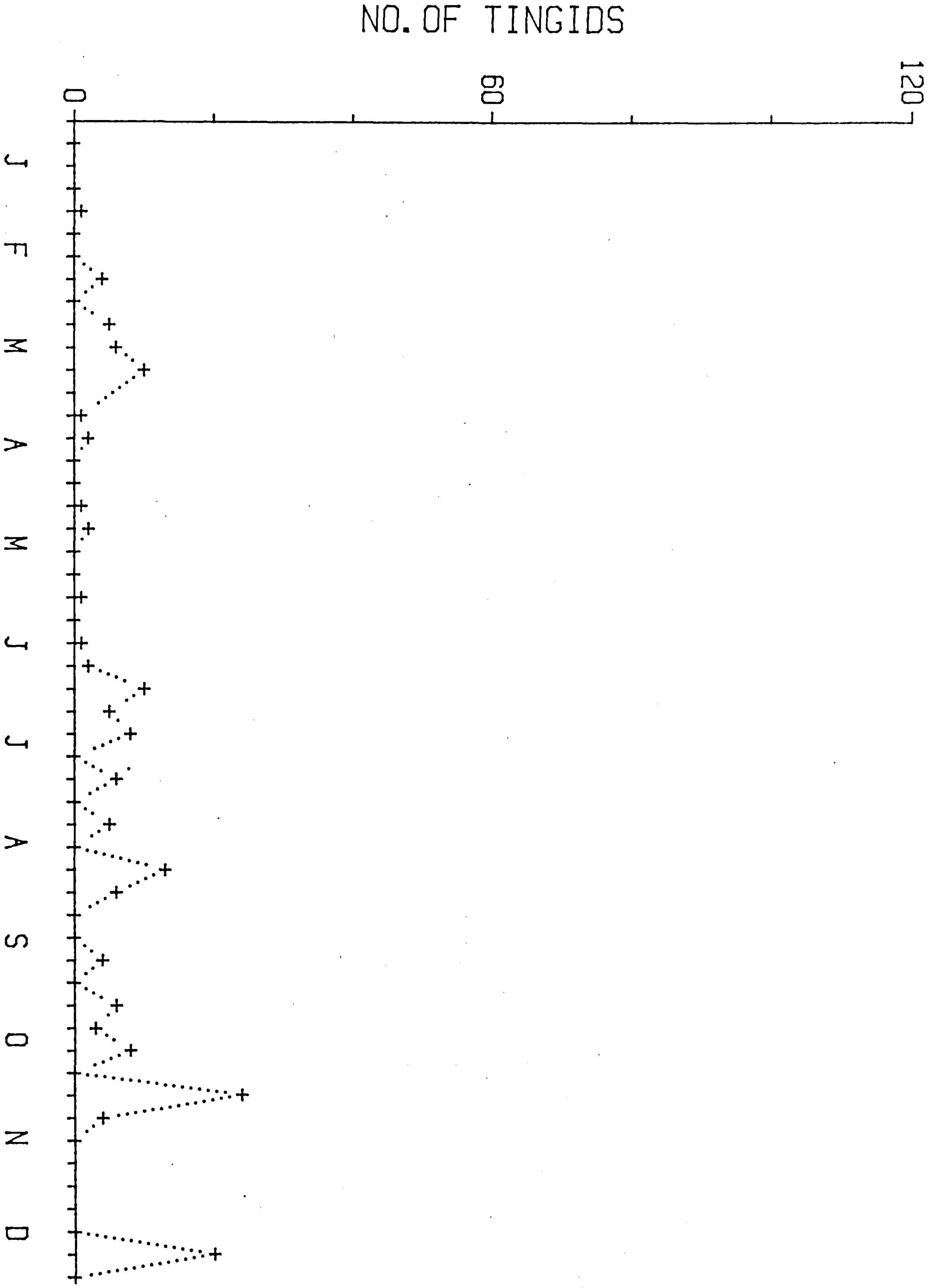
Graph 60. The abundance of symphilids and geophilomorph centipedes in 1983.



Graph 61. The abundance of *Myrmica scabrinodis* in 1983.



Graph 62. The abundance of spiders in 1983.



Graph 63. The abundance of Acalypta platychila in 1983.

	Values of coefficient b +/- 95% C.I.		
	1983	1984	1985
Staphylinidae (+ Agriotes)	1.043 +/- 0.163	1.258 +/- 0.193	1.309 +/- 0.180
Collembola	1.477 +/- 0.159	1.668 +/- 0.210	1.408 +/- 0.241
Myrmica scabrinodis	2.889 +/- 0.090	2.924 +/- 0.058	2.975 +/- 0.077
Spiders	1.174 +/- 0.080	1.373 +/- 0.051	1.243 +/- 0.154
Predatory mites	1.577 +/- 0.193	1.624 +/- 0.196	1.259 +/- 0.206
Phytophagus mites	1.449 +/- 0.151	2.072 +/- 0.183	2.104 +/- 0.186
Symphyla + Geophilomorphs	1.547 +/- 0.100	1.836 +/- 0.113	1.438 +/- 0.019
Acalypta platychila	1.809 +/- 0.102	2.241 +/- 0.070	1.255 +/- 0.207

Table 32. Indices of clumping for soil organisms.

	Comparison of sections of the year					
	I-II	II-III	III-IV	IV-V	V-VII	VI-VII
Ant activity	0.01 (increase)	0.001 (increase)	N/S	N/S	0.05 (decrease)	0.001 (decrease)
Staphylinids + Agriotes	N/S	0.001 (decrease)	0.001 (decrease)	N/S	0.001 (increase)	0.05 (increase)
Spiders	N/S	0.001 (decrease)	N/S	0.001 (increase)	0.05 (increase)	N/S
Myrmica scabrinodis	N/S	N/S	0.05 (decrease)	N/S	N/S	N/S
Collembola	0.001 (decrease)	0.01 (decrease)	0.001 (decrease)	0.05 (decrease)	N/S	0.1 (increase)
Phytophagus mites	N/S	0.001 (decrease)	0.001 (decrease)	N/S	N/S	0.001 (increase)
Predatory mites	0.001 (decrease)	0.01 (decrease)	0.001 (decrease)	N/S	N/S	0.001 (increase)
Acalypta platychila	0.001 (increase)	0.01 (decrease)	0.001 (increase)	0.05 (decrease)	N/S	N/S
Symphyla + Geophilomorphs	N/S	0.01 (decrease)	0.001 (decrease)	N/S	0.001 (increase)	0.05 (decrease)

Table 33. The seasonal variation of soil organisms with respect to Lasius flavus activity.

Ant activity

	1983				1984				1985			
	RHO	p	Tau	p	RHO	p	Tau	p	RHO	p	Tau	p
Collembola	-0.32	0.023	-0.21	0.015	-0.33	0.038	-0.24	0.028	-0.50	0.010	-0.35	0.008
Staphilinids + Agriotes	-0.25	0.082	-0.17	0.042	-0.14	0.448	-0.09	0.247	-0.28	0.179	-0.16	0.146
Myrmica	0.15	0.592	0.10	0.321	-0.08	0.656	-0.06	0.328	0.19	0.363	0.13	0.205
Spiders	-0.56	0.001	-0.41	0.001	-0.42	0.014	-0.31	0.008	-0.58	0.002	-0.41	0.003
Predatory mites	-0.25	0.079	-0.16	0.05	-0.30	0.090	-0.19	0.063	-0.66	0.001	-0.52	0.001
Phytophagus mites	-0.51	0.001	-0.36	0.001	-0.07	0.689	-0.06	0.318	-0.48	0.015	-0.36	0.007
Myriapods	0.01	0.949	0.002	0.493	0.06	0.746	0.04	0.390	-0.16	0.434	-0.12	0.206
Acalypta	-0.53	0.005	-0.41	0.003	0.05	0.150	0.39	0.065	0.42	0.035	0.33	0.014

Table 34a. Non parametric correlations between ant activity and numbers of soil organisms.

Rainfall

	1983				1984			
	RHO	p	Tau	p	RHO	p	Tau	p
Collembola	-0.14	0.343	-0.11	0.155	0.25	0.169	0.17	0.096
Staphylinids + Agriotes	0.06	0.687	0.05	0.342	0.10	0.577	0.18	0.275
Myrmica scabrinodis	-0.01	0.998	-0.01	0.491	-0.04	0.848	-0.04	0.413
Spiders	-0.05	0.712	-0.04	0.365	0.11	0.558	0.08	0.275
Predatory mites	-0.02	0.870	-0.02	0.439	0.21	0.239	0.17	0.102
Phytophagus mites	-0.10	0.495	-0.07	0.269	0.26	0.144	0.21	0.055
Symphyla + Geophilomorphs	0.14	0.334	0.10	0.183	0.04	0.815	0.03	0.426
Acalypta platychila	0.22	0.130	0.18	0.066	-0.35	0.049	-0.28	0.029

Table 34b. Non parametric correlations between rainfall and numbers of soil organisms.

	Temperature							
	1983				1984			
	RHO	p	Tau	p	RHO	p	Tau	p
Collembola	-0.38	0.007	-0.27	0.003	-0.62	0.001	-0.42	0.001
Staphylinids + Agriotes	-0.64	0.001	-0.48	0.001	-0.49	0.005	-0.35	0.001
Myrmica scabrinodis	-0.07	0.648	-0.05	0.317	0.05	0.805	0.04	0.396
Spiders	-0.33	0.020	-0.22	0.013	-0.32	0.080	-0.23	0.040
Predatory mites	-0.51	0.001	-0.37	0.001	-0.48	0.006	-0.34	0.004
Phytophagus mites	-0.64	0.001	-0.44	0.001	-0.14	0.439	-0.10	0.212
Symphyla + Geophilomorphs	-0.43	0.002	-0.30	0.011	-0.60	0.001	-0.43	0.001
Acalypta platychila	0.26	0.068	0.20	0.032	0.19	0.305	0.14	0.164

Table 34c. Non parametric correlations between temperature and numbers of soil organisms.

Humidity

	1983				1984			
	RHO	p	Tau	p	RHO	p	Tau	p
Collembola	0.29	0.041	0.21	0.019	0.55	0.002	0.38	0.002
Staphylinids + Agriotes	0.14	0.320	0.11	0.149	0.25	0.183	0.19	0.078
Myrmica scabrinodis	0.05	0.752	0.04	0.375	-0.13	0.489	-0.01	0.260
Spiders	0.40	0.004	0.28	0.003	0.06	0.772	0.02	0.443
Predatory mites	-0.04	0.811	-0.08	0.384	0.33	0.073	0.23	0.040
Phytophagus mites	0.23	0.105	0.16	0.053	0.37	0.042	0.24	0.032
Symphyla + Geophilomorphs	-0.08	0.579	-0.07	0.243	0.14	0.470	0.08	0.289
Acalypta platychila	-0.09	0.519	-0.07	0.278	-0.35	0.050	-0.26	0.038

Table 34d. Non parametric correlations between humidity and numbers of soil organisms.

All the soil organisms considered vary inversely with ant activity, with the exception of Myrmica scabrinodis which shows no overall difference in abundance, and Acalypta platychila whose pattern is unrelated to ants or other soil animals. It is interesting that those animals of smallest size follow the trends of ant activity most closely, and with staphylinids, geophilomorphs, symphyla and wolf spiders, there is a lag between the rise of ant activity, and the corresponding decrease in soil organism numbers. Hence this hints that some animals are more sensitive to ant activity than others.

To further elucidate the relationship between ant activity and soil organisms, correlation coefficients were determined between ant activity and the number of soil organisms. The abiotic factors temperature, humidity and rainfall were also analysed, as it is already known that temperature and humidity affect ant activity (Peakin 1960). Abiotic measurements were taken at Silwood Park, Ascot, Berkshire, about five miles from Staines Moor. No measurements were taken in 1985.

Due to the problems encountered in transforming the ant data, non-parametric methods were used i.e. Spearmans rank correlation coefficient RHO and Kendalls rank correlation coefficient Tau. Both methods rank the same information, but the final formulation is different. Kendalls coefficient Tau is the most sensitive to correlations between variables and is regarded as the better more tractable test (Bradley 1968). Both coefficients vary from -1 (perfect negative correlation) to +1 (perfect positive correlation). The results are presented in tables 34a-d.

Rainfall It is not likely that rainfall would affect soil organisms except under the most extreme conditions. This is what was found (see table 34b); only Acalypta platychila shows any hint of a negative correlation, which may reflect its non subterranean existence.

Humidity Small terrestrial arthropods possess a large surface area to volume ratio, therefore desiccation is always a problem and a slight positive relationship maybe expected, especially during periods of dry weather. The only clear correlation found was with soil Collembola ($0.002<p<0.041$), with a hint that spiders in 1983 may have been negatively associated with humidity ($0.003<p<0.004$). Of all the soil animals considered, Collembola were the smallest and poorly sclerotized, therefore most susceptible to low humidity.

Temperature All groups except Myrmica scabrinodis and Acalypta platychila show negative correlations, implying that the effects of temperature on soil animals are deleterious. With spiders this is less marked, presumably because they are mobile enough to escape the worst consequences of high temperature. The mode of action of temperature is not clear. Relative humidity may provide one method, equally the effect of temperature increasing ant activity may also be important. It is not suggested that temperature directly causes any form of mortality, but may serve to drive soil organisms deeper into the nest.

Ant activity Many soil organisms have been found in larval food from Lasius flavus, including soil collembola, geophilomorph centipedes, wire worms (Pontin 1958). Other animals are assumed to be attacked by Lasius flavus by the occurrence of their corpses in soil samples e.g.predatory mites. Soil collembola, spiders and predatory mites all show strong negative correlations with ant activity. Acalypta platychila shows slight signs of correlation in all three years, but that these vary between positive and negative emphasises the dubious relationship of tingids to ants. Phytophagus mites show high negative correlations with ants in 1983 and 1985 ($0.001<p<0.015$), but not in 1984. Staphylinids, Myrmica scabrinodis, symphyla and geophilomorphs are shown not to be affected by ant activity.

Although strongly associated with ant activity, soil collembola are even more strongly correlated with temperature and humidity. This implies that ant activity may not be the major factor affecting their density, but humidity. If predation was the dominant factor, it would be expected that collembola would be most common away from the nest mound, which is not the case. Relative humidity rarely is not saturated in the ant nest (Peakin 1960), except during prolonged dry spells.

Some species of staphylinids (e.g.Dinarda) are guests in the true sense of the word (see section 1.3), but the majority are opportunistic predators of ants. Myrmica scabrinodis has also been recorded as a predator of Lasius flavus (Donisthorpe 1927a). The lack of correlation with ant activity is not surprising, staphylinids are heavily sclerotized, and possess repugnatorial glands, therefore can defend themselves against Lasius flavus. Myrmica scabrinodis is a larger ant than Lasius flavus with more powerful jaws. Pontin (1969) regarded it as a 'habitual predator' and in contests over nest mounds usually prevails. Spiders despite including at least two biologically distinct groups (types I and II of Donisthorpe 1927b), are consistently negatively correlated with ant activity only. They are also considered to be opportunistic predators of ants.

Predatory and phytophagus mites show high correlations with both temperature and ant activity. Due to the number of species included in these groups, their habits are very variable. In general predatory mites are more negatively associated with ant activity than phytophagus mites. Phytophagus mites may be tolerated to a greater extent because of their small size and hard exoskeleton. The relationship between ants and predatory mites is many sided: some suck blood, others feed on the dead bodies of ants, other insects and larvae, and others devour the young of other mites. Some may even be predators of ant trophobionts.

Symphyla and geophilomorphs, show no correlation with ant activity, which is surprising as <u>Geophilus</u> remains have been identified from the food remains of ants. Hence predation pressure may not be very intense. Of the other factors, only temperature shows any correlation. Maybe at higher temperatures, the symphyla burrow to feed upon the deeper plant roots.

If staphylinids, spiders and predatory mites are true predators of ants and their larvae, then it would be expected that these groups would be excluded from larval brood chambers. Mann-Witney U-tests were carried out to see if differences exist between samples containing brood and those taken from other areas of the nest mound. The results are presented in table 35. At the time of year when brood were present, the frequency of staphylinids, spiders and predatory mites was already low and a further reduction was not expected.

	1983 p	1984 p	1985 p
Staphylinids (+ Agriotes)	0.00003	0.03488	0.000001
Predatory mites	0.000001	0.00006	0.00117
Spiders	0.09338	0.00177	0.00025

Table 35. Probability values for the difference between numbers of ant predators in the nest mound and brood chambers.

	November 1946 (upper 6")	November 1983
Hymenoptera	0.1	12.3
Coleoptera	1.5	2.8
Collembola	23.7	22.8
Hemiptera	8.4	21.3
Acarina	65.9	25.9
Araneia	0.1	1.3
Myriapoda	0.3	0.1

Table 36. Comparison of the number of soil organisms extracted by Raw et al 1948, and 1983 results.

However, with the exception of spiders in 1983, the trend is clear: beetles, spiders and predatory mites are excluded from brood chambers, their abundance being far lower there than at any other part of the ant nest. Predatory mites show this trend most consistently, presumably because their smaller size makes them easier to deter. For staphylinids the picture is biased as in many cases their mode of foraging is to attack an ant, then retreat before it is pursued.

One of the few comparable field studies was conducted by Salt, Hollick, Raw and Brian (1948) on ten year old grazed pasture in Cambridge. Four inch diameter soil cores were taken, up to a depth of 6", and then further cores from 7-12". Flotation methods were used to extract the animals. The most accurate counts were made in November 1946, and were compared with rough estimates taken in May 1946. Percentage abundance of selected groups of soil animals for November 1946 and November 1983 are given in table 36.

The main differences occur with the Hymenoptera and Hemiptera. Salt et al were sampling mainly for Agriotes and therefore did not only sample ant mounds, but the most common ant found was Lasius flavus (with smaller numbers of Myrmica sulcinodis, M.scabrinodis and M.laevinodis). Of the Hemiptera found in 1983, 95% were root aphids. The paucity of them in 1946 again probably reflects the lack of ant mound samples. All the other groups of animals considered show similar levels to those found by Salt et al (the smaller number of mites in 1983 is not significantly marked), which attests to the equal accuracy (inaccuracy) of both methods. All those animals sampled in May 1946 occurred in the same abundance as in November, except for Hemiptera which were nine times more common in May ($p<0.01$).

5.4 Conclusion

(i) The number of aphids found in the nest mound is independent of temperature, air humidity and rainfall.

(ii) In general aphids are positively associated with ant activity and the biomass of the larval brood. The exceptions to this are *Aploneura lentisci* which is not ant tended and *Trama troglodytes* which may not have a high enough reproductive rate to cope with the increased predation.

(iii) In general aphids are negatively associated with the presence of alate ants. The exception to this is *Anoecia corni* which is found away from the nest mound when the alates are present, and when they are absent.

(iv)The abundance of coccids appears to be independent of temperature, humidity, rainfall, ant abundance and the state of the brood.

(v) The abundance of other soil organisms varied with season. Except for *Acalypta platychila*, all animals decreased in abundance with increasing ant activity and reached their lowest level in June-August.

(vi) Spiders and predatory mites are strongly negatively associated with ant activity, and this is the dominant factor affecting their abundance. They are considered to be predators of ants and/or their brood, and together with staphylinids seem actively excluded from brood chambers. Staphylinids are not strongly influenced by ant activity because of their heavy sclerotization, comparatively large size and repugnatorial glands.

(vii) Soil collembola show a negative association with ant activity, however, temperature and humidity provide even stronger negative correlations, and are considered to be more important in limiting distribution than predation.

CHAPTER SIX

FURTHER CONSIDERATIONS OF THE RELATIONSHIP BETWEEN ANTS, APHIDS AND OTHER ENVIRONMENTAL FACTORS

6.1 Introduction

Previous chapters have dealt with individual factors, both biotic and abiotic, which affect the abundance of ants, aphids and soil organisms. However, no indication has been given of the relative importance of the twenty-one factors which have been measured each week. The objective of this chapter is to create a model which can predict ant activity and aphid abundance using these environmental variables. Of all the multivariate techniques available, multiple regression is the appropriate method. It calculates the regression of a predicted variable, upon a weighted combination of predictor variables. By considering the variance of the model using all possible variables, and the variance of each variable in turn, one can assess the contribution of each variable to the prediction. Having created the model, the actual and simulated series can be compared to examine the seasonal fluctuations and forecast future values. One may then be able to control the system, but equally importantly a sound model is a sign of a clear understanding of the interactions of the system.

Essentially multiple regression assigns weights to the twenty variables which maximizes the correlation with the predicted variable. This is achieved by assessing the differences between successive weeks' results, i.e. for 1983, solving 49 simultaneous equations each with twenty-one variables. This is most easily done by matrix algebra, and the method of Seal (1966) has been followed throughout.

6.2 The multivariate model

Initially, six regression equations were calculated, to predict ant activity and aphid abundance in 1983, 1984 and 1985. The respective coefficients for each factor are presented in tables 37 and 38. Measures of nest size were not taken every week in 1984 and 1985, and no abiotic data were available for 1985. An analysis of variance was conducted on each model and the percentage of the total sum of squares accounted for by each biotic factor is recorded in tables 39-40. In general it seems that the state of ant brood accounts for a large proportion of the variation of the ant model, but the causes of aphid abundance are not so clear.

Each of the possible models was then used to predict data for each year. The percentage of the total variance accounted for by the models is presented in table 41. It is not surprising that regression models designed to fit certain years, explain away most of the variance incurred by sampling in that year, indeed it is surprising that they did not explain it all. Obviously there are further factors to take into account e.g. sampling errors. What is interesting is that the 1983 ant model also explains away a high percentage of the 1984 and 1985 variance.

Reassured by this, product-moment correlation coefficients were calculated between the predicted and observed values per year (see table 42). Again high correlations exist between predicted and observed values for the years which the models were calculated for ($p<0.001$).

Variable	1983	1984	1985
Aphids	-0.1	-2.47	0.78
Larval brood	17494.4	-494.83	-7274.61
Adult brood	10653.9	1987.52	-2171.38
Total brood	-1675.4	-508.37	1918.89
Coccids	0.3	-41.90	20.05
First instar coccids	5.5	1.39	33.38
Staphylinids + Agriotes	1.1	-16.53	-9.07
Collembola	0.3	0.10	-0.56
Predatory mites	-2.3	7.25	0.18
Phytophagus mites	-0.9	0.27	-0.13
Geophilomorphs + Symphyla	8.2	0.70	7.04
Acalypta platychila	-11.8	97.01	-21.60
Spiders	-14.0	-7.65	-137.46
Nest size	0.1		
Ground temperature	-15.8	30.59	
Mean weekly temperature	19.0	-64.25	
Humidity	-26.0	28.83	
Mean weekly humidity	1.6	-22.63	
Rainfall	-12.7	12.13	
Mean weekly rainfall	-37.3	-9.75	

Table 37. Coefficients of regression equations to predict ant activity.

Variable	1983	1984	1985
Ants	-0.04	-0.06	0.06
Larval brood	4648.83	1044.37	1027.45
Adult brood	-3219.28	-617.78	-98.16
Total brood	342.06	379.04	-21.26
Coccids	3.56	-2.63	-13.65
First instar coccids	1.58	0.89	-2.91
Staphylinids + Agriotes	-2.60	-1.96	2.16
Collembola	0.44	-0.02	0.16
Predatory mites	-2.73	1.37	-1.73
Phytophagus mites	0.48	0.22	0.23
Geophilomorphs + Symphyla	-4.93	-4.19	2.90
Acalypta platychila	-19.11	19.85	-3.69
Spiders	8.99	1.72	10.20
Nest size	0.04		
Ground temperature	-24.31	-0.67	
Mean weekly temperature	20.54	-9.63	
Humidity	-27.44	-0.61	
Mean weekly humidity	24.80	-3.06	
Rainfall	9.23	4.42	
Mean weekly rainfall	-14.20	-16.15	

Table 38. Coefficients of regression equations to predict aphid activity.

Variable	1983	1984	1985
Aphids	26.4	5.3	3.3
Larval brood	21.9	9.6	27.4
Adult brood	22.4	54.2	5.2
Total brood	0.2	1.5	0.5
Coccids	0.5	2.6	1.1
First instar coccids	0.7	0.8	22.2
Staphylinids + Agriotes	1.3	0.02	0.9
Collembola	3.2	1.1	2.5
Predatory mites	2.0	3.0	0.1
Phytophagus mites	10.0	1.2	2.1
Geophilomorphs + Symphyla	3.6	0.3	0.2
Acalypta platychila	5.9	18.5	12.8
Spiders	1.9	1.9	21.7

Table 39. Percentage of regression sum of squares to predict ants accounted for by biotic factors.

Variable	1983	1984	1985
Ants	33.8 1	6.9	5.8
Larval brood	5.0	19.4 2	0.0
Adult brood	5.3	2.7	2.8
Total brood	0.4	0.008	0.0
Coccids	1.3	7.1	6.0
First instar coccids	0.1	6.2	11.2 3
Staphylinids + Agriotes	13.6 3	4.2	0.8
Collembola	12.0 4	2.4	2.4
Predatory mites	18.9 2	5.5	53.2 1
Phytophagus mites	0.1	0.4	0.3
Geophilomorphs + Symphyla	3.5	2.1	13.3 2
Acalypta platychila	5.2	42.4 1	0.2
Spiders	0.8	0.8	4.1

Table 40. Percentage of regression sum of squares to predict aphid abundance, accounted for by biotic factors.

		PREDICTED		
		1983	1984	1985
OBSERVED	1983	99.2	92.9	87.5
	1984	94.1	99.5	49.1
	1985	81.8	42.8	97.8

Table 41a. Percentage of total variance accounted for by ant models.

		PREDICTED		
		1983	1984	1985
OBSERVED	1983	98.6	81.8	87.0
	1984	28.5	98.8	50.9
	1985	28.8	37.5	93.2

Table 41b. Percentage of total variance accounted for by aphid models.

		PREDICTED		
		1983	1984	1985
OBSERVED	1983	0.850	-0.466	0.360
	1984	0.623	0.946	-0.193
	1985	0.404	-0.178	0.813

Table 42a. Product-moment correlation coefficients for ant models.

		PREDICTED		
		1983	1984	1985
OBSERVED	1983	0.772	-0.295	0.353
	1984	0.042	0.877	-0.199
	1985	0.132	-0.159	0.611

Table 42b. Product-moment correlation coefficients for aphid models.

Variable	F-value
Aphids	2.56 -
Larval brood	1.25
Adult brood	1.32
Total brood	3.52 -
Coccids	2.47 -
First instar coccids	2.42 -
Staphylinids + Agriotes	2.51 -
Collembola	2.42 -
Predatory mites	2.69 -
Phytophagus mites	2.20 -
Geophilomorphs + Symphyla	2.40 -
Acalypta platychila	2.29 -
Spiders	2.37 -
Nest size	2.02
Ground temperature	2.47 -
Mean weekly temperature	2.46 -
Humidity	2.19 -
Mean weekly humidity	2.47 -
Rainfall	2.46 -
Mean weekly rainfall	2.43 -

F 15,29 (0.05) = 2.03
(0.01) = 2.73
(0.001) = 3.80

Table 43. Results of F-tests carried out on predictor variables of 1983 ant model.

Variable	F-value
Ants	2.94
Larval brood	2.41
Adult brood	2.75
Total brood	2.83
Coccids	2.85
First instar coccids	2.86
Staphylinids + Agriotes	2.60
Collembola	2.62
Predatory mites	2.10
Phytophagus mites	2.91
Geophilomorphs + Symphyla	2.71
Acalypta platychila	2.42
Spiders	2.85
Nest size	2.70
Ground temperature	3.07
Mean weekly temperature	2.79
Humidity	1.91
Mean weekly humidity	2.67
Rainfall	2.85
Mean weekly rainfall	2.81

$F_{15,29}$ (0.05) = 2.03
(0.01) = 2.73
(0.001) = 3.80

Table 44. Results of F-tests carried out on predictor variables of 1983 aphid model.

The 1983 ant model is a closer fit for all years observations than would be expected by chance, and therefore has some meaning as a model. No model predicts aphid abundance in all three years, the best model is again 1983, when the correlation coefficients were all positive. The main reason that the 1983 results provide a better model is because it is based upon the longest time series, and thus it gives a better estimate of the variability of each factor. This point is demonstrated by considering the 1984 data in which sampling was only started when larval brood biomass was high, therefore the ant model underestimates the effect of larval brood, and over estimates the effect of the alates in compensation.

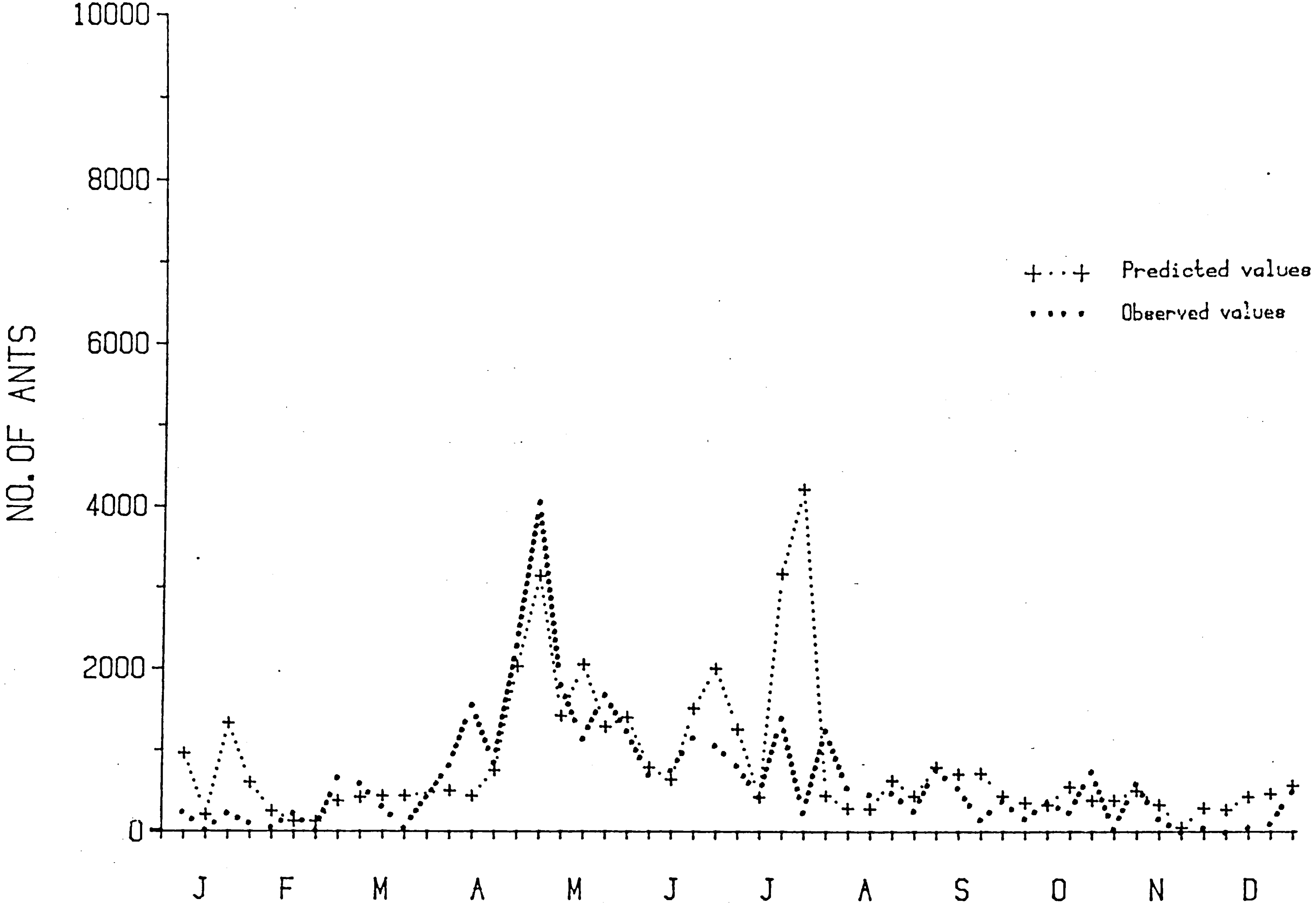
Having found the best regression equation to predict ant and aphid numbers using all twenty predictors, it would be useful to compare the effect of each factor, and establish whether there are any that contribute so slightly to the overall model that they can effectively be set to zero. This is achieved by comparing the variance of the single factor 'restricted' model to the variance of the full model. The ratio of these values is a variate of the F-distribution. The full model is considered to be the most accurate model and therefore if the restricted model under consideration is a major component of it, then it should not deviate significantly from it. The results of these F-tests are shown in tables 43 and 44.

It can be seen that the only factors which are significant in predicting ant activity are the biomass of the larval brood and the biomass of the alates, and maybe the size of the nest, a factor which should be included because of the work of Nielsen et al.

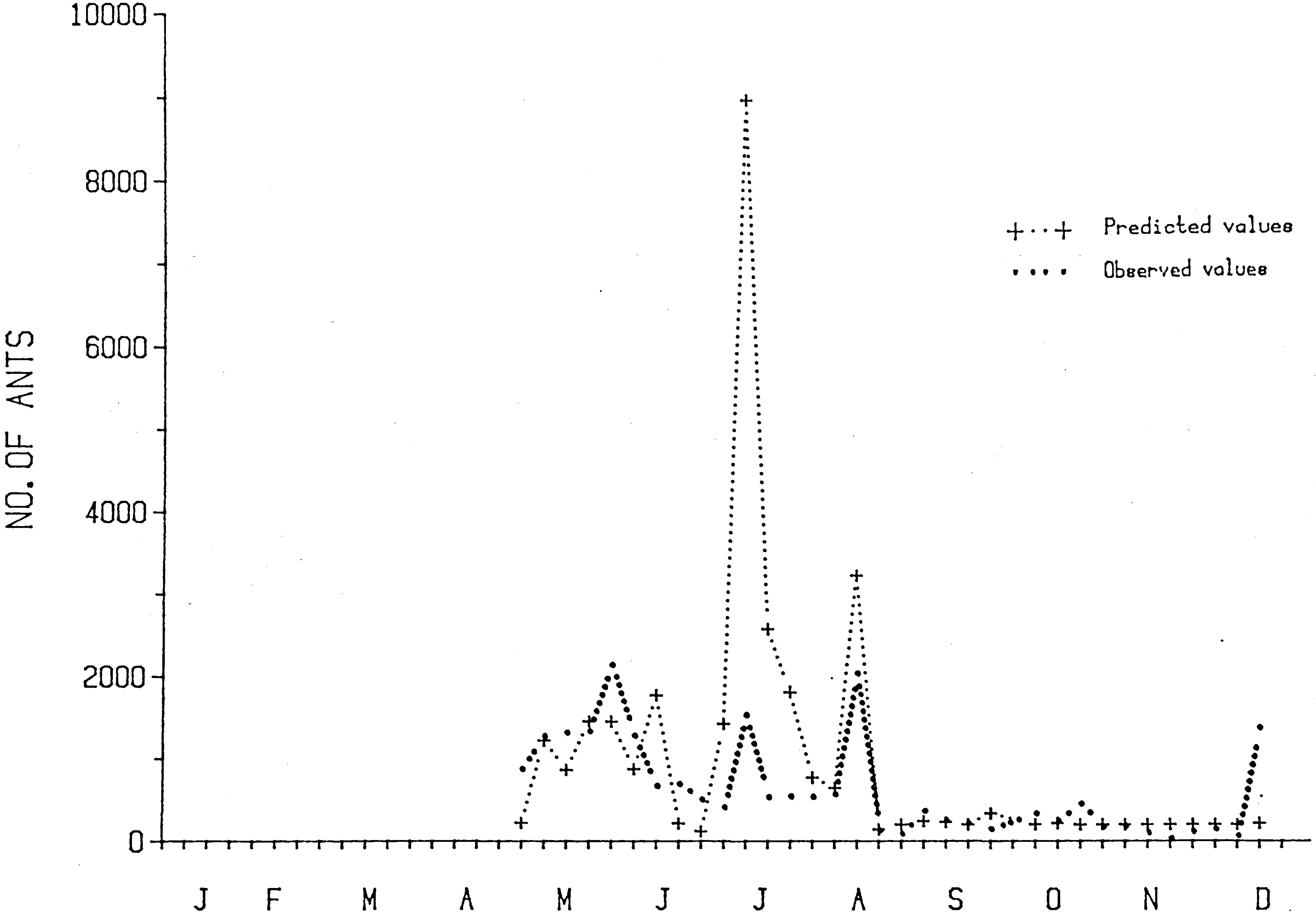
Ant activity = 17494 larval brood biomass (g) + 10654 alate biomass (g) + 0.1 base area of nest mound (sq.cm) + c

This model is far more manageable and has certain implications; ant activity can almost totally be explained by the state of the ant brood. It increases with increasing larval brood biomass presumably due to a higher degree of foraging. This may also account in part for the increased activity when the alates emerge, but at this time of year there are also other tasks e.g. construction of the flight chambers and feeding up of the queen prior to peak egg laying. When no brood are present, ant activity is proportional to nest size. Although this latter point supports the work of Nielsen et al, it is slightly unrealistic in as much as Winter values are much lower than predicted. Temperature makes little contribution to the overall model, in keeping with the findings of Chapter 3.4, but what is important are the extremes of temperature (under $10^{\circ}C$ and over $23^{\circ}C$). By finding the gradient of the best fitting line through the graphs of ant number against temperature, it is found that for each degree centigrade under $10^{\circ}C$, 37 less ants are expected, and for every degree centigrade over $23^{\circ}C$, 58 less ants are expected to be sampled. This shows that ant activity is more susceptible to high temperature than low, presumably via the effect of lower humidity. Adding the effect of extreme temperature to the model immediately improves the prediction.

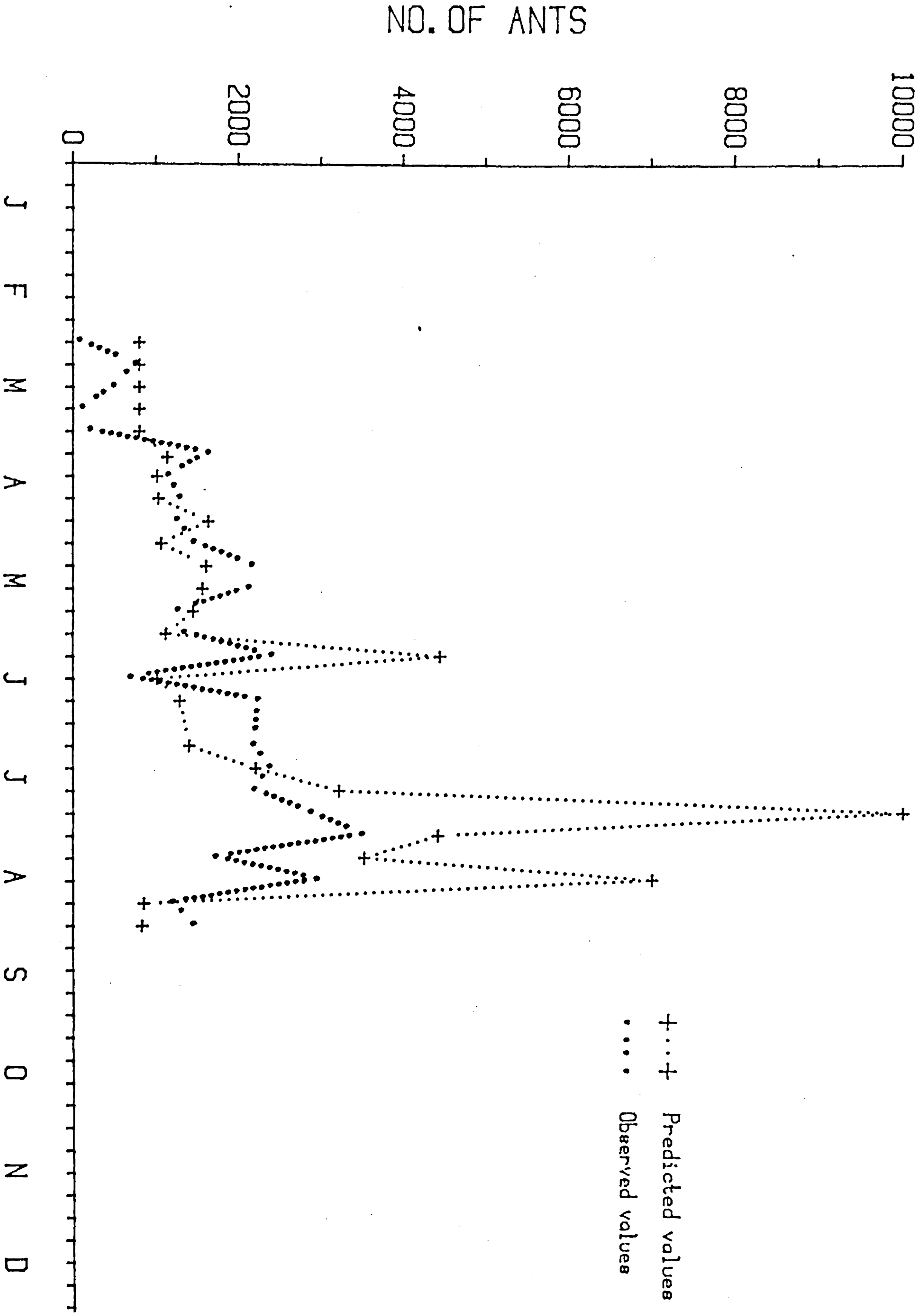
The relationship between the observed and predicted number of ants for 1983, 1984 and 1985 are shown in graphs 64-66. When comparing these curves, the most striking feature is still the individual variation between nests, however, the model does reflect the main features in each year i.e. at low Winter temperatures there is little activity, but as temperature increases, so does ant activity. Ant activity further rises when the larval brood are found, but this increase is far more rapid than observed in the field.



Graph 64. Comparison of the observed and predicted number of ants for 1983.



Graph 65. Comparison of the observed and predicted number of ants for 1984.



Graph 66. Comparison of the observed and predicted number of ants for 1985.

This is one of the subtle flaws of the model; as it is dependent on the presence or absence of brood, it gives an 'all or nothing' response, whereas in the field in late March, the larvae are present and causing an increased foraging rate, but as yet are not being incubated in the top 10 cm of the soil. As the larvae begin to pupate, ant activity drops and in early-mid June there is a lull in activity when the brood are mostly pupae. After this ant activity rises with the hatch of the alates, and very high ant activity is found just before the nuptial flight (one main flight in 1983 and 1984, two flights in 1985). After this ant activity levels are similar until the Winter temperatures begin. The model can overestimate the effect of larval and adult brood. This is most noticeable at peak alate captures, which occur when the flight chambers are sampled by chance. In such a case the model provides a much larger estimate of ant activity than is observed, and demonstrates how the model is susceptible to sampling error.

The fit of the model is less good in 1984 because nest sizes were not measured, and even less precise in 1985 as the temperature data are not available (yet). However, the shape of the ant activity curve is almost identical for 1983 and 1984, and similar to 1985, and the curves can almost be superimposed by translating the time scale. This demonstrates the reproducibility of results, presumably because there is a set development time of ant brood, given 'normal' weather conditions, and the differences in time scale are determined by the type of year it is. 1984 was a very dry year, with more days in excess of 25°C than 1976. 1985 was by far the wettest Summer of recent years, and 1983 was intermediate. In neither 1983 nor 1984 was Spring pronounced, being especially late in 1984, whereas 1985 had a warm spell in late March to April and again in mid-May. Hence ant activity rises earliest in 1985, but is a much more prolonged peak due to the lack of Summer. The main nuptial flight was in the third week of July. In 1984 larvae were not found in abundance until early May (c.f. mid April in 1983), reaching peak numbers in early June, by which time in 1983 the majority had pupated. Due to the hot Summer the larvae rapidly developed, and alates emerged late June in both years. In 1984 the weather conditions were not right for the nuptial flight (due to low air humidity and dry hard earth) until early August, whereas in 1983 the nuptial flight was in the third week of July, as in 1985.

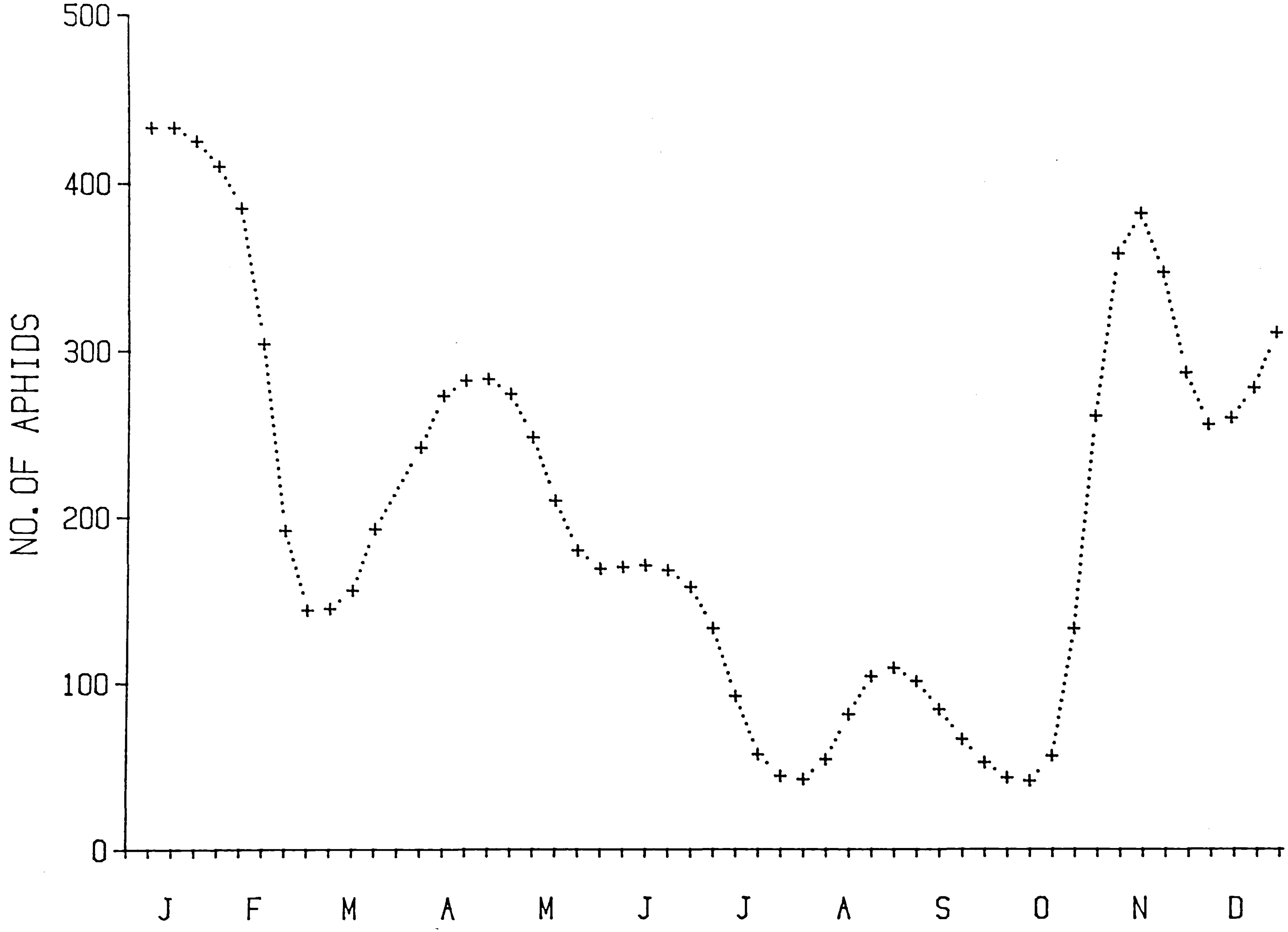
Returning to the aphid model, it seems that no simple combination of biotic factors can influence aphid numbers to such an extent that they alone can predict aphid abundance. It is surprising that alate biomass, a factor which was strongly negatively correlated with aphid abundance in Chapter 5.2, is not an important factor in this model. But this only emphasises the different approach of multiple regression, a feature that only occurs for three weeks a year, cannot be used as a main factor in predicting aphid abundance throughout the year. Upon reflection, it seems likely that aphid numbers could not be accurately modelled because of the large sampling error. As it is the seasonal trends in aphid abundance, rather than the precise values which are of interest, it was possible to 'smooth' curves to bring out the salient features, thus minimizing sampling variation. This is commonly done by using a 'floating mean'. The statistical package MINITAB (T.A.Ryan 1982, Pennsylvania State University) uses a running median of three consecutive values, together with a running mean computed as:

$$z(t) = 0.25y(t-1) + 0.5y(t) + 0.25y(t+1)$$

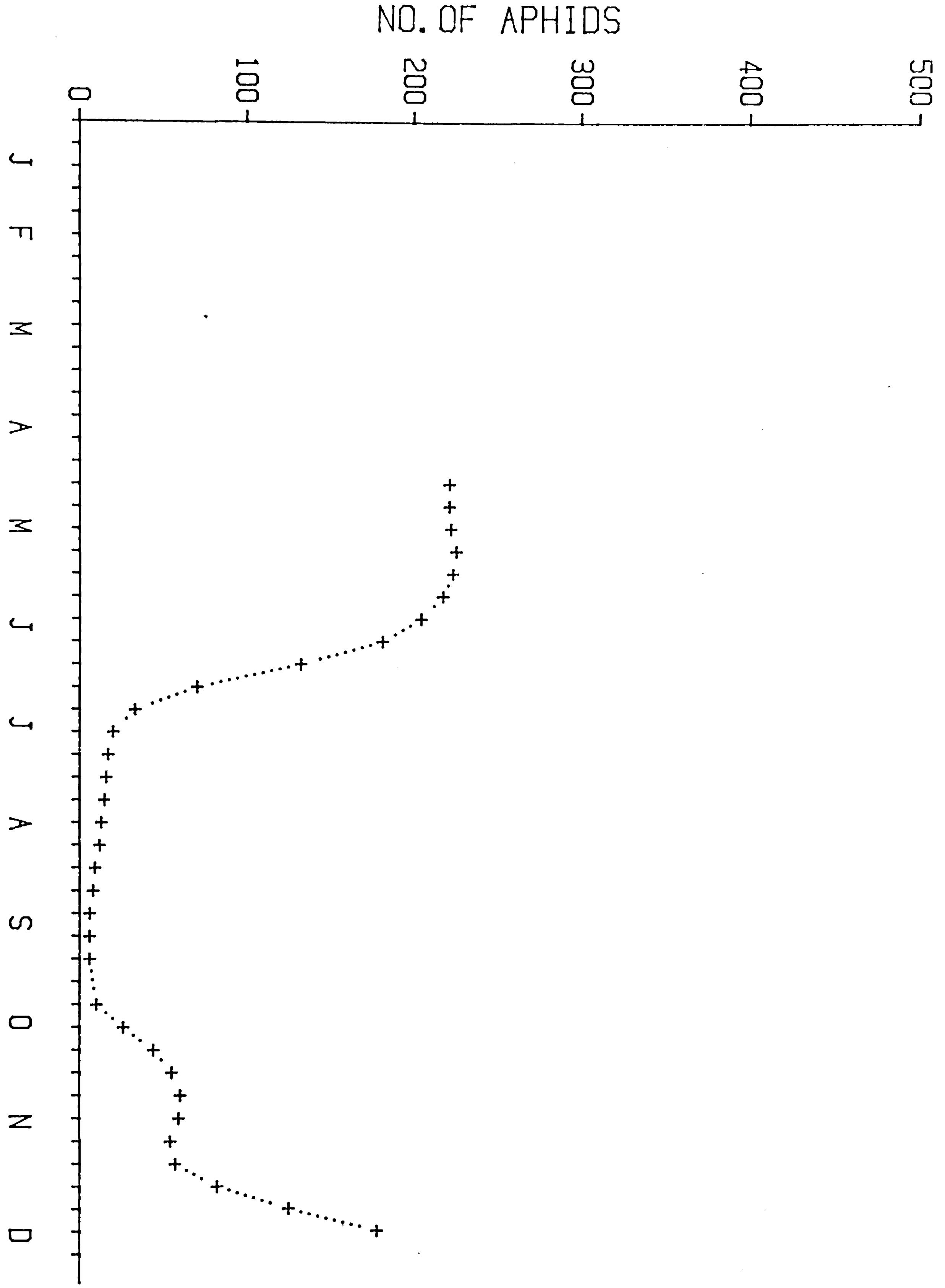
until there are no further changes. This was used to create graphs 66a-66c. Using these new values, the same multivariate technique was applied. The regression coefficients are presented in table 44a.

It can be seen that the major factors (larval biomass, adult biomass, total brood biomass and ant activity) are of approximately the same size each year. However, when the respective years' models are used to predict aphid abundance for other years, as before, no single model is suitable (table 44b). In fact when the correlation coefficients for these 'smoothed' curves are compared with the correlation coefficients for the unsmoothed results (table 42b), it shows the smoothed curves give far inferior values. It seems that the minor oscillations in aphid abundance are of extreme importance in multivariate analysis.

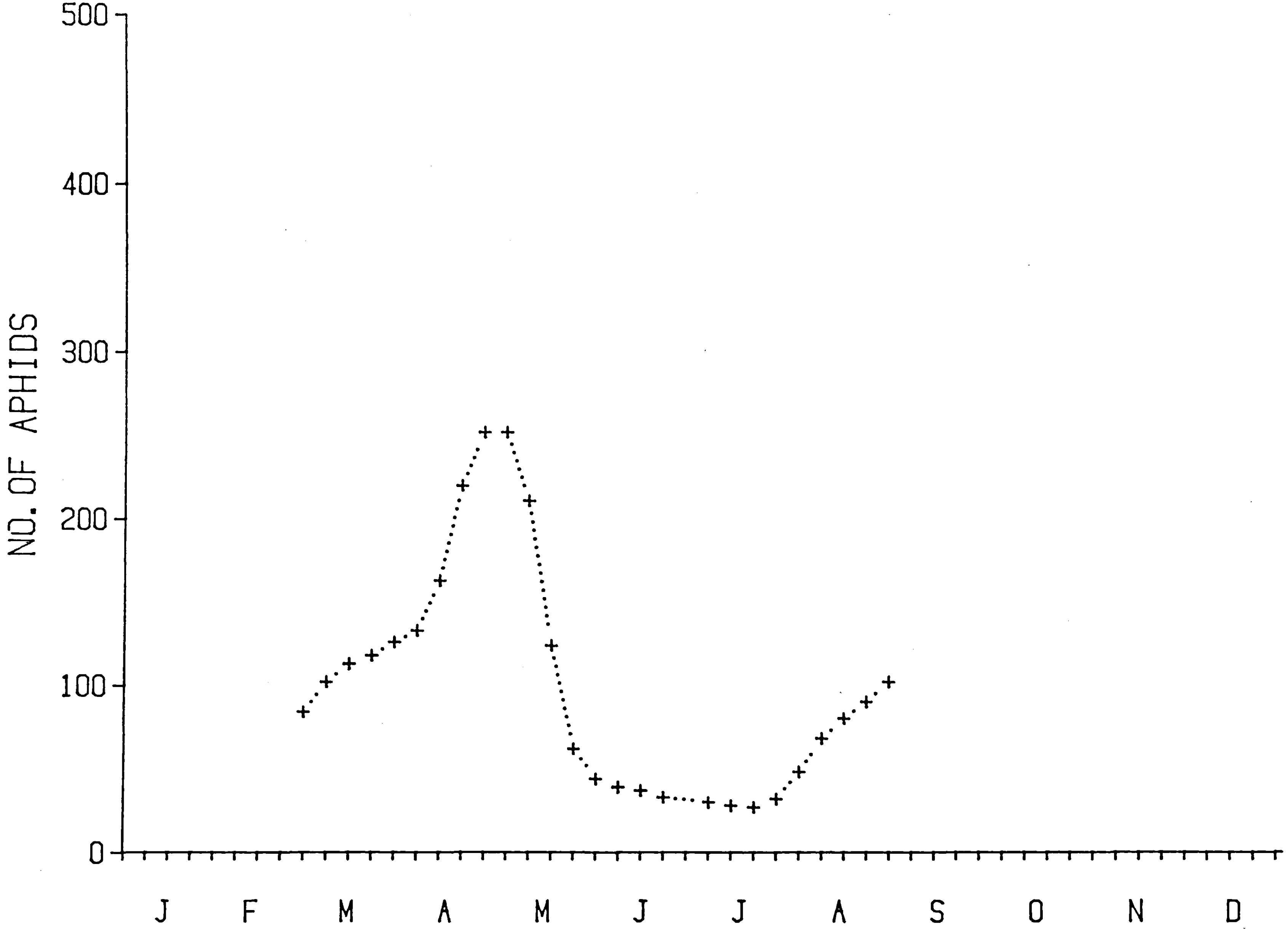
What is interesting is that these smoothed curves can be superimposed upon each other to show the same trends. This is achieved by superimposing 1984 by two weeks in advance of 1983, and 1985 by one week in advance of 1983, thus synchronizing the alate hatch (see table 44c). It was reasoned that the time lags shown must reflect ant development as this is the main pressure upon aphid numbers. To some extent this must be influenced by the type of year it was; 1984 had a late Spring, but very hot Summer (therefore brood well developed). 1985 had a warm spell in early April, therefore the brood were found far sooner than other years, but this initial benefit was partially lost due to low Summer temperatures.



Graph 66a. The effect of 'smoothing' the 1983 aphid abundance curve.



Graph 66b. The effect of 'smoothing' the 1984 aphid abundance curve.



Graph 66c. The effect of 'smoothing' the 1985 aphid abundance curve.

Variable	1983	1984	1985
Ants	0.002	-0.006	-0.007
Larval biomass (g)	-303.385	-701.746	-455.659
Adult biomass (g)	-73.536	-50.783	-45.208
Total brood biomass (g)	34.099	140.000	63.269
Coccids	-3.064	0.771	0.172
First instar coccids	0.605	-0.570	0.711
Staphylinids + Agriotes	0.102	0.314	0.667
Collembola	-0.110	-0.035	-0.021
Predatory mites	-0.176	-0.167	0.003
Phytophagus mites	0.064	0.034	0.015
Geophilomorphs + Symphyla	0.808	-0.676	0.371
Acalypta platychila	0.367	0.198	1.001
Spiders	-0.972	0.767	-2.949
Nest size	-0.003		
Ground temperature	2.139	0.196	
Mean weekly temperature	-0.777	-0.690	
Humidity	0.323	-0.291	
Mean weekly humidity	-1.562	0.433	
Rainfall	0.257	1.327	
Mean weekly rainfall	1.792	-5.928	

Table 44a. Coefficients of regression equations to predict 'smoothed' aphid abundance.

		PREDICTED		
		1983	1984	1985
OBSERVED	1983	0.613	0.046	0.090
	1984	-0.061	0.846	-0.082
	1985	0.087	0.090	0.368

Table 44b. Product-moment correlation coefficients for 'smoothed' aphid models.

	1983	1984	1985
Time of:			
first alates	22/7	4/7	16/7
main nuptial flight	22/7	8/8	13/8
first small larva	20/4	already medium	1/4
first medium larva	29/4	28/4	9/4
first large larva	8/6	9/5	17/5
first pupae	16/6	30/5	1/6

Table 44c. The different rates of ant brood development with year.

Although the brood developed more quickly in some years, the nuptial flight was often delayed. In 1983 the alate hatch was followed very quickly by the main nuptial flight, and as a result, aphid recovery from low numbers was most rapid in this year. In 1984 the consequence of high temperatures and dry soil was that there were many smaller nuptial flights, the main one being in the second week of August. This extra time the alates were in the nest caused the aphid population to recover much more slowly. In 1985 again the nuptial flight was again a long time after alate hatch (but this time for the opposite reasons), therefore again giving a much slower aphid recovery than 1983.

Hence despite the failings of multi-variate analysis, we do have an empirical graphical method to predict aphid abundance, as outlined above and in Chapter 4.2. Moreover, these trends between years are so similar, that it can be predicted which species will be most abundant at a certain time of year. To succeed with a multi-variate model, it appears that a measure incorporating weather conditions and larval biomass is needed i.e. the rate of larval development.

6.3 Conclusion

(i) Ant activity can be modelled to the equation:

Ant activity = 17494 x larval brood dry biomass (g) + 10654 x adult reproductives dry biomass (g) + 0.1 x base area of nest mound (sq.cm) + c

The correlation of the observed and predicted values gives a probability of $0.0001<p<0.002$

(ii) No such linear model can be created to account for aphid abundance using multiple regression. Such an analysis shows aphid numbers to be independent of ant activity and ant brood, thus suggesting there is no distinct management of aphids by the ant *Lasius flavus*.

CHAPTER SEVEN

GENERAL DISCUSSION

In general ant nests are of ecological significance because they contain societies of insects, which are to some extent isolated from the rest of the ecosystem. This is especially true of Lasius flavus in which the mound is practically a closed system. Lasius flavus obtains the majority of its food from the aphids it tends on the underground parts of grasses, many of which have no alternate host plant in this country. Due to the success of this relationship Lasius flavus seldom forages above ground and both it and its aphids are adapted to a permanently subterranean lifestyle.

A further point of interest with these aphids is that they all (except Trama troglodytes) feed on the same range of grasses. Although many plants are attacked by a large number of aphid species, relatively little is known about these assemblages of aphids with respect to how species differ from each other, and what selection pressures cause the differences. Lasius flavus mounds lend themselves well to this analysis, because they are both abundant and highly visible, and most of the aphids remain on the grass roots all year round and can occur in high densities.

Donisthorpe (1927a,1927b) collated many observations on which soil organisms were common in British ant nests. Way (1963) reviewed the extent of the interaction between ants and root aphids, and Heie (1980) and Paul (1980) provided useful accounts of the taxonomy and lifestyle of myrmecophilous aphids. Hence much of the background work had been completed. Addicott (1979) looked at four aphid species which occur on Fireweed (Epilobium augustifolium), in terms of the time of colonization of the aphid, the time of maximum colony number, and differences in feeding position and relationships to tending ants. Pontin (1978), working on Lasius flavus nest mounds, studied the seasonal abundance of aphids and differences in their nest position. Pontin (1963) had already observed different feeding positions amongst subterranean aphids.

From such work, various principles emerged about the associations between assemblages of aphids. On Fireweed, aphid species abundance is separated temporally, the arrival of each species from its primary host differs by approximately two weeks, and this temporal difference is further reflected in the occurrence of the maximum number of colonies per aphid species. Differences were also found in feeding positions and whether or not the aphids were ant tended. Whereas with Pontins mainly anholocyclic species, found in nests all year round, very little temporal difference in abundance between those species was observed. Different nest positions were not found in these aphids by Pontin, neither were any host preferences, contrary to the work of Muir (1959). First instar mortality amongst aphids was found to be high in the Summer months and Pontin (1958) proposed that aphid numbers were regulated by ants dependant upon a protein/carbohydrate balance i.e. large numbers of aphids produced excess honey-dew, therefore the ants removed a proportion of the population until a balanced protein/carbohydrate diet was resumed. This mechanism accounted for the continued presence of aphids in ant mounds i.e. restrained workers from destroying the whole population.

Working on the same site as Pontin, many of the biological parameters concerning Lasius flavus agree; mean nest diameter (0.83m), and estimates of the number of ants per nest (see chapter 3.5). No differences were found between the number of ants in each quadrant of the nest mound, unlike Nielsen 1976. This was attributed to the time of sampling (@ 1500hrs), when the ground temperature was highest, therefore the differential effects of insolation were minimized. The total number of workers extracted from the ant nest could not be correlated with nest size, because the abundance of ants in the top 10cm of the nest varied seasonally with factors such as temperature and state of brood (see chapter 3.4, chapter 6). Activity in the surface of the nest increases as the temperature rises to 10°C. Temperature then has little effect on the abundance of ants except at extremes (>23°C), when the ants move to deeper parts of the nest due to the reduced humidity (Peakin 1960). During Spring the larvae were also brought to the surface of the mound, and as the brood increased in biomass, so did ant activity, presumably due to increased foraging. There seemed to be a slight lull in ant activity when the brood pupated (although not statistically marked), and then renewed activity when the alates emerged due to flight chamber construction and further feeding. When there was a real increase in worker numbers (late August-September), this passed almost unnoticed. As well as variation in ant numbers with depth, ant abundance also falls off with distance away from the centre of the nest mound. Generally the number in the epicentre of the nest is similar to that at 20cm radius, less are found at the edge of the ant mound (35cm), and far fewer near the edge of the territory (about 70cm). The presence of brood tends to lessen these differences, as more ants forage throughout the ant territory, extreme cold accentuates these differences as the ants congregate in the nest mound. It was found that the temperature at the base of the nest mound may be up to 6°C higher than that of the ground in early Winter. These cyclical changes observed in all three years, and modelled in chapter 6, were not observed by Pontin (1978). It is thought that this is because his cores were taken away from the nest mound, where the differences are less obvious.

Aphids occur together in the nest mound throughout the majority of the year, therefore show positive temporal associations. The only exceptions to this are Anoecia corni (an heteroecious species) and Aploneura lentisci (not ant tended), which implies that they are not an integral part of the community. Especially marked temporal associations exist between Geoica utricularia, Geoica setulosa, Tetraneura ulmi, Baizongia pistaciae and Forda formicaria, (but not statistically significant between T.ulmi and B.pistaciae). However, when these aphids are found together in soil cores, there is very little evidence of interaction between them (see chapter 4.4) and no mosaics are formed.

Of all the factors influencing aphid abundance, ant activity (especially during the emergence of alates) was found to be most important (see chapter 5.21). Aphids are highly abundant in Winter when ant activity is low. As the ant brood develops, there is an increasing reduction in aphid numbers. This is especially noticeable amongst the first instars, and and upon consideration of age classes there seems to be high mortality, although the number of adult aphids is almost unchanged. When the alate ants emerge, aphids of all age categories practically disappear from the nest mound. *Anoecia corni* is the only exception to this, returning to the nest late May to June, and reaching maximum abundance in late August. It avoids much of the aphid predation by colonizing the outlying nest territories. Aphid species seem to have different breeding rates over Winter, and thus reach maximum abundance at different times, similarly to Addicott (1979). Of the five gramnivorous species analysed (*Tetraneura ulmi*, *Forda formicaria*, *Anoecia furcata*, *Baizongia pistaciae*, *Aploneura lentisci*), *T.ulmi* did not reproduce over Winter and *B.pistaciae* reproduced much less than the rest of the aphids. As a result, *F.formicaria* and *Aploneura lentisci* reached maximum abundance in February, whereas *T.ulmi* and *B.pistaciae* only reached this in May.

Having postulated that interspecific competition should play a less important role than intraspecific competition in determining aphid abundance, it was reasoned that interspecific competition may only become obvious at times of high aphid density i.e. January-March and

November-December. When such periods were analysed, no differences were shown between the probability of finding an individual of an aphid species at any given nest location i.e. the chance of finding an aphid species at a certain point is proportional to its abundance. When mean densities were compared, certain aphids were found to be more abundant at different nest locations, thus implying that there is a spatial separation between aphids at high density, some surviving and breeding best at certain nest locations. It was found that B.pistaciae was significantly more common at 20cm from the centre of the nest mound, F.formicaria was more common near the edge of the nest mound, Geoica setulosa was most abundant 35-70cm from the nest mound, and Anoecia corni was most abundant at the edge of the territory when it occurred, which was in part responsible for its survival and abundance immediately after the marriage feast. Tetraneura ulmi was significantly more common at 70cm, despite also being very abundant at 20cm from the centre of the nest mound.

This distribution remained whilst the major dietary requirement of the nest was carbohydrate, but as the demand for protein to feed the brood grew, the distribution broke down. Experimental evidence to support the importance of protein demand can most simply be shown by reducing the demand upon the aphid population. This can only be carried out in March-April, when larvae are first brought to the nest surface. Such field experiments are outlined in the section on future work. To explain the set distribution observed; it is suggested that there are various degrees of interdependence between ants and root aphids, and these differences in ant attendance help maintain this distribution. All the aphids studied possess a circlet of hairs around the anus, often referred to as the 'trophobiotic organ', but there are also other structural adaptations which may encourage/discourage the attention of ants. Trama troglodytes has elongated hind legs, and is reported to use these to simulate worker 'communication' during trophobiosis. Therefore it is highly ant-adapted, and in keeping with its expected tolerance it is often found in the centre of the nest, even in brood chambers (Dr.Pontin, personal communication). However, it is fully mobile even as an adult, and its foodplants (Compositae) may influence its distribution far more than ant attendance. On the other hand, aphids which are customarily found at 70cm e.g. Anoecia corni are heavily sclerotized and still possess rudiments of siphuncles. Tetraneura ulmi also has rudimentary siphuncles and is very waxy. A phylogenetically similar aphid, Eriosoma lanigerum is totally avoided by ants because the waxy excrement is not attractive (Heie 1980). Aphids of intermediate ant tolerance maybe waxy e.g. B.pistaciae, Geoica spp. or have a very high reproductive rate e.g. B.pistaciae, but there is no sclerotization.

Of prime importance to the continued survival of aphid populations is the attentiveness of Lasius flavus. Reviews of myrmecophily differ in the benefits derived by aphids; but aphid eggs are treated in the same manner as ant eggs (Pontin 1958), aphids are carried alongside brood during heat extraction and can often be seen being carried around artificial nests (although this latter response may be maladaptive as the aphids are often moved from suitable host plants and placed in nest chambers), therefore aphids are obviously a prized resource. What is not so clear is the ultimate benefit that aphids derive in terms of fitness, very few alates are produced, and this seems to be the only way to spread their genes (see chapter 5.22, appendix D1).

A secondary aspect of this relationship is whether ants purposefully regulate the number of aphids in the nest. Pontin (1978) proposed a protein/carbohydrate balance to account for the relatively constant number of aphids he found in the nest territory. To test this extra sucrose/melizitose was added to ten mature Lasius flavus nests during August (1985), a time of year when aphid populations were small, thus any additional carbohydrate would be easily recognised. Ants were observed using this food source, and in one nest there were battles between Lasius flavus and Lasius niger to possess it. Subsequent statistical analysis showed no difference between the number of aphids in the experimental and control nests (see appendix A5). This shows restraint upon the part of workers from further reducing the aphid population despite having excess carbohydrate, therefore the balance is in doubt. Furthermore when whole nests are continually studied, it is found that aphid numbers are not constant, but susceptible to almost complete extinction in the nest mound, when alate predation is high.

Aphid numbers fall with the development of the ant brood. Mortality is mainly from the immature stages (especially first instar), implying that workers can match the size of prey to the size of the larvae to some extent. Although it should be noted that the immature stages are most abundant, smaller, less waxy and unsclerotized, thus are most liable to predation. The number of adult aphids remain at approximately the same level throughout Spring until July, therefore this does not noticeably seem to reduce the breeding population. Highest aphid mortality coincides with the emergence of the alate ants (late Summer). All age groups of aphids are reduced until they practically vanish from the nest mound. It is thought that the feeding up of the new queens accounts for this, as they prepare to fast until they have reared their first brood. Aphids recolonize the nest mound during the next three months, presumably from the surrounding territory (but it is possible that alates produced from other ant nests aid this). Those species which recolonize the nest first have high reproductive rates and some form of protection from ant predation e.g. Tetraneura ulmi, Anoecia corni.

I can find no evidence for a protein/carbohydrate balance. Once a worker is mature, it has little need of aphid protein, its requirements maybe satisfied by the amount of amino acids in honeydew or additional sources from scavaging. When larvae are present the protein demand rises, and workers harvest the aphid population to match this, presumably in response to larval surface pheromones. This demand occurs at a time of rapid aphid reproduction and does not noticeably damage the breeding population. During the time of larval pupation and alate emergence, flight chambers are constructed in the surface galleries (those parts of the nest most frequently sampled). This initially displaces some aphids (and other soil organisms) out of the nest mound, and this situation is accentuated by alate predation, and results in the observed lack of aphids in the nest mound. It should be emphasised that the number of aphids in the territory remains approximately constant and although the captures are low, these still provide a sizeable crop because of the large area involved (appendix D2). After the alates have left the nest, there is a gradual recovery of aphids into the nest mound.

The only need of regulation/restraint in the system is so that the number of larvae present does not exceed aphid supply. There are strong selective pressures against this, especially in the light of the subsequent need for food from the alate ants. Such regulation must originate from the queen. During the majority of the year (except in late Autumn and Winter) she receives protein to build up her ovaries and maintain egg production. Thus she gains some indirect estimate of aphid crop. Once her ovaries are mature she can still suppress egg production to some extent if food becomes scarce, and it is significant that maximum egg laying only occurs when larval feeding pressure subsides (when the queen larvae prepare to pupate).

Ants, aphids and coccids make up 68% of the total number of organisms extracted from the ant nest. The other organisms included; soil collembola, beetles (80% of which were staphylinids), spiders (mainly wolf spiders), predatory and phytophagus mites, symphyla and geophilomorph centipedes, the ant <u>Myrmica</u> <u>scabrinodis</u> and various meadow bugs including froghopper nymphs and the tingid <u>Acalypta platychila</u>. Insects frequent the nest for many reasons, higher temperature and humidity, a ready source of refuse (e.g.dead ants, pupae exuviae), plentiful fresh food e.g.ants and their brood as well as other soil organisms. The abundance of staphylinids, collembola, phytophagus mites, spiders and to a lesser extent myriapods and predatory mites decreases from April onwards with the maturation of brood, reaching lowest levels with the emergence of alates, therefore correlations were calculated with ant activity (see chapter 5.42, table 33).

Soil collembola are common decomposition animals in ant nests and showed strong negative correlations with ant activity, it is thought that these are used as a further food source during high demand (May-July). Staphylinids, spiders, predatory mites and Myrmica scabrinodis are all facultative predators of ants and their brood. Spiders and predatory mites are not heavily sclerotized and are often of similar size to L.flavus workers, hence these are killed or driven from the ant nest as ant activity rises, as indicated by the strong negative association. On the other hand M.scabrinodis is a larger ant with more powerful jaws, and 'is adapted to living near hostile L.flavus colonies' (Moxon 1980). In mixed laboratory nests, M.scabrinodis reacts passively to L.flavus attacks, although they tend to restrict L.flavus access to common areas by blocking their nest entrances. However, in the field M.scabrinodis take dead L.flavus workers and pupae, and once part of the nest mound has become inhabited by M.scabrinodis, L.flavus extend the nest in the opposite direction. Thus the lack of a negative correlation between L.flavus and M.scabrinodis may mask a number of complexities. Staphylinids are common predators of Lasius flavus. Some survive in the mound by acquiring the colony odours, others possess trichomes which secrete 'appeasement substances' which calm the ants. Many symphilic species have adapted structurally e.g. morphological mimicry, modification of antennae for communication or carrying. Most staphylinids however, are opportunistic predators relying on quick forays, or ambushes in the less frequented galleries. Even when attacked by large numbers of ants, they usually survive, because they are more powerful, highly sclerotized and can produce repugnatorial substances from glands in the tips of their abdomens. Staphylinids show little correlation with ant activity. Phytophagus mites also become more scarce as brood matures, but despite this there is no significant correlation with ant activity. This implies that phytophagus mites maybe tolerated in the nest due to their small size and hard exoskeleton. Symphyla and geophilomorph centipedes also follow this trend, but in this case temperature seems to be important; summer temperatures may drive these myriapods deeper into the soil beyond the core depth.

If staphylinids, spiders and predatory mites were predators of ants and their larvae, it was reasoned that these groups would be excluded from the larval brood chambers. This was found to be true (see table 35), especially amongst predatory mites which may be the easiest to deter.

To determine how soil organisms were distributed within the ant nest, measures of aggregation were calculated using Taylors coefficient b. These are presented per year for workers (table 5), aphids (table 17) and other soil organisms (table 32). The most highly clumped species was Myrmica scabrinodis; when this ant invades L.flavus nests, it forms small dense groups, not distributed throughout the nest mound. Next most clumped were the aphids and coccids, each of which had values well in excess of 2. These clumps were presumably produced by 'family' groups of aphids on neighbouring plant roots. Estimates of clump size and density are given in table 18. In each case the clump is larger than the core diameter and aphid density varies with taxa; Fordinae > Eriosomatinae > Anoeciinae > Traminae. Lasius flavus was the next most clumped species. Of the remaining soil organisms, aggregation values vary quite widely because one is dealing with multi-species groups, but it can be seen that the main predators of L.flavus nests, staphylinids and spiders (and to a lesser extent predatory mites) are randomly distributed within the nest, indicating their solitary hunting behaviour. Other soil organisms have slightly clumped distributions.

Further information on the distribution of these animals was gained by examining the frequency distribution (see appendix C). For predatory mites, staphylinids, spiders, phytophagus mites and collembola, all the distributions fit a negative binomial, which is to be expected when regularly sampling across an environmental gradient. However, both ants and aphids have distributions which are more clumped than this, and have been found to fit a reciprocal distribution which reflects a further level of clumping beyond that due to the environmental gradient i.e. aphid clones on neighbouring grass roots and ants in chambers.

Conclusion

Subterranean aphids from Lasius flavus nests provide another example of competing organisms which continue to coexist. There is evidence of some resource partitioning i.e. different grasses from the same range may be preferred; space maybe partitioned by different root feeding positions and/or different positions in the nest mound when aphids are at high abundance. Furthermore although aphids reproduce all year round, some species were more successful at certain times of year. Due to the slight partitioning of resources, intraspecific competition is expected to be higher than interspecific competition and this would be a stabilizing influence on the coexistence of species.

Although ant activity appears responsible for the seasonal pattern of aphid abundance, no evidence of deliberate regulation of aphid numbers could be shown. Indeed indiscriminate predation of aphids by Lasius flavus could contribute to the stability of the aphid community. Despite this some species do seem to have a closer relationship with L.flavus e.g. Trama troglodytes, although this too becomes significantly reduced in numbers when predation pressures are high. In general it is those aphids which are heavily coated by wax/sclerotized and have the highest reproductive rate that seem most abundant in L.flavus mounds, far more so than 'ant-adapted' aphids.

High levels of aphid predation (due to high larval biomass) occur at a time of year when the aphids are breeding most rapidly. As a result the breeding population remains about the same level throughout Spring. Nevertheless, this predation reduces the aphid population to a level where the effect of intraspecific competition becomes greater than interspecific competition and the spatial separation of aphid species breaks down. The period of lowest aphid numbers coincides with the hatch of alate L.flavus, indeed the queens' abdomen almost doubles in size from the time of hatch until the nuptial flight. In addition at this time of year flight chambers are being excavated in the superficial nest galleries, which may passively force aphids out of the nest mound. These chambers become densely packed, even larvae are moved from the centre to the margins of the nest mound. Laboratory observations over this period show that the response of L.flavus workers towards aphids was unchanged. They were not fed to alates, and they were carried around the nest as usual.

Irrespective of abundance and the degree of ant attendance, success in Lasius flavus tended aphids seems slight. Alate aphids are rare, and as success can only be measured in terms of gene propagation, then lack of dispersal must severely limit this.

Future work

Throughout the period of research, two main problems arose, relating firstly to the destructive method of sampling and secondly to my inability to culture aphids in the laboratory. Each week a new nest was sampled which created a continually changing source of variation. Although this can be overcome by statistics, as a result these can only predict trends rather than real numbers. The problem with taking cores from the same nest in successive weeks, is that after the first week, one is not sampling a natural population. Therefore some measure of inter-nest variation should be taken by sampling a large number of nests per week, unfortunately this was beyond the scope of my apparatus and time.

Despite many variations of technique, no aphid cultures were totally successful. It would be useful to have more accurate measures of fecundity, maybe from dissection, and thus calculate better estimates of aphid mortality. In the absence of experimental replacement series, an assessment of aphid-aphid interactions is still needed, presumably by field work, maybe by examining their abundance in other situations e.g. <u>Lasius niger</u> nests, or artificially aphid free mounds and study the recolonization more thoroughly.

From consideration of aphid dispersion patterns, it was shown that at high density, they separate spatially throughout the nest presumably in response to interspecific competition facilitated by differential ant attendance. It was further proposed that this pattern breaks down due to larval predation. This can be tested by removing larvae from one set of nests thereby limiting predation and comparing them with control nests. This is most easily accomplished in mid-March when small larvae are first brought to the surface of the nest. It is hypothesised that the aphid distribution pattern in the experimental nests should remain far longer than usual.

The converse experiment of adding extra larvae can also be carried out. If these larvae are accepted by the workers as readily as they are in the lab, then this should increase the predation level to such an extent that aphid numbers are seriously depleted in May-June, so that by the time of the nuptial flight, there is not enough food to feed the alates. This has three predictions: nests sampled in May-June should contain more larvae and less aphids than the controls. Alate queens emerging from the nest should have a lower live weight than queens from control nests. In the experimental nests, low aphid abundance should cause the alates to emerge earlier from the nest.

Lasius flavus workers face a conundrum, on one hand tending aphids for carbohydrate, on the other killing the aphids for their larvae thus depriving themselves of a food source. It would be interesting to manipulate these opposing motivational states, by adding/removing larvae to ant-aphid laboratory cultures (if these are ever possible!), especially noting different treatments of different species of aphid. It is expected that when carbohydrate is the main dietary requirement that there should be little difference in attention to the aphid species. When the larvae are introduced, it is expected that ant behaviour would change towards aphids; some being killed, and that a preference would be shown for small, less waxy aphids. Thus providing support for different degrees of ant attendance.

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The management of ~~subterranean~~ aphids and other soil NEST INHABITANTS ~~organisms~~ by the ant *Lasius flavus* (F.).

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APPENDIX A1

THE EFFICIENCY OF EXTRACTION

Results

	Mean number extracted per core	Mean number remaining per core	Percentage extracted
Worker ants (Winter)	14.0	0.2	98.6
(Summer)	113.4	0.8	99.3
Pupae	43.5	5.8	88.2
Male alates	20.7	0.0	100.0
Female alates	6.6	0.8	89.2

Table 45. The mean number of ants extracted and remaining in soil cores at different times of year.

Discussion

Many methods of extracting animals from soil have been published in scientific literature. The most widely used types either involve heat extraction or flotation methods, but other techniques have been used e.g. Salt et al (1948) used a high powered water jet to force the soil animals through successively finer wire meshes. This method is most suitable when extracting a certain species or size range of animals, and is not universally applicable. Not only did they initially lose many of the smaller arthropods (especially mites), through their finest mesh, but the more delicate organisms were beyond identification by the end of the extraction process.

In an effort to assess the percentage efficiency of extraction, for five week periods in both Winter and Summer, all soil samples were hand sorted after extraction to determine the numbers of organisms remaining. The most abundant organisms remaining in the soil cores were _Lasius flavus_. Although many more workers were found dead in the Summer samples (due to mechanical damage from the overall compression of the core and by being trapped at the edge of the sample by the corer), the percentage lost in this manner is lower than the Winter samples. Worker and alate males show an almost complete extraction whereas the number of alate females is lower. This is attributed to the size of the wire mesh immediately below the soil core, although the majority managed to wriggle through the wire mesh, those recently emerged either did not have the strength or had problems with their expanding wings, and remained around the bottom of the soil core. Pupae showed an even lower percentage of extraction. This demonstrates the problem with any 'repellant' technique, that it is harder to obtain the dormant stages such as pupae and eggs. Egg masses were never found in the post-extraction samples. It is interesting that the efficiency of extraction of pupae seems to decrease with increasing distance from the nest centre. This may demonstrate that the extraction of non-locomotory stages e.g. pupae as well as ant larvae, aphids and other soil organisms, maybe via carrying by ants. Preserved ants were often seen with aphids in their mandibles, and aphid carrying is a common occurrence in laboratory nests.

Other soil organisms were searched for, but few were found except the occasional body remnants of beetles. Presumably they were damaged during sampling, but it is possible that they were killed by ants or a combination of both factors. The remains of soft bodied arthropods were never recorded, which is perhaps understandable following a weeks desiccation.

Nielsen et al (1976) claimed an extraction efficiency of 96% for _Lasius flavus_; my own estimate can be no higher than 88%. Therefore the numbers claimed in the preceding chapters are not precise measures, but what was important were the relative changes in the population density of the soil organisms.

APPENDIX A2

THE FORMATION OF MOSAICS BY APHIDS

Introduction

The problem with disjunct core samples is that one is never sure what happens in between; whether the dominant species in one core is found in neighbouring cores, or whether aphid clumps are more limited in size. The sampling pattern of 1985 answered the questions of aphid clump size, density and spatial distribution within the nest, but back in 1983 attempts to discern this were also made, not by contiguous linear transects, but by almost totally sampling the surface of the ant mound. The object was to find whether or not aphids formed a mosaic of species i.e. there were distinct zonal boundaries between species.

Discussion

Diagrams I-V show the distribution of the four commonest aphids found in the five, twenty-five core samples. An 'in depth' analysis of which aphids are present at each time of year has been covered elsewhere, suffice to say that these observations are in complete concordance.

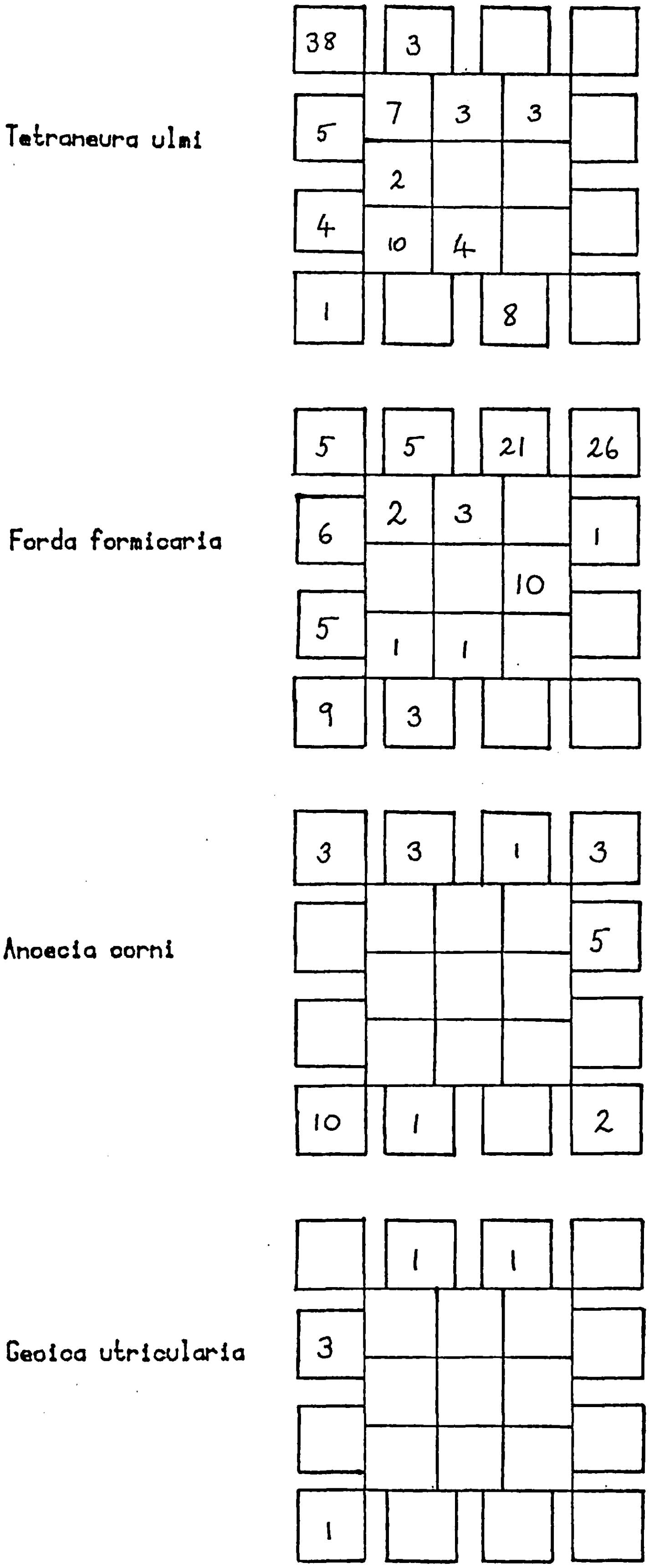


Diagram I. The spatial distribution of aphids from the twenty-five core sample on 15/7/85.

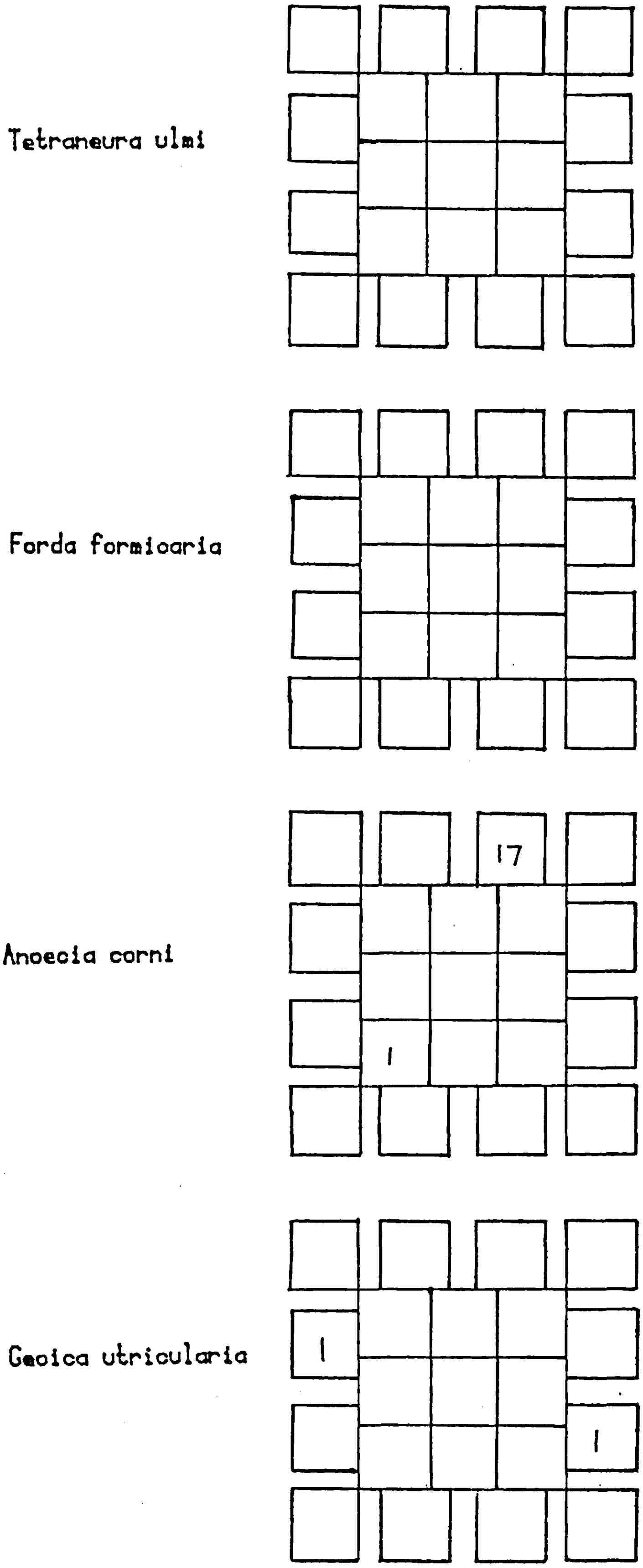


Diagram II. The spatial distribution of aphids from the twenty-five core sample on 8/9/85.

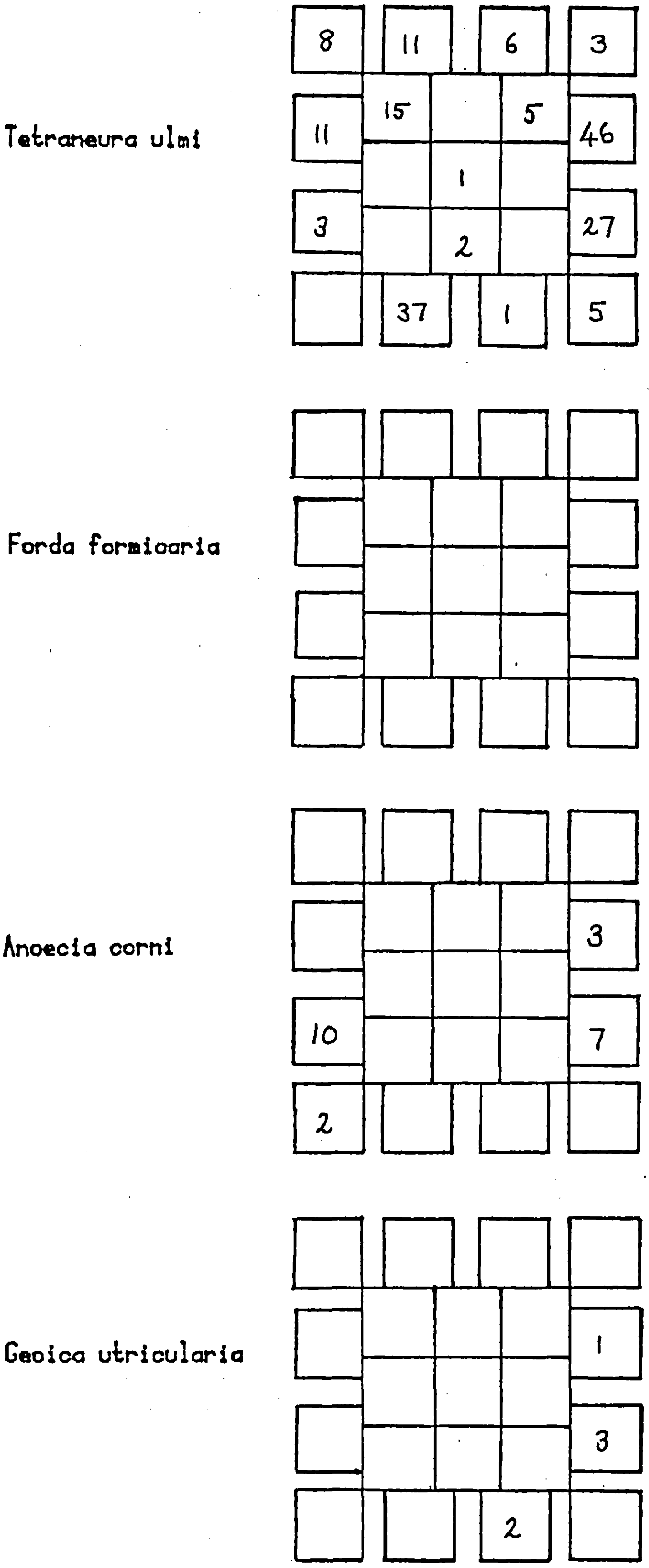


Diagram III. The spatial distribution of aphids from the twenty-five core sample on 13/10/85.

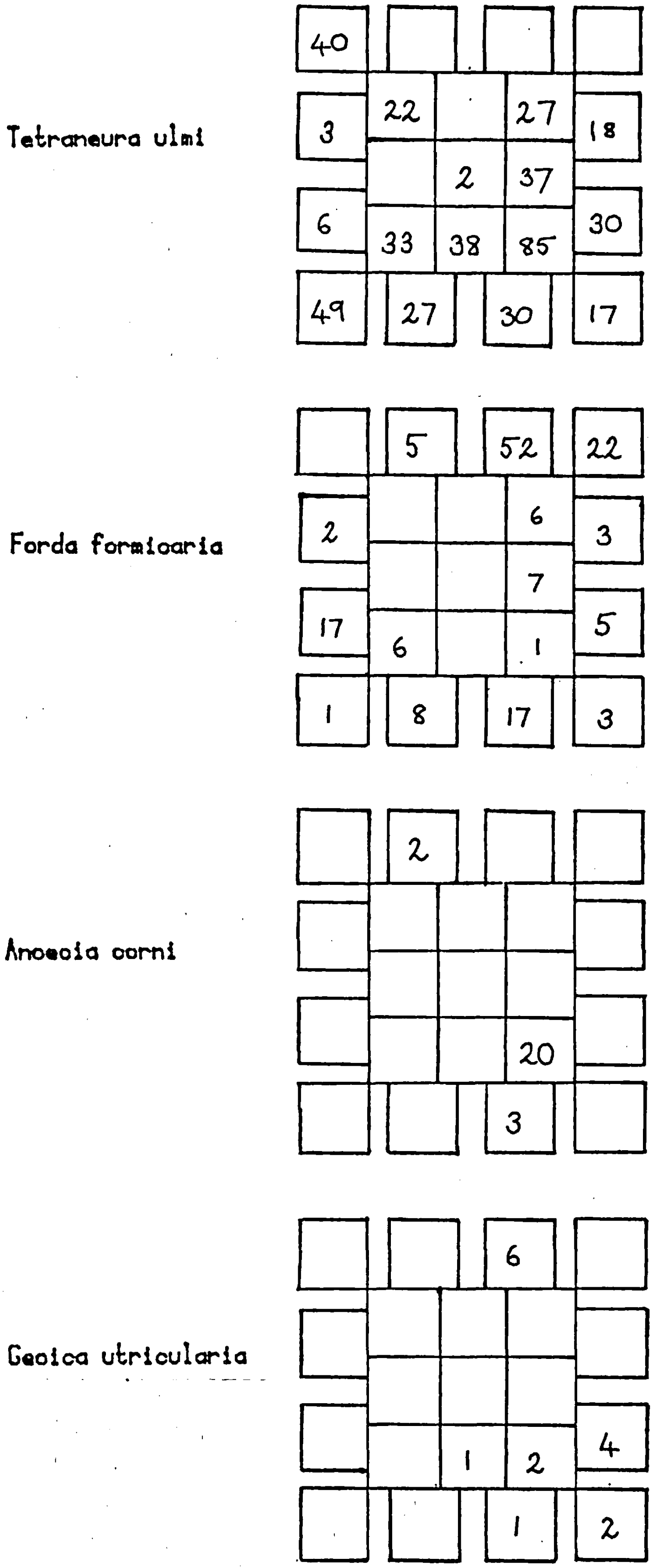
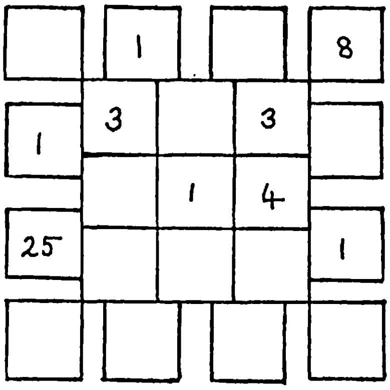
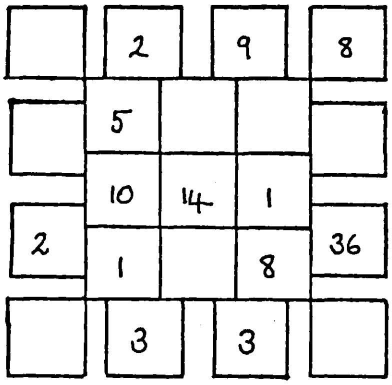


Diagram IV. The spatial distribution of aphids from the twenty-five core sample on 10/11/85.

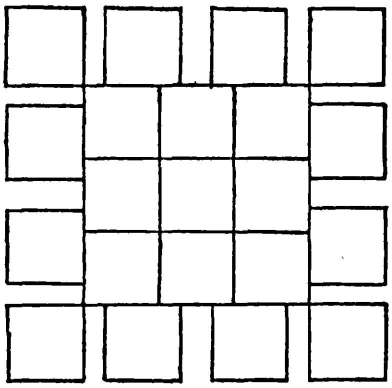
Tetraneura ulmi



Forda formicaria



Anoecia corni



Geoica utricularia

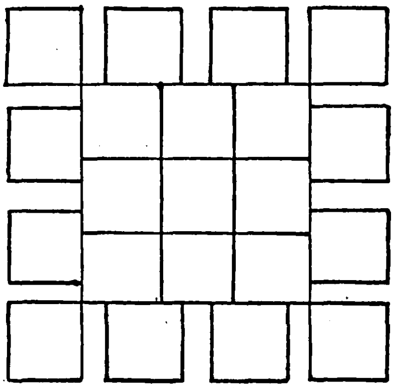


Diagram V. The spatial distribution of aphids from the twenty-five core sample on 13/12/85.

It can be seen that mixed species cores are of most common occurrence;

the probability of a mixed species core = 0.47

the probability of a single species core = 0.34

the probability of a null species core = 0.21

although the difference in probability between mixed and single species cores could be due to chance. Thus it was concluded that when aphids were at the levels of abundance found over the study period (July-early December), they did not form mosaics of species within the ant mound. This was to be expected from consideration of the mean clump size (chapter 4, table 17). Although an ant nest cannot be considered a uniform environment, grass roots are abundant throughout, therefore there are no physical boundaries between gramnivorous species. But in general intraspecific competition between the members of the same clone is going to be more severe than interspecific competition, and this alone provides a strong pressure against the formation of mosaics.

However, it should be noted that when aphids were at low density i.e. after larval brood pupation and during the 'recovery phase', when food was not limiting, the most common species overlapped less than when the aphids were at high abundance. Hence different aphid species only interact as food and space become limiting, and only then does interspecific competition become an important factor.

APPENDIX A3

INVESTIGATING THE REALITY OF THE 'MARRIAGE FEAST'

Introduction

By early Autumn 1983, it was becoming clear that there was a drop in aphid numbers coincident with the hatch of alate ants, followed by a slow rise in aphid abundance as they recolonized the ant mound. Pontin (1978) sampling away from the nest mounds found no such drop in abundance, therefore in mid-October, samples were taken from ten ant mounds in addition to the normal weekly sample to see if this drop in aphid abundance was a local phenomenon due to chance or whether it was widespread in Lasius flavus mounds. The mounds were sampled from all parts of Staines Moor, the cores being taken 20cm from the centre of the nest mound.

Results

Nest number	Number of ants	Number of aphids	Species of aphids
1	37	2	Anoecia corni
2	75	5	A.corni, Trama troglodytes, Aploneura lentisci
3	30	0	
4	36	0	
5	61	0	

Nest number	Number of ants	Number of aphids	Species of aphids
6	67	0	
7	22	0	
8	72	0	
9	18	0	
10	55	0	

Discussion

The range of ant values is in keeping with the variation found in 20cm samples from other nests, therefore there is no reason to think these ant nests unusual. The number of aphids extracted is low, matching the counts measured in previous weeks. It is also interesting that the most abundant aphid species was Anoecia corni, which is one of the earliest recolonizing aphids, maybe because unlike other species it may still be migrating from its alternate host.

From this it was concluded that the reduction in aphid numbers around the time of the nuptial flight is of widespread occurrence in Lasius flavus mounds. It may take up to four months for aphid numbers to recover to density levels equivalent to those prior to the alate hatch. This trend is also shown in the outlying territories, but to a much lesser extent, and recolonization is far more rapid.

APPENDIX A4

INVESTIGATING THE CAUSES OF VARIATION BETWEEN NESTS

Introduction

During the seasonal cycle of ant activity, there are periods of relative stability e.g. mid-Winter and periods of rapid increase/decrease with large fluctuations between nests e.g. late Spring and Summer. During the weeks approaching the nuptial flight, when inter-nest variation is high, adjacent nests were sampled each week in an effort to determine how much sampling error could be attributed to individual variation, and how much could be explained away by different states of brood development.

Discussion

Table 46a compares the ant activity of the three double samples. It can be seen that the variation between samples collected on 18/7 and 25/7 could be accounted for by chance, but that there is a real difference between samples collected on 8/8. Therefore numbers of brood were examined for each nest, both in terms of numbers and dry weight biomass (g), shown in tables 46b and 46c respectively.

	NEST 1			NEST 2			
	Total ants	Mean	Variance	Total ants	Mean	Variance	F-test
18/7	543	45.3	1787	637	53.1	2357	1.32
25/7	539	44.9	2135	234	19.5	1066	2.00
8/8	2034	169.5	40035	536	44.7	1295	30.92

Table 46a. The variation in ant activity.

	NEST 1				NEST 2				
	Larval numbers	Pupal numbers	Alate numbers		Larval numbers	Pupal numbers		Alate numbers	
18/7		261	381	1		102	1	70	20
25/7		217	4	13		5		3	
8/8	6	11	357	34		3		48	

Table 46b. The variation in brood numbers.

	NEST 1			NEST 2		
	Larval biomass	Pupal biomass	Alate biomass	Larval biomass	Pupal biomass	Alate biomass
18/7		0.1044	0.1564		0.0436	0.1080
25/7		0.0868	0.0536		0.0020	0.0012
8/8	0.0033	0.0044	0.2788		0.0012	0.0192

Table 46c. The variation in brood biomass.

At this time of year there are very few larvae around, and those that are present are a mixture of almost fully grown workers, and very small sexuals which will not mature until the next season. The number of pupae rapidly declined over the study period, as the alates and new workers emerged.

On 18/7 the sex ratio of the alates differs, but the overall biomass is similar and likewise the ant activity. On the 25/7 although there is a disparity between alate biomass, both levels are so low that these do not cause a significant difference between nests. However, on 8/8 there is a very large difference between the number of alates in the nest and even larvae are still being attended in addition in nest one. This may be responsible for the difference, and further support is given by the ant model from chapter 6, which predicts values of 3228 and 405 ants respectively, thus more than compensating for the observed difference.

In general ant activity is most similar between nests which contain the same biomass of brood. Large differences between nests can often be explained in this way. However, there are smaller variations which cannot be so explained, contributory features maybe; differences in physical constants e.g. nest size and temperature, as discussed in chapter 6, inaccuracies in extraction; the heat of extraction causes some alates to hatch prematurely, thus contributing to the 'active biomass' of the sample, without necessarily increased ant activity. There are also errors caused during sampling; when disturbed, some ants investigate the disturbance, whilst others carry the brood to deeper parts of the nest.

APPENDIX A5

INVESTIGATION OF THE PROTEIN/CARBOHYDRATE BALANCE IN LASIUS FLAVUS

Introduction

Pontin (1958) suggested that Lasius flavus regulates aphids according to a protein/carbohydrate balance, and provided some experimental evidence in support of this (Pontin 1978). It seemed to me that a sound test of this would be to administer the excess sugar solution during the 'recovery phase' when aphid numbers were already low, so that the excess sugar would be readily noticed. Sugar solution and tap water (as a control) were administered at 24 hour intervals throughout August as described in Chapter 2.3.

Results

EXPERIMENTAL NEST

Number of ants	Biomass of brood(g)	Biomass of pupae(g)	Number of aphids
132			6
166	0.0005		60
250			4
262	0.0017		2
58	0.0010		15
115			11
75	0.0004		9
33			0
53			0
94			21

Table 47a. Composition of ants and aphids in experimental nest.

CONTROL NEST

Number of ants	Biomass of brood(g)	Biomass of pupae(g)	Number of aphids
222	0.0020		4
128			1
98			27
41			11
95	0.0004		62
52			12
10			1
89	0.0004		12
79			18
111	0.0005		5

Table 47b. Composition of ants and aphids in control nest.

	EXPERIMENTAL NEST			CONTROL NEST		
	Sum	Mean	Variance	Sum	Mean	Variance
Ants	1238	123.8	6423.1	925	92.5	3300.3
Aphids	128	12.8	320.6	153	15.3	334.2

F test (ants) F = 1.95 F 9,9 (0.05) = 3.18

F test (aphids) F = 1.04

Mann-Witney U-test (aphids), U = 41 U 10,10 (0.05) = 23

Table 47c. Analysis of results.

Discussion

Despite the large variation between ant samples, F-tests showed that the control and experimental ants were not from significantly different populations. This implies that the excess sugar solution caused no ill effects upon *Lasius flavus*. Unlike Pontin however, no difference was found between the number of aphids in the experimental and control nests. Therefore I can find no evidence to support a protein/carbohydrate management system by *Lasius flavus*, or at least such a system breaks down in the period immediately after the nuptial flight, when carbohydrate, not protein is the prime requisite for the worker diet.

APPENDIX A6

THE EFFECT OF DIFFERENT NEST FLORA

Introduction

Having observed the ant mound flora every week, it was noted that a small proportion of the ant nests were not covered by the usual mixture of grasses and annuals, but were dominated by just one plant, most commonly Mouse-eared hawkweed (Hieracium pilosella). It was thought that an over-abundance of this Composite would change the ratio of aphid species in favour of Trama troglodytes rather than gramnivorous species.

Results

NEST 1

	Ants	Anoecia corni	Forda formicaria	Geoica utricularia	Tetraneura ulmi	Trama troglodytes	Aploneura lentisci
20N	91					1	
20E	79	3					
20S	23			2			2
20W	44						

NEST 2

	Ants	Anoecia corni	Forda formicaria	Geoica utricularia	Tetraneura ulmi	Trama troglodytes	Aploneura lentisci
20N	129	1	4		3		
20E	258				1		
20S	84				9		
20W	30				1		

Table 48. The abundance of aphid species in Hieracium pilosella dominated nests.

	Total aphids	Mean per core	Variance per core	t-test
Hieracium pilosella dominated nests	27	3.4	11.7	0.05
'Standard nests'	28	3.5	17.0	

Table 49. Summary of the difference between aphid numbers in Hieracium pilosella dominated and 'standard' nest mounds.

	Anoecia corni	Forda formicaria	Geoica utricularia	Tetraneura ulmi	Trama troglodytes	Aploneura lentisci
Hieracium pilosella dominated nests	0.15	0.15	0.07	0.52	0.04	0.07
'Standard' nests	0.71	0.07		0.22		

Table 50. The proportion of each aphid species found in each vegetation type of nest mound from 27/8/85-3/9/85

Discussion

The most abundant species in each vegetation type were the same i.e. Aneocia corni, Tetraneura ulmi, and Forda formicaria. The range of aphid species was also similar, the only difference being that Aploneura lentisci found in H.pilosella nests were replaced by Baizongia pistaciae in 'standard' nests, but this trend cannot be distinguished from chance.

It seems that at this time of year, the nest flora does not influence the variety of aphid species in the nest mound. Grasses are found even in H.pilosella dominated nests and these seem to be able to support the gramnivorous species. Due to low aphid abundance, it is unlikely that food is a population limiting factor, and thus some species may survive at this time, only to be replaced by Trama troglodytes at a later stage. Few cores were taken per nest, therefore these findings are not definitive.

APPENDIX A7

THE DESIGN OF LABORATORY APHID CULTURES

Introduction

As discussed in chapter 2.4, one method to assess interspecific competition is by replacement series. This necessitates aphid cultures in the laboratory, therefore the various methods tried and problems encountered are outlined

Method and Discussion

Initially aphid cultures were raised on the roots of *Agrostis tenuis* using the method shown in diagram 3a. A glass tube was used so that aphids could be regularly counted. The tube was then covered by black paper, to darken it so that the aphids were less inclined to wander off the root. The root tips were submerged in a dish of water so that the plant did not need to be changed as often.

Three major problems were encountered; firstly condensation on the inside of the tube. This was especially common at the union of the tube and the dish containing water, therefore different bungs were used e.g. plasticine, 'blu-tac' and cotton wool, none of which noticeably reduced the condensation. The condensation obscured vision, encouraged mildew to develop on honeydew and in some cases aphids drowned. The second main problem was that in the absence of ants, honeydew eventually covered some aphids, got colonised by fungus and the aphid perished. Some aphids seemed more susceptible to this than others, *Geoica* was

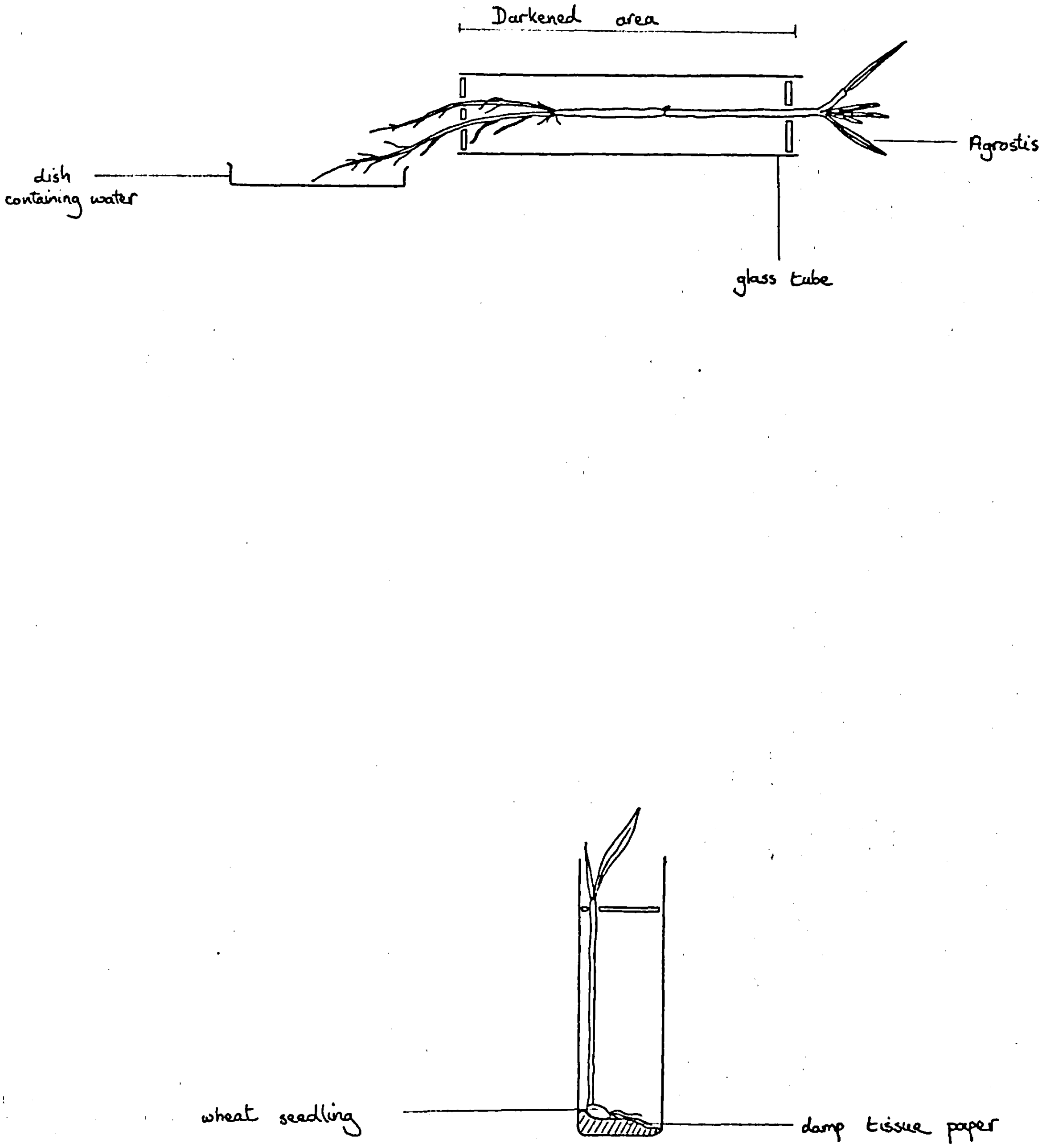


Figure 3. Techniques used in the rearing of subterranean aphids.

almost unaffected, presumably due to its waxy cuticle. The final problem was that aphids tended to wander all around the tube, and this behaviour may have reduced their fecundity. This was most common amongst first instar aphids, especially Tetraneura ulmi, and these are considered to be the main dispersal stages amongst subterranean aphids, this is certainly the case in the Aster root aphid (Pemphigus trehernei)(Foster and Treherne 1978). The mechanism for first instar dispersal is unknown, but it may be similar to that found by Hoffman et al 1985 i.e. the height of the root hairs prevented the first instars from feeding on certain areas of the root.

Various modifications were subsequently made to the design, the most successful method is outlined in diagram 3b. In this case the foodplant used was wheat seedlings, which the aphids accepted, most readily amongst the Fordinae. The wheat was germinated in water, then transferred to a 3x1 vial when the second leaf was beginning to develop. Blotting paper was used to supply moisture to the root and this also seemed to absorb condensation. The problem of aphid wandering was less serious as it was easier to refind and mount the root. The lack of ant attendance was again a problem, but at the time of year these experiments were conducted (late Spring to early Summer), they were not included because this added yet another unknown variable to the system, and because of fears of predation.

Fecundity estimates most closely allied to those in the field were found by transferring adults from the field to the laboratory and measuring how many young were produced in the first two days. These estimates are presented in table 28, chapter 4. From these estimates of field fecundity, together with a measure of the proportion of reproducing females per nest, one can calculate the standard 'egg' production (Hebert 1977), a measure of reproduction independent of the size structure of the population. Within the confines of the fecundity estimates it is found that the number of aphids predicted is up to 700 more than observed i.e. this number of first instar aphids may be lost to ant predation each day. In fact this is a minimum estimate of mortality and should be multiplied by the length of time in days that the first instar lasts (about 4 days in *Forda formicaria*). This brings it more in line with the estimate of 3000 aphids lost per day at Summer production levels by Pontin (1978).

APPENDIX A8

OBSERVATIONS FROM ARTIFICIAL LABORATORY ANT NESTS

Artificial nests were set up as described in chapter 2.4. One nest containing unmated alate queens and workers, originated from individuals which escaped from the cores before extraction. The other originated from unmated alate queens which had survived the extraction process. At this time of year, the wings of the alates do not sink, but remain upon the meniscus of the preservative and allow a platform to form for other ants. Any workers which fall onto this, die from desiccation, but the queens seem far more resistant to this, as would be expected.

To each of these nests were added about one dozen Aphis fabae and some worker pupae. The aphids were tended by workers and queens alike, but carrying was only done by the workers. What is surprising is that these ants will tend non-subterranean aphid species. Despite this, both sets of aphids vanished from the nest within two days, giving some support to the 'marriage feast'. Worker pupae were also tended by both castes, but again only the workers carried them around. Such was the attention of queens, that one worker which was having trouble emerging, was assisted by the queens (and workers), by enlarging the exit hole. As the worker subsequently emerged perfect, I do not think this was an attempt at predation.

Small numbers of workers (less than the number in the nest) were added to the artificial colonies from different nests. Although these ants distanced themselves from the main group of queens, when they encountered the original nest occupants, no aggressive acts were observed, and after four days, mixed with rest of the ants, presumably having acquired the nest odour.

Boomsma et al (1981) have documented many physical variables which are associated with the nuptial flight. I would like to propose a further cue for this; food shortage. It has become apparent that from the time of alate emergence until the nuptial flight there is a vast drop in the number of aphids in the nest mound, if this is due to alate ant predation, then there must come a time when the benefit of laying down future fat reserves is outweighed by the extra energy to find aphids (or at least rate lost due to intraspecific competition). This was investigated by depriving one nest of sugar solution, and not the other. The results were not immediate, but six days into the experiment, increased alate activity was observed in the experimental nest. Queens became positively phototactic (beforehand they lived under the tissue paper and in self-constructed burrows), wandered around the top of the perspex box, and used their wings when they fell off the sides. On the seventh day activity was far less and on the eighth day the alates were back under the tissue paper. Despite a further weeks starvation, no further activity peaks occurred. The nests were not in direct sunlight, the relative humidity of the artificial nest was always saturated, wind velocity was nil and the temperature did not fluctuate noticeably in the laboratory, thus all Boomsmas cues were controlled and flight activity was still induced. However, it should be mentioned that this increased activity occurred two days before the main nuptial flight, and it is possible that some innate factor may have been responsible. After five weeks a group of three queens had settled together in a burrow, and were attending/being attended by seven newly emerged workers, despite not having been mated. Pontin (personal communication) regards the quality of virgin-queen attention to be much poorer than usual. These queens are not licked as often as mated queens, possibly due to the retention of wings, but even if they are artificially dealeated, they are still not treated similarly.

APPENDIX B1

RECORDS OF OBSERVATION NESTS

Date	Observations	Temperature			Weather conditions
		Air	Ground	Nest	
15/7	Lasius niger - Alate chambers made, ♂ and ♀ alates active, but haven't flown yet Lasius flavus - In some nests chambers have been made, others not. Some alates present, but few. Many pupae at surface, ♂ and ♀ pupae warming at separate sides of nest. (To synchronize hatch ?)	20	26	26	Light breeze, cloudy, overcast.
17/7	Lasius niger - Most ♀ hatched, complete male hatch in 50% of nests. Lasius flavus - More ♀ hatched, ♀ + ♂ pupae at top of nest, but markedly less than last time. Flight chambers made Myrmica scabrinodis - Lots of full grown larvae.	22	25	28	Medium West wind, sunny, 50% cloud, 50% blue sky
23/7	Lasius flavus - In 'sunny' nests odd ♂ alates, no ♀ or pupae. In 'shaded' nests, ♂ alates with less ♀ alates and pupae present.	27	31	33 (25 in shaded nests)	Light breeze from S-W, sunny, 90% clear sky.
24/7	Lasius niger - Alates flew at 4 p.m. today. (Temperature had dropped to 25°C) Lasius flavus - Very few workers in nests in sun. In others ♂ + ♀ alates present, but no pupae.	27	28	31	30% cloud, sunny.
25/7	Lasius niger - Little activity Lasius flavus - Little activity, few workers and odd ♂'s. Myrmica scabrinodis - Still have larvae	28	34	32	10% cloud, sunny.

Table 51. Records of Alderhurst observation nests 15/7/85-25/7/85.

Date	Observations	Temperature			Weather conditions
		Air	Ground	Nest	
26/7	*Lasius flavus* - Only workers found except for one nest which also had worker pupae	21	18	20	Medium wind from S-W. Completely overcast, no sun.
29/7	*Lasius niger* - Workers and small pupae present, alates found in one nest. *Lasius flavus* - Most with workers, male alates and small pupae, others also have a few ♀ alates	18.5	20	20	Completely overcast, raining.
30/7	*Lasius niger* - ♀ alates present in two nests *Lasius flavus* - Alates and worker pupae found in all nests. Further flight chamber excavation has been carried out.	22	24	26	Rained all morning, sunny by 2p.m. Very humid.
31/7	*Lasius flavus* - Many ♂, ♀, workers and small pupae present	22.5	26.5	27	Intermittent sunshine, 50% cloud cover.
1/8	*Lasius flavus* - Many ♂'s + ♀'s + workers + some small pupae.	23.5	25.5	25	75% cloud cover, sunny spells, slight Southerly wind.
2/8	*Lasius flavus* - Workers, no pupae, no ♀ alates, a few ♂ alates only found in 10% of nests	16	18	19	Rained for most of day, completely overcast.
5/8	*Lasius flavus* - Workers + ♂ alates + odd ♀ present	21	22	23	60% cloud cover, sunny
6/8		21	20.5	21.5	90% cloud cover, but bright!

Table 52. Records of Alderhurst observation nests 26/7/85-6/8/85.

Date	Observations	Temperature			Weather conditions
		Air	Ground	Nest	
7/8	*Lasius flavus* - Workers abundant, but less male alates and even fewer female alates seen. No pupae.	19	19	18	Overcast, light rain.
8/8	*Lasius flavus* - Workers, males and females abundant. 4.20 p.m. ♀ alates climb up grass stems; nuptial flight.	21	21	26	Sunny, warm, slight cloud cover.
9/8	*Lasius flavus* - ♂ + ♀ alates + workers + worker pupae abundant	20	24	23	
13/8	*Lasius flavus* - ♂ + ♀ alates + workers abundant. Not many pupae.	21.5	22	23	Medium Southerly wind, 30% cloud cover, sunny.
14/8	*Lasius niger* - 9 a.m., second emergence from under tarmac. Some nests have emerged twice, but less this time. *Lasius flavus* - Did not emerge from Alderhurst	19	19	18	60% cloud cover, sunny.
15/8	*Lasius flavus* - Workers and males abundant, few females	20	21	23	60% cloud cover, sunny spells between rain showers.
16/8	*Lasius flavus* - Workers and pupae abundant, but few males and no females	18	21	21.5	70% cloud cover, heavy showers and sunny spells
20/8	*Lasius flavus* - Workers present, but only one ♂ alate seen.	16	14	20	Complete cloud cover, windy from West.

Table 53. Records of Alderhurst observation nests 7/8/85-20/8/85.

Date	Observations	Temperature			Weather conditions
		Air	Ground	Nest	
28/8	4.30 p.m. flight of *Lasius niger* (mainly males) 5.00 p.m. flight of *Formica rufa*	27	29	28.5	40% cloud cover, sunny, slight wind from South-West.
30/8	*Lasius flavus* - In sunny nests, a few workers and odd ♂ alate. In shaded nests, more workers and worker pupae	27.5	26	29	30% cloud cover, sunny.

Table 54. Records of Alderhurst observation nests 28/8/85-30/8/85.

APPENDIX B2

THE EFFECT OF HIGH TEMPERATURE ON NESTS WITH HIGH RELATIVE HUMIDITY

Introduction

Two nests were selected to be of similar size, both were unshaded and only five feet apart. The experimental nest was irradiated at its surface by an infra red lamp. The temperature was kept at a constant 30°C (+/-2°C) by moving the lamp away from or closer to the nest. Four samples were then taken from each nest, 20cm from the nest mound centre. The samples were extracted and counted in the usual way. At a later date the nests were sampled once again to see if there was any real difference between them in colony size.

Results

	Experimental nest	Control nest
Nest size (l)	49.6	46.6
Temperature (2/5)		
Ground	19	19
Half way up nest	21	21
Nest surface	23/30	23
Temperature (17/5)		
Ground	19	19
Half way up nest	18	18
Nest surface	22	22

Table 57. Physical data on experimental nests

	Experimental nest	Control nest
Ant counts (2/5)	117, 252, 287, 195	95, 482, 396, 429
Ant counts (17/5)	301, 412, 399, 462	204, 334, 455, 389

Table 58a. The results of the temperature experiment

	Experimental nest		Control nest
2/5			
Mean	212.7		350.5
Variance	5512.3		30268.3
Kruskal Wallis			
one-way analysis (experimental vs control)		1.33	
Quenouille test	"	1.33	
Wilcoxon matched pairs	"	1.00	
t-test	"	1.46	
17/5			
Mean	393.5		345.5
Variance	4540.3		11345.7
t-test (experimental vs control)		0.76	
t-test (experimental 2/5 vs experimental 17/5)		3.61	

Table 58b. Statistical analysis of temperature experiment

Discussion

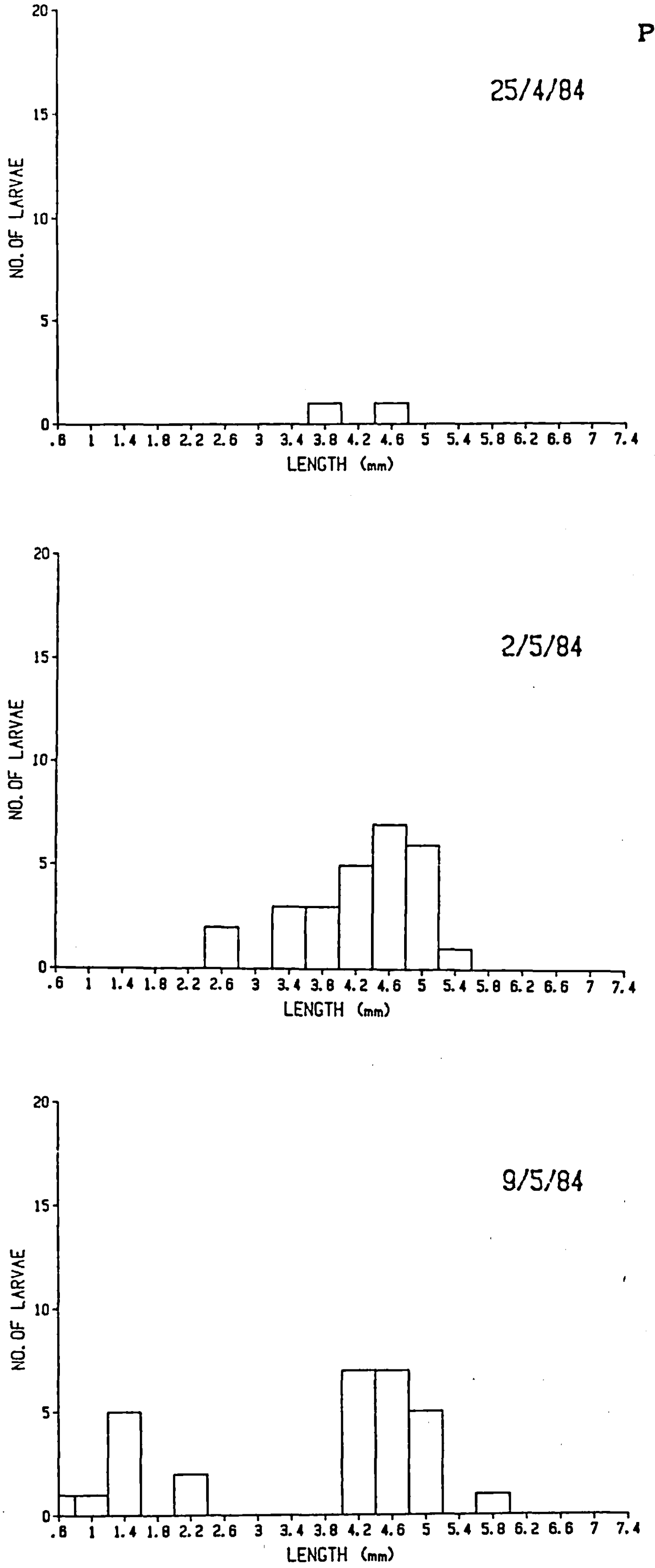
As recorded in chapter 3.4, high temperature does not seem to reduce ant activity in the presence of high humidity. However, there is a suggestion that there may be a difference between the number of ants found in the experimental nest on 2/5 and 17/5/85 ($p<0.05$). Unfortunately there are many ways to account for this; an increase in ant activity due to larger brood biomass, increased activity to repair the nest. Besides the probability level is sufficiently low, that the difference may well be meaningless.

APPENDIX B3

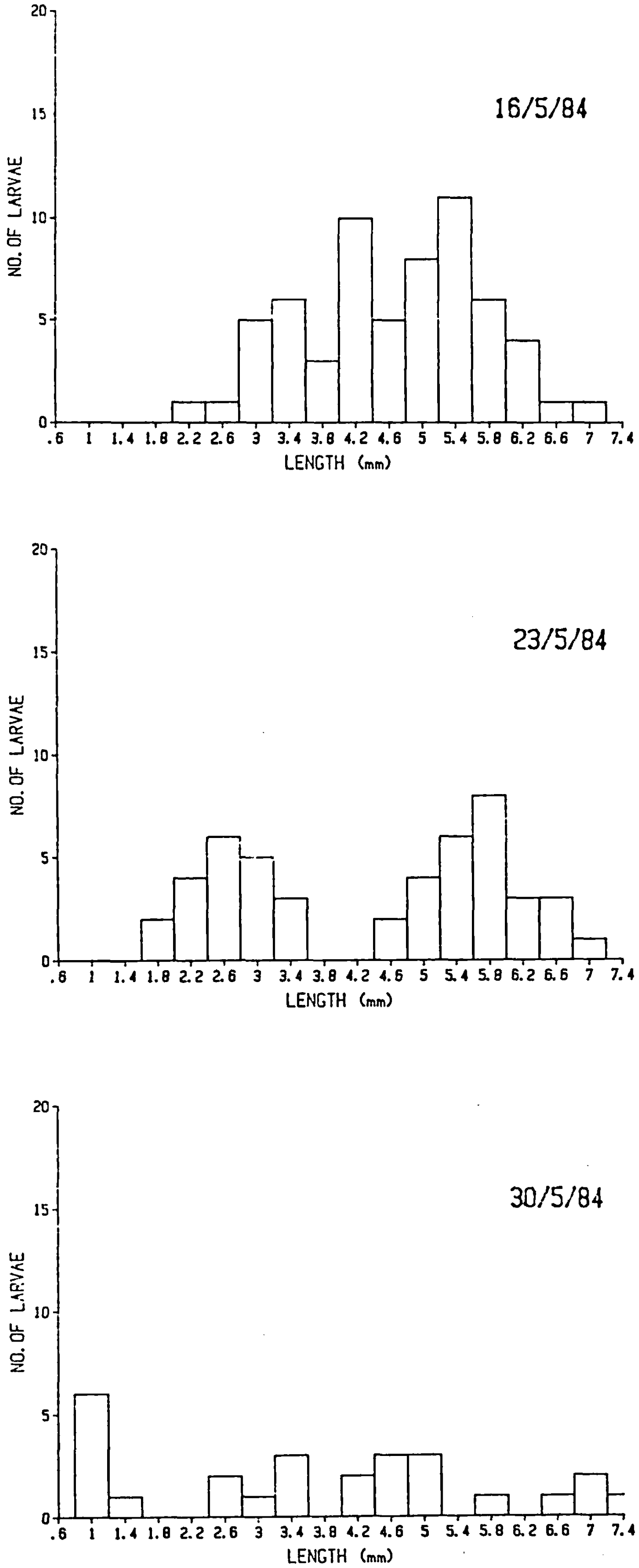
OBSERVATIONS ON THE DEVELOPMENT OF LARVAL BROOD

Introduction

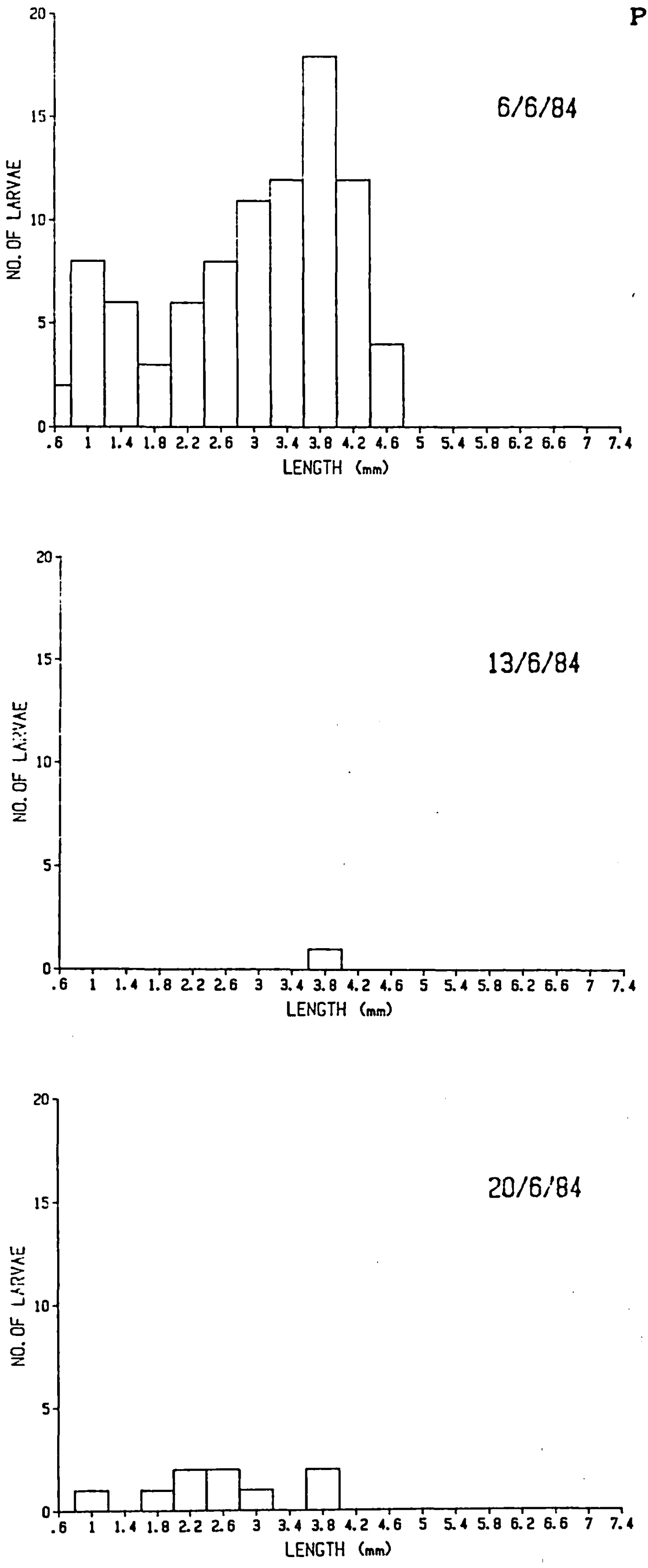
The size classes of larvae recorded in 1983 showed that although originally quite large larvae were found,as the season progressed, the majority of larvae were much smaller before pupation. This was further investigated in 1984 by detailed measurement of larval size. This is summarized in graphs 67-70.



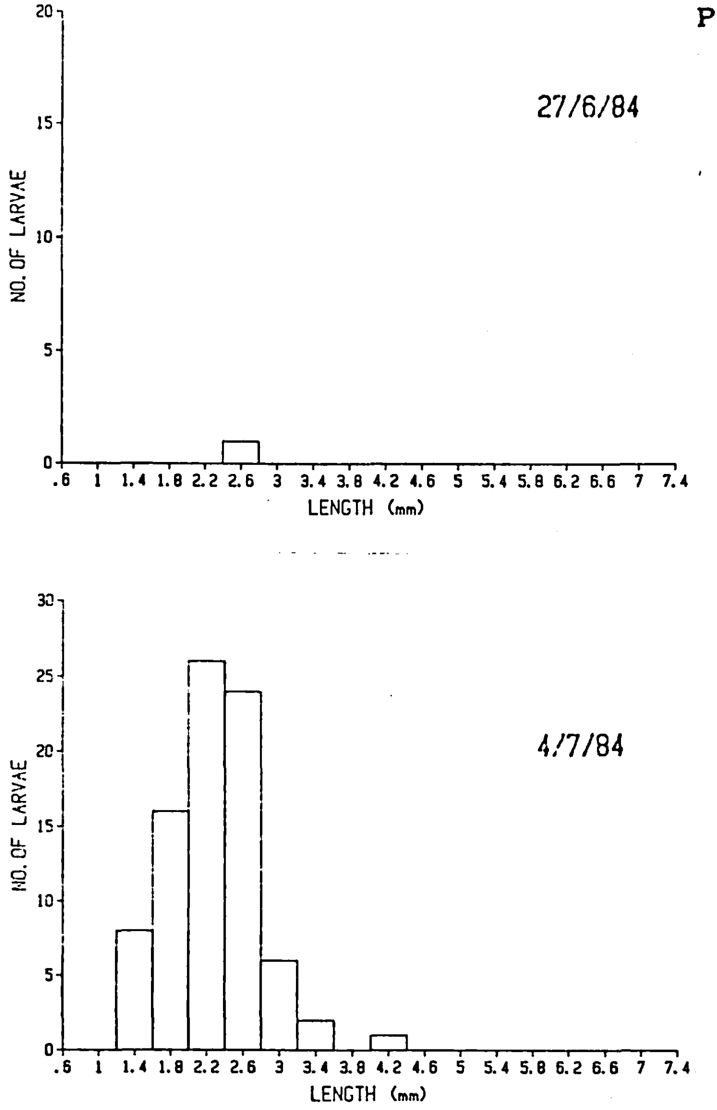
Graph 67. Variation in larval size 25/4/84-9/5/84.



Graph 68. Variation in larval size 16/5/84-30/5/84.



Graph 69. Variation in larval size 6/6/84-20/6/84.



Graph 70. Variation in larval size 27/6/84-4/7/84.

Discussion

By early May there was an almost continuous range of larval sizes up to 5.4mm. A week later the majority of larvae are in the same size range, but there is a smaller group of larvae also present in the top 10cm of the ant nest. By mid-May these two size ranges had coalesced, but even so, it can be imagined that these larvae can be split into two different size ranges, with the peak at 4.2mm caused by the overlap in size range of the lower and upper group. The samples from the 23rd May certainly show this. At this stage it is proposed that the larger group are the future queens, and the smaller group are the future males. By the end of May the queen larvae have pupated, and a new group of smaller larvae are found. This is further demonstrated by the two different size ranges found in early June. The next three weeks show little except the gradual increase in size of the smaller larval size group. Over this period the males pupate, as supported by the size and increased number of pupae found. It is further proposed that this new group of larvae are the new workers, and by the beginning of June they are nearing pupation. These proposals have some support from the order of emergence of the castes, first the queens, closely followed by the males and then later by the workers. The size ranges of the mature larvae is commented upon in chapter 1.1. The slight overlap in the size ranges of males and workers causes problems in separating the pupae. This becomes easier as the male develops, first the wings show, and then the pupae darken due to sclerotization.

This temporal separation in brood maturation and difference in larval size, reflects the different investments of the colony in the next generation. Kin selection theory predicts that there will be queen-worker conflict over whether males or new workers should receive more nest resources. This time difference shows how the queen neatly side-steps the problem.

APPENDIX B4

THE DIFFICULTIES IN TRANSFORMING ANT COUNTS

Introduction

To use parametric statistics, the most widely recognised statistical tests, one has to have data which conform to a Normal distribution i.e. the variance and mean of the sample must be independent and the components of the variance should be additive. If these three criteria are not fulfilled, the data must be transformed; the original counts being replaced by a mathematical function of the count. For unusual functions, the coefficient b derived from Taylors Power Law can be used to select the appropriate transformation of data, by entering it in the equation:

$$p = 1 - b/2$$

where p is the transformation value. The new estimates of population mean and variance are then replotted to make sure that the relationship has been broken. If the relationship is still present, then the transformation process is repeated using the new value of b. The correct transformation of the data satisfies the above criteria for parametric statistics.

Discussion

In the case of all the ant results the first transformation did not break the relationship between mean and variance. The second transformation broke the 1984 results, but after three attempts neither the 1983 nor the 1985 results had independent means and variances, therefore the transformation process was curtailed. Moreover, it becomes increasingly mysterious what these strange powers signify. For these reasons non-parametric statistics were often used.

From consideration of the above equation, it can be seen that for a value of $b=2$, $p=0$, therefore the transformation process is meaningless. The two most obstinate years (1983 and 1985) have b values of 1.803 and 1.919 respectively, which is getting close to 2. To see if this was indeed the case, other organisms with similar values of aggregation were also transformed i.e. phytophagus mites ($b=2.072$), symphyla and geophilomorph centipedes ($b=1.836$). In both cases the relationship was not broken, significant relationships still linking the mean and variance ($0.01<p<0.05$).

APPENDIX B5

VARIATION IN ANT AGGREGATION

Introduction

In chapter 3.3 it was found that worker activity at certain nest locations varied with the time of year (see tables 11-14, graph 6a-g). From this it was reasoned that if more ants were foraging in the nest territory, then less would be found in the mound thus giving lower measures of aggregation. To assess the degree of seasonal variation in ant aggregation, Taylors coefficient b was recalculated for worker numbers in each of the seven sections of the year, (see page 79 for explanation of sections).

Results

Section of year	b value, 1983
I	1.719
II	1.531
III	2.189
IV	1.486
V	2.029
VI	1.745
VII	2.031

Table 59. Measures of ant aggregation for different periods of the year.

Discussion

The results show that my previous ideas were an over simplification of ant aggregation. Large amounts of foraging imply high nest demand, and this usually coincides with extensive brood care. Thus the increased number of ants foraging in the territory although reducing the potential for clumping, does not do so significantly.

In late Winter it appears that ants are not highly clumped, but this may be misleading as ants are out of sampling range. Certainly in the field when ants are encountered at this time of year they seem densely packed. From consideration of ground temperatures it seems logical that ants should congregate in the nest mound. In section II low temperatures may again be masking the true degree of clumping, but by mid March ants (and aphids) can be found at the nest surface, so overall it seems that there is little clumping. When the largest larval biomass is present, despite extensive foraging, there is a high (the highest) degree of clumping presumably due to larvae being tended in the brood chambers. After larval pupation and during the main alate hatch, ant aggregation reaches its lowest level. This implies that pupae require less attention than larvae and likewise alates. This is initially surprising, but in contrast to larvae, future queens are quite capable of feeding themselves, and alates reach such densities in the flight chambers that workers may be physically excluded.

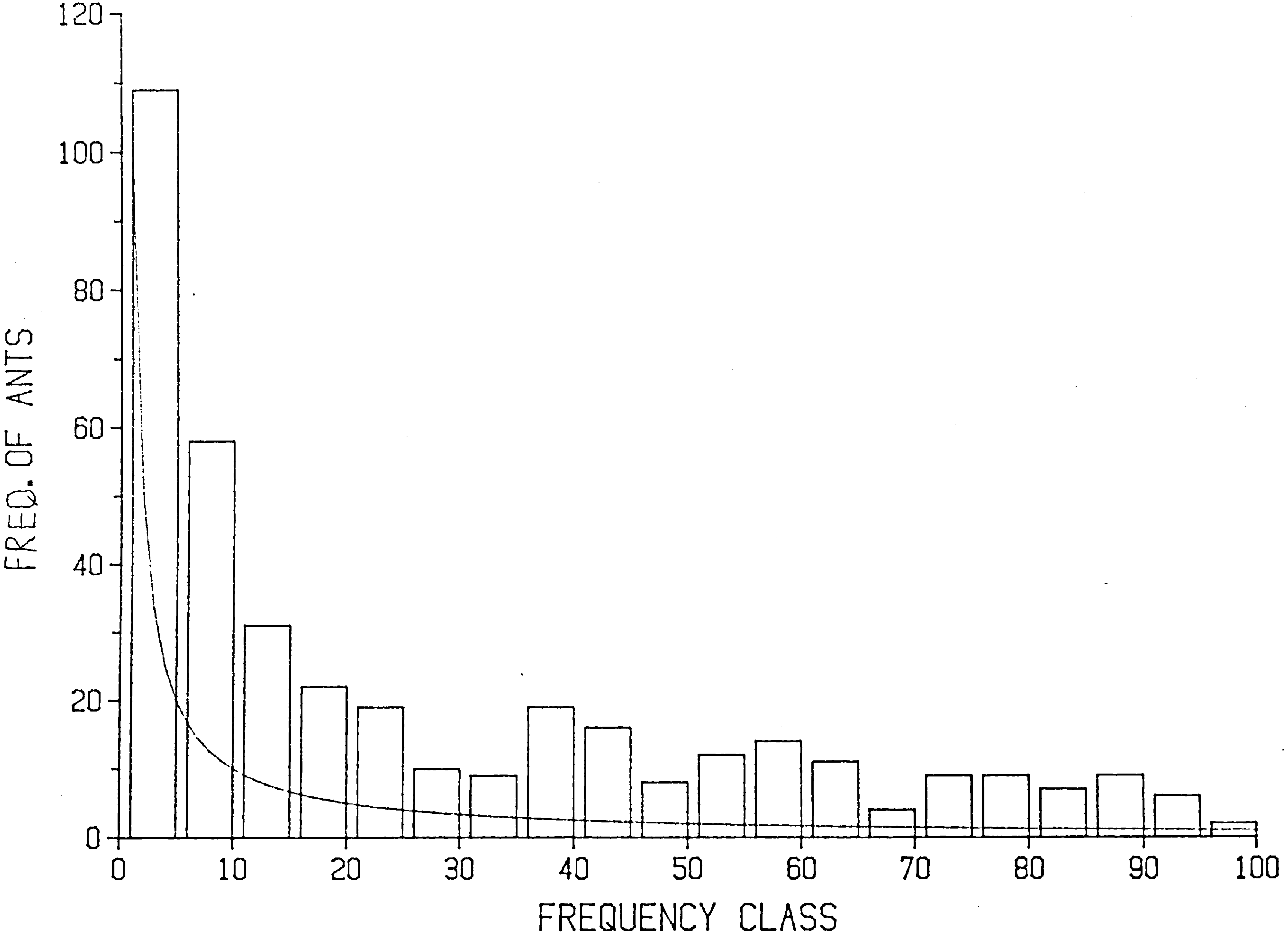
Section V represents the main hatch of workers from the pupal chambers. New workers were included in these counts, and therefore may account for this; but this is a very short section and thus the coefficient of aggregation may not be important statistically. In Autumn workers are less clumped. As Winter temperatures return ants become more concentrated in the nest mound.

APPENDIX C

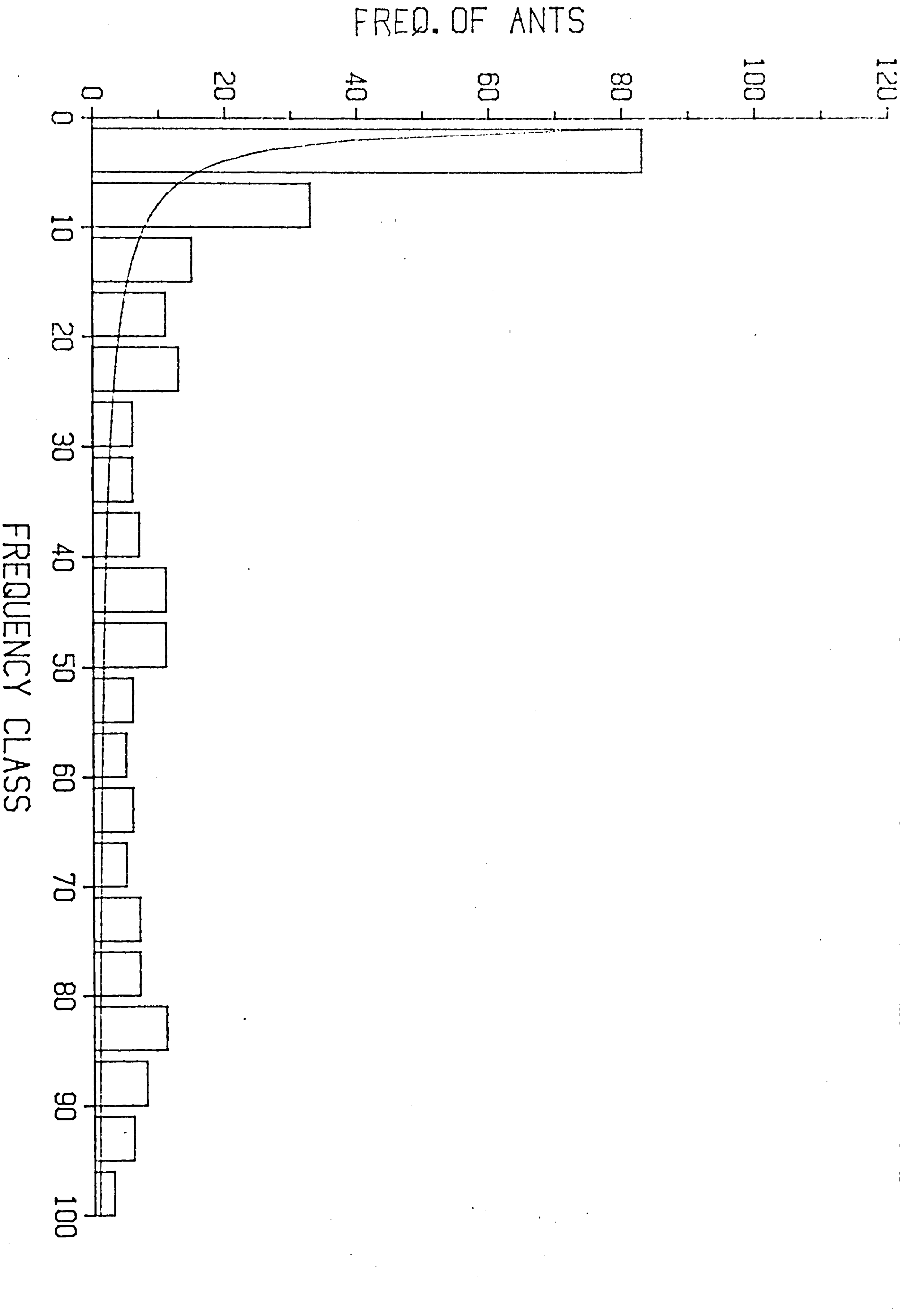
THE RECIPROCAL DISTRIBUTION

Seldom in nature are animals not found in clumps. Clumping can occur for a multitude of different reasons including; food resources, hatching from the same egg mass, for mating, for defence. Even plankton in a reservoir (an almost uniform environment) occur in clumps, and these may still persist after the water has been circulated both artificially by jetting and by the wind (Steel 1975). This distribution has already proved successful for aphid species in 1983, 1984 and 1985, and that portion of Dr.Pontins 1974 data that I have started analysing also fits (see appendix F). Lasius flavus also has a reciprocal distribution (see graphs 71,72). The exceptions to this reciprocal distribution are perhaps more informative as to the limitations of this model. Collembola, predatory and phytophagus mites, despite being clumped are best fitted by a negative binomial distribution ($0.82>p>0.1$). Staphylinids and Agriotes, and spiders which are not highly clumped are also fitted best by a negative binomial distribution.

Many invertebrates are attracted to ant mounds because of the increased warmth, refuse as a food source, increased ventilation of soil (see chapter 1.3). Therefore when regularly sampling across this environmental gradient, a



Graph 71. The frequency distribution of <u>Lasius flavus</u> 1983.



Graph 72. The frequency distribution of *Lasius flavus* 1984.

non-Normal distribution is expected, and this is expressed as a negative binomial. If however there is a further level of clumping within this environment e.g. aphid clones on neighbouring grass roots, ants in brood chambers, then a different frequency distribution arises, which can be fitted by the reciprocal model.

The reciprocal model was derived from the following considerations:

(i) The clump size of aphids has been found to be larger than the diameter of the corer (Pontin 1978, chapter 4.31)

(ii) Therefore when the nest is sampled, one only obtains some fraction of the clump;

$$1/x$$

(iii) As all aphid species differ in abundance, then allowance should be made for their different numbers. Therefore use:

$$y = N/x$$

(iv) This equation can be modified to produce a good fit by introducing a variable k:

$$y = N/kx$$

k was initially found by iteration of successive Chi-squared tests. But it can also be calculated from a weighted population mean i.e. average value of: number of single aphids + number of "two counts" x2 + number of "three counts" x3 .....etc.

(v) When $x = 1$, i.e. $1/x$ = unity, the whole clump has been sampled, then the equation reduces to:

$$y = N/k$$

which provides the number of aphids per clump.

(vi) Therefore k is some measure of dispersion of the aphids over the nest. Indeed those values of k calculated from the largest numbers of aphids vary inversely to Taylors clumping coefficient b.

APPENDIX D1

THE PRODUCTION OF ALATE APHIDS IN LASIUS FLAVUS NESTS

Introduction

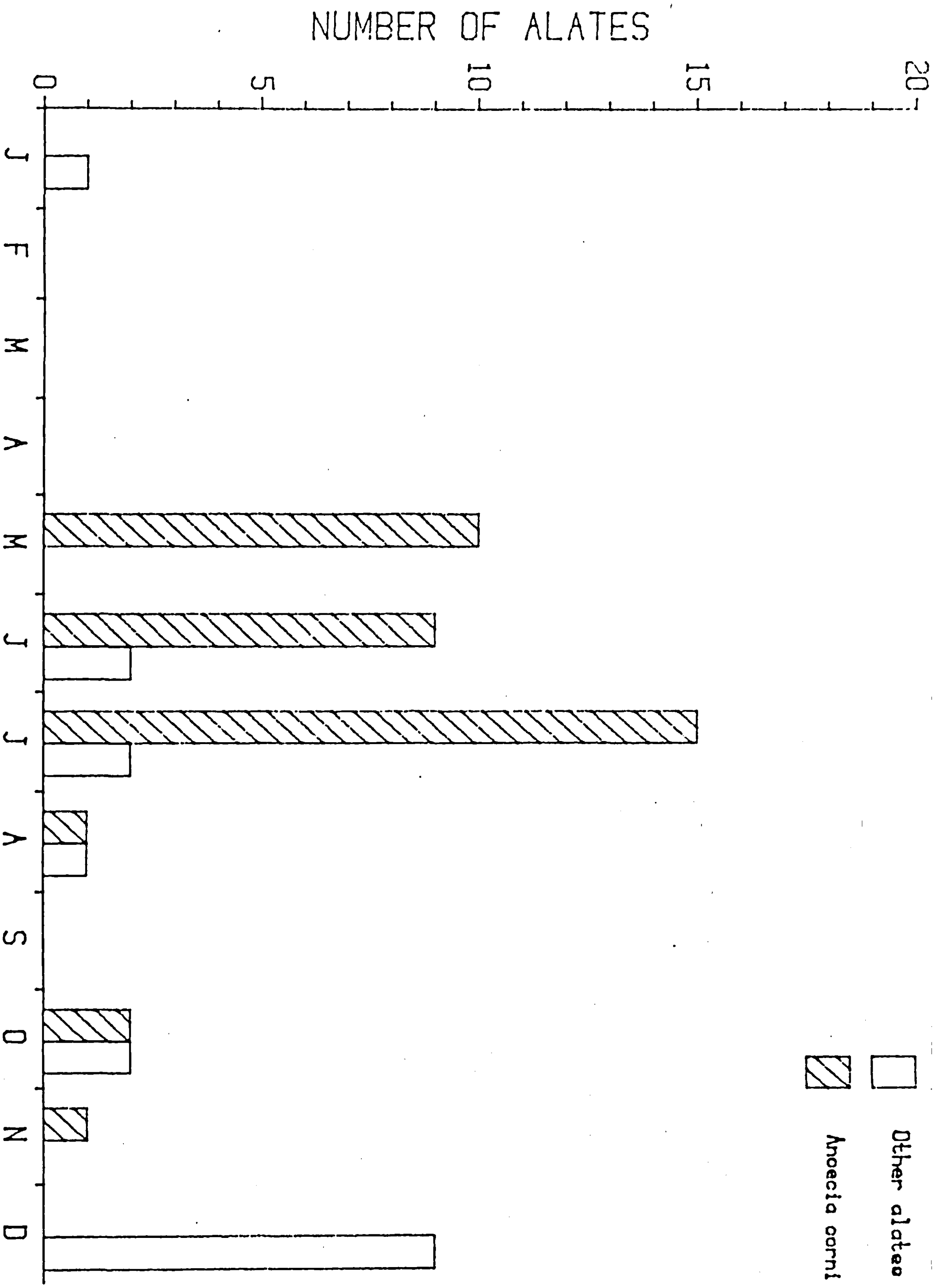
One of the clearest indications of the balance of the 'mutualism' between Lasius flavus and subterranean aphids is the almost total lack of alate aphids. Far fewer than are produced in nests of Lasius niger with the possible exception of the heteroecious species Anoecia corni. Winged forms are known from the majority of the subterranean aphids found on Staines moor, the exception being Geoica setulosa (Heie 1980). Geoica utricularia, Forda formicaria, Baizongia pistaciae and Aploneura lentisci do not have an alternate host plant in this country, therefore alates are rare. Anoecia corni, Anoecia furcata and Tetraneura ulmi do have alternate host plants, but only in Anoecia corni is the host alternation obligate.

The development of alate morphs is linked to crowding, ant attendance, quality of host plant, temperature and photoperiodism, and intrinsic factors. Crowding stimulates alate production possibly due to the increased amount of aphid-aphid tactile contact; although when ants tend aphids the tactile response seems to have the opposite effect on them, so this may not be the complete answer. A reduction in the quality of the host plant causes alate production.

The mechanism is unknown, but this most commonly occurs as the host plant becomes dormant causing a reduction in the flow of phloem, and translocation of sugars and minerals from the leaves to the roots. Low temperature and short day length also encourage alate production. For root aphids which live in continual darkness at a relatively constant temperature, it is likely that food quality and ant attendance are the most important factors.

Discussion

Anoecia corni was the most abundant alate captured, presumably due to its obligate host alternation. Captures were highest in early Summer when it was migrating to grasses. High numbers also occurred in late Autumn, at which time all the adults found were alate, when it was returning to Dogwood. Other alates found on Staines moor included Anoecia furcata, Baizongia pistaciae, Aploneura lentisci, Forda formicaria and Tetraneura ulmi, all were uncommon. The majority were found in Winter (see graph 73), when a high proportion of the adults were alate (see table 60). Of these Tetraneura ulmi and Anoecia furcata alone have alternate hosts in this country, therefore this behaviour in other aphids is presumably a reflection of what happens in Central Europe, which has not been totally selected against because of the lack of genetic mixing. Tetraneura ulmi, Forda formicaria and Aploneura lentisci alates were also found in Summer (prior to the nuptial flight), and it is possible that these alates were not leaving the grass to alternate hosts, but to disperse to other grasses, thus favouring the retention of alate morphs.



Graph 73. The number of alates produced per month.

	Tetraneura ulmi	Forda formicaria	Baizongia pistaciae	Anoecia corni	Anoecia furcata	Aploneura lentisci
Percentage of adults accounted for by alates:						
Summer	67	20		20		50
Winter		100	100	100	50	

Table 60. The percentage of the number of adult aphids which were alates, found in Lasius flavus nests at different times of year.

APPENDIX D2

AN ESTIMATE OF THE NUMBER OF APHIDS PER NEST

Introduction

In appendix A7, it was concluded that as many as 2800 first instar aphids may be lost from an ant mound per day. This appendix seeks to put this in perspective by making estimates of mean nest aphid population. These were calculated for certain times of year, using the same method as ants (chapter 3.5) i.e. calculating a mean abundance per core and estimating density in successive concentric rings. The times of year were chosen to represent low ant activity (late and early Winter) and periods of high ant predation pressure at times of maximum larval brood and alate biomass.

Results

Time of year	Mean aphid density/nest	S.E. of mean	t-test between successive periods	
			t	p
Late Winter (12/1-15/2)	6562	+/- 1962		
			2.12	N/S
Maximum larval brood (8/6-8/7)	2354	+/- 318		
			2.67	0.05
Maximum alate biomass (15/7-3/8)	1098	+/- 348		
			2.53	0.05
Early Winter (10/11-29/12)	3243	+/- 773		

Table 61. Estimates of aphid number per nest 1983.

Discussion

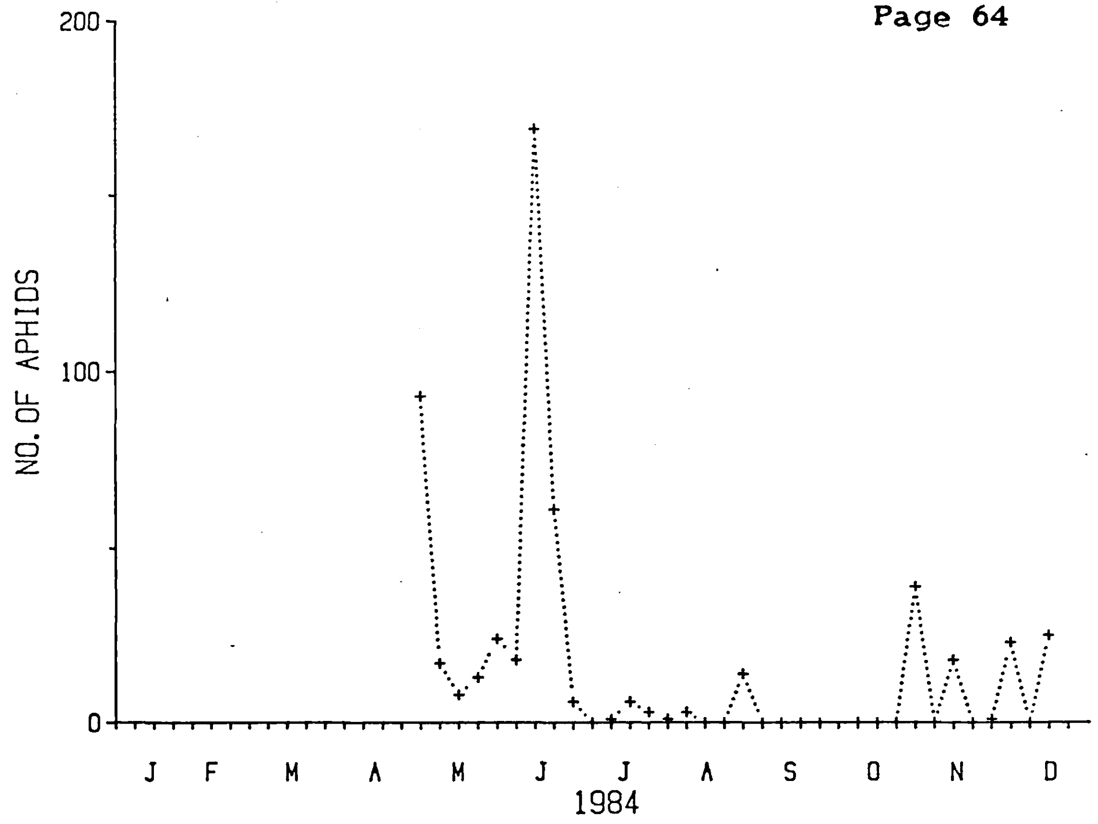
From consideration of table 60, it seems that even after a long period of low ant activity, there is considerable variation in the number of aphids per nest. The estimated daily mortality represents quite a large proportion of this, however, at high larval brood biomass, the number of aphids remaining in the nest is not significantly different from the Winter levels, so as stated elsewhere, despite the high mortality, the overall breeding population seems undamaged. Once the alates have emerged, many less aphids are found in the nest, the number being significantly lower than at the maximum brood biomass level; but even at times of very low aphid abundance in the nest mound, the outlying territory still provides a large crop. These aphids survive not because they elude workers (they need honeydew removed, and can only live in spaces cleared by workers), but because the workers do not wish to eat them. In early Winter after the 'recovery phase', aphid numbers are noticeably higher than the level found prior to the nuptial flight, and comparable to the late Winter level ($t=1.57$, $p>0.1$).

Three thousand first instar aphids per day represents a dry weight biomass of approximately 0.06g, therefore it is likely that other animals and aphid instars may be killed to account for the rise in larval biomass.

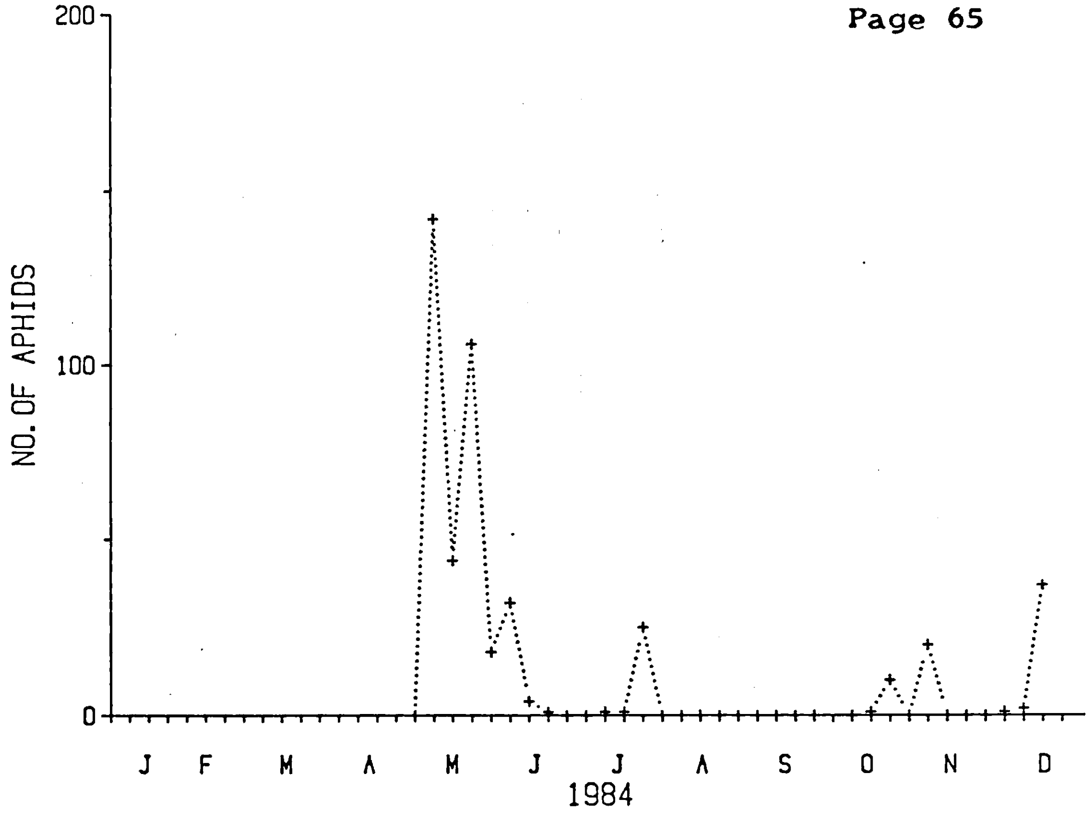
APPENDIX E1

Abundance of aphid species throughout 1984 and 1985

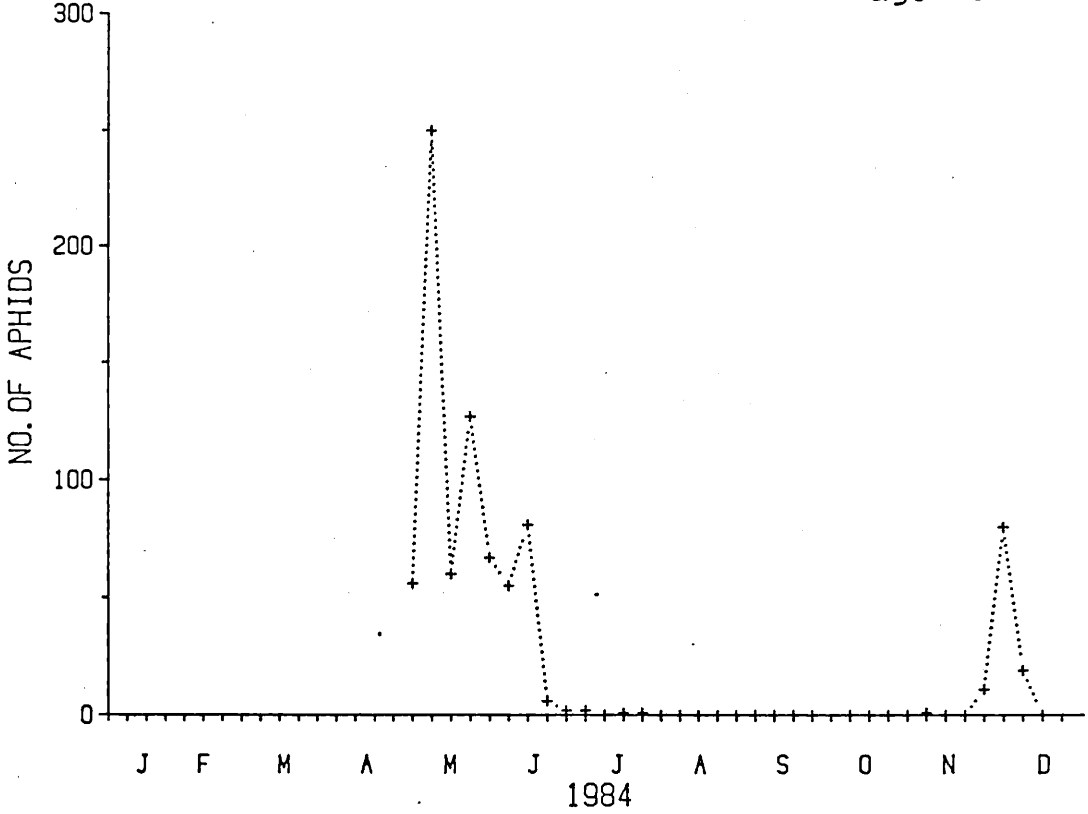
(Graphs 74-87)



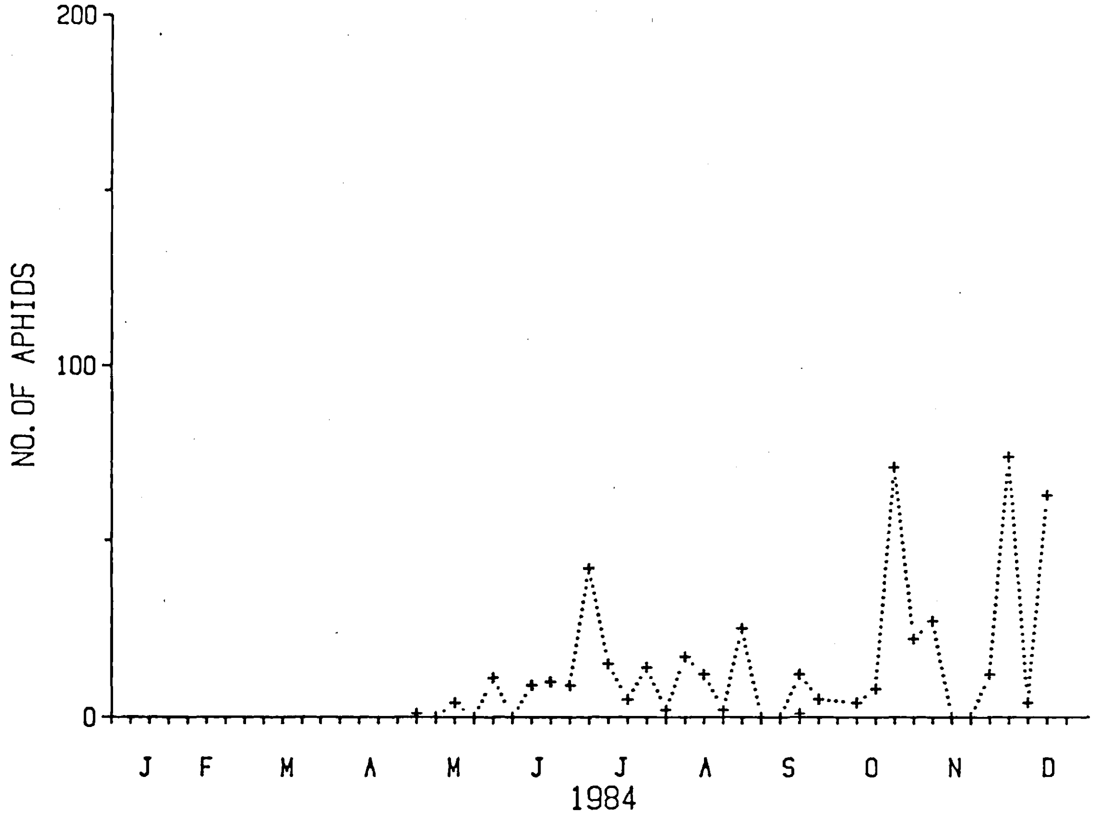
Graph 74. The abundance of Tetraneura ulmi throughout 1984.



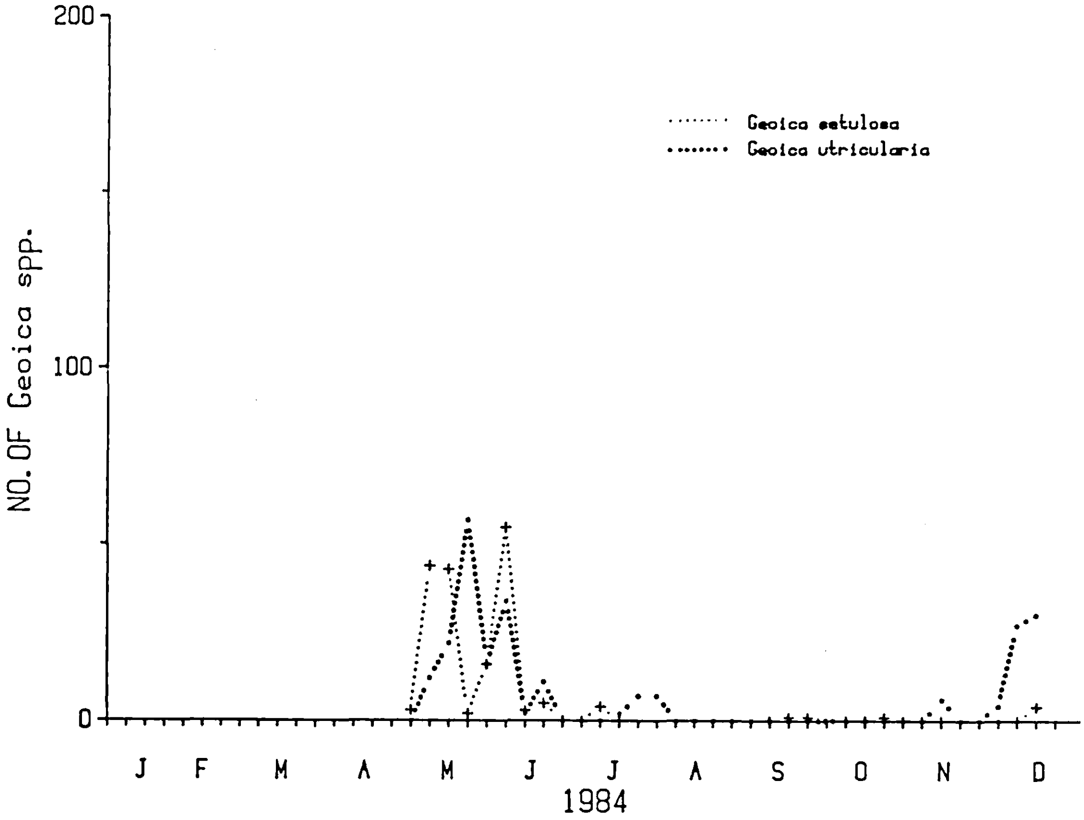
Graph 75. The abundance of <u>Baizongia pistaciae</u> throughout 1984.



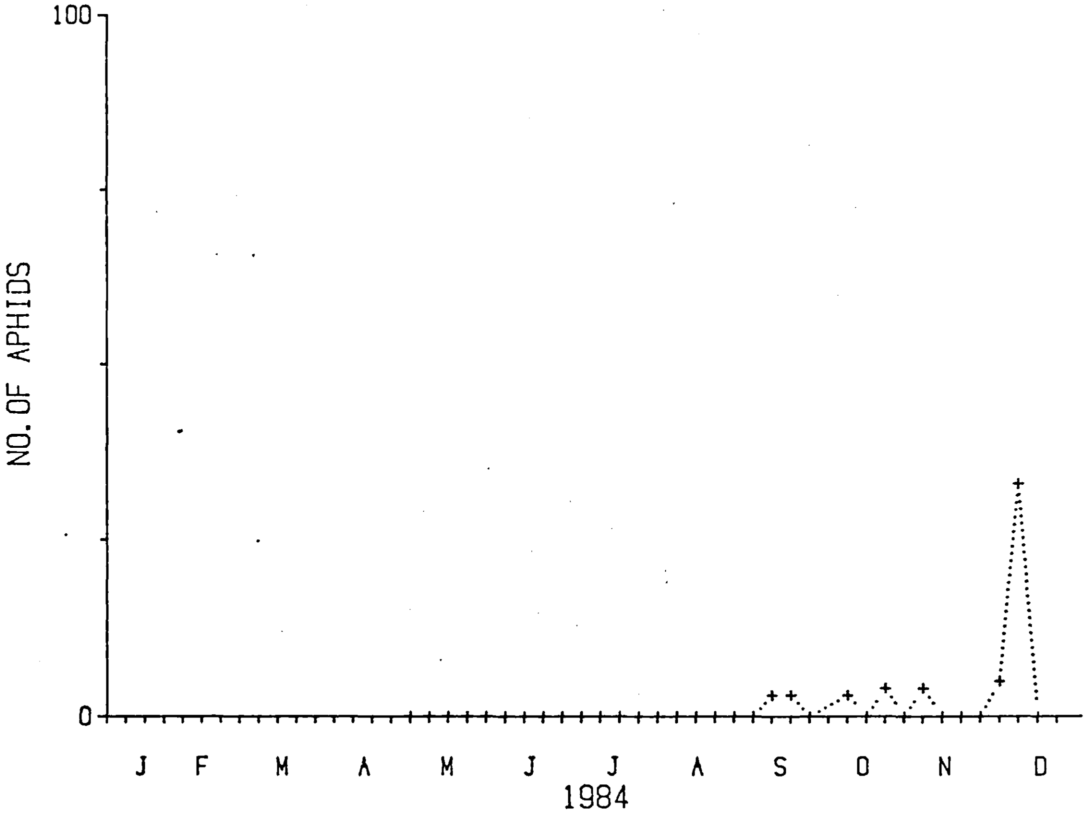
Graph 76. The abundance of <u>Forda formicaria</u> throughout 1984.



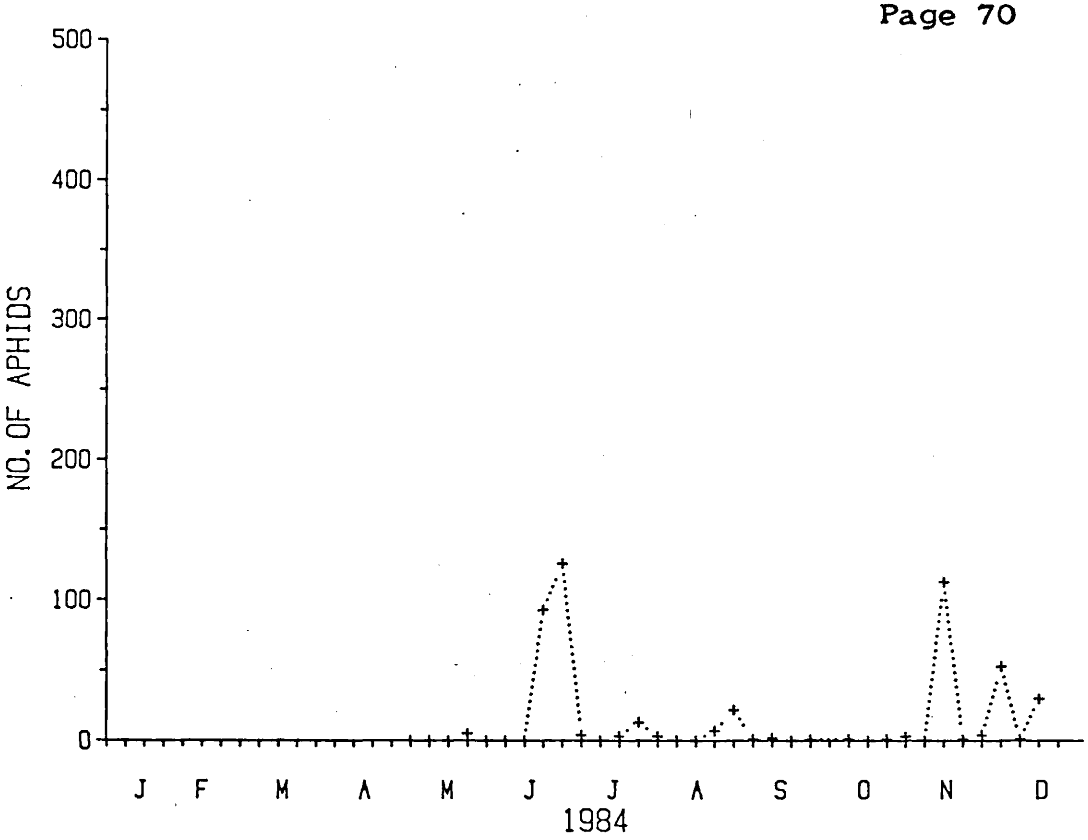
Graph 77. The abundance of <u>Anoecia corni</u> throughout 1984.



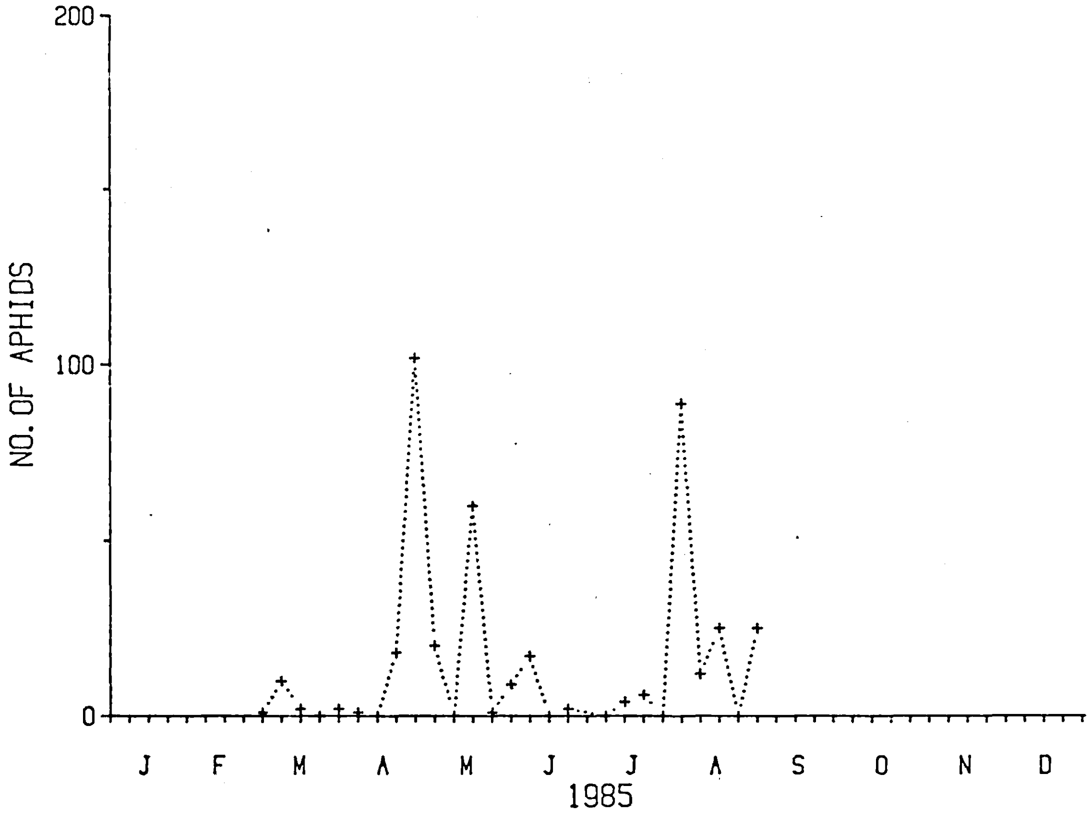
Graph 78. The abundance of <u>Geoica setulosa</u> and <u>Geoica utricularia</u> throughout 1984.



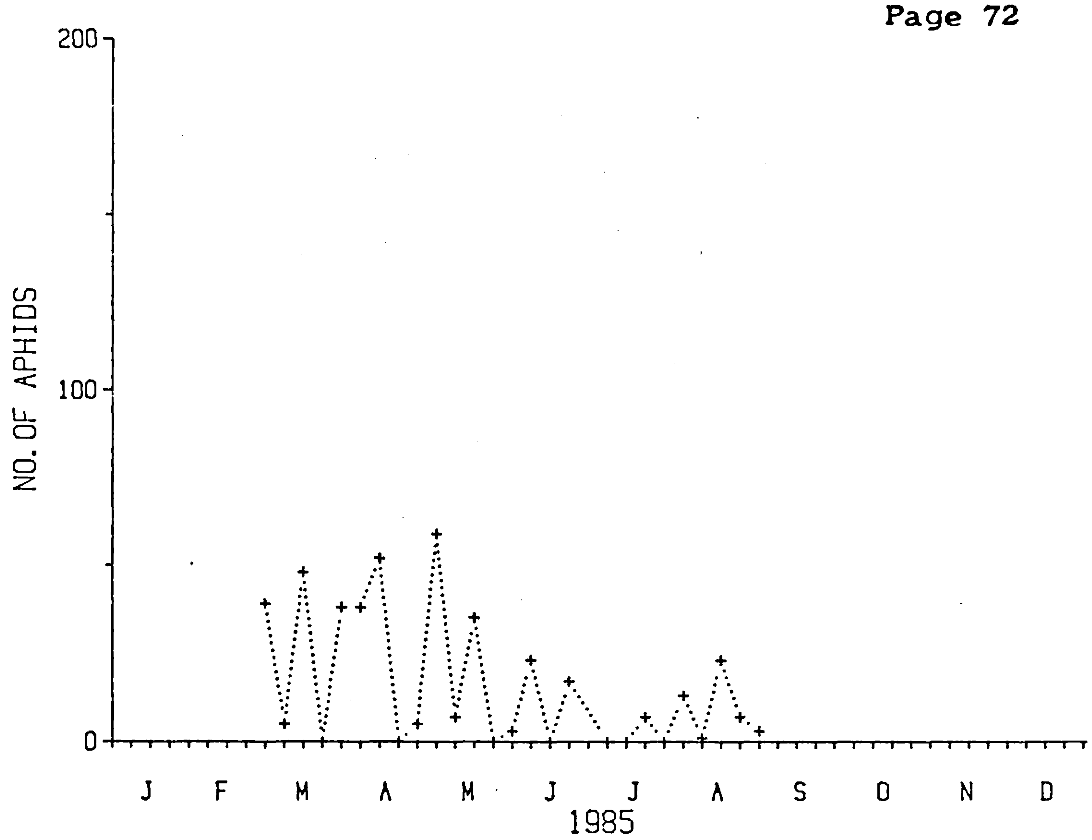
Graph 79. The abundance of Trama troglodytes throughout 1984.



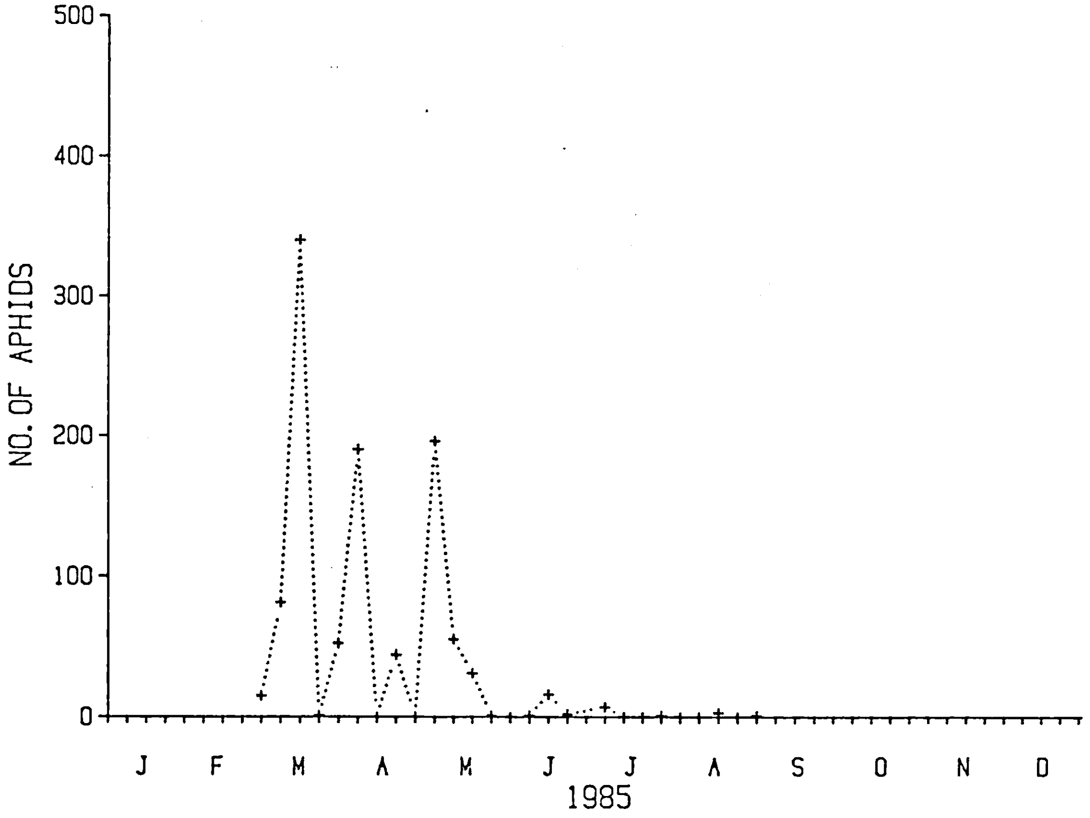
Graph 80. The abundance of <u>Aploneura lentisci</u> throughout 1984.



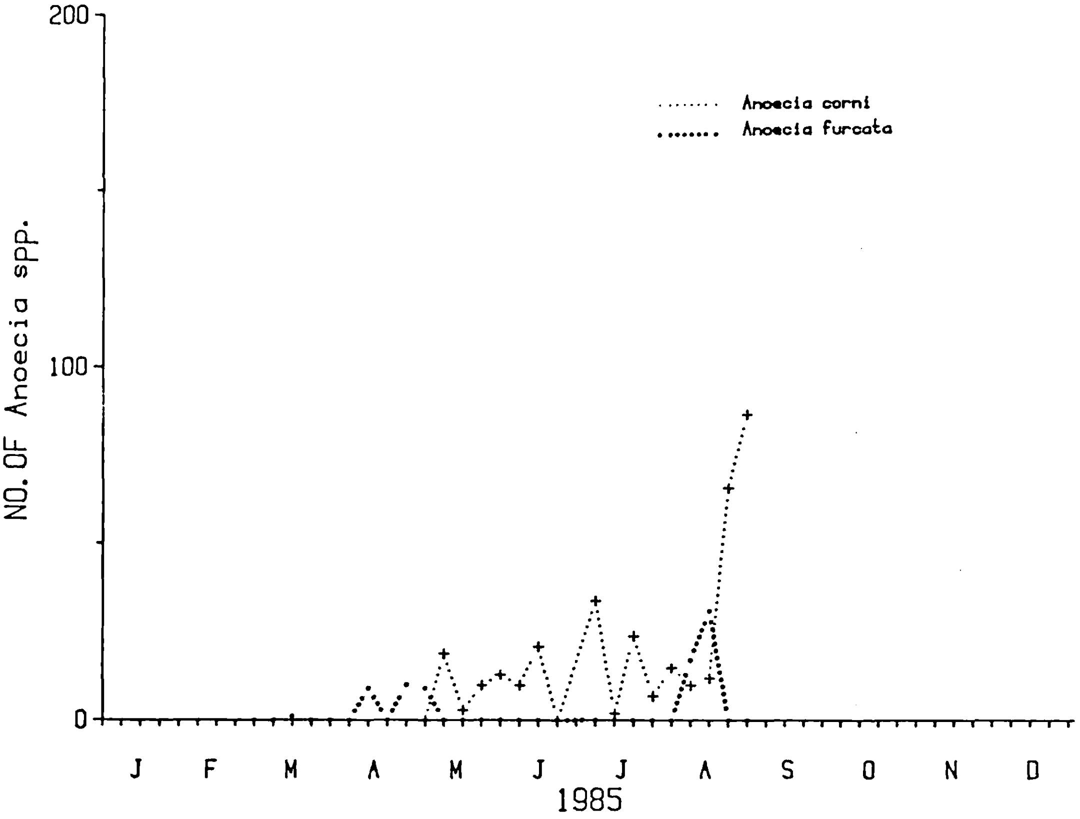
Graph 81. The abundance of Tetraneura ulmi throughout 1985.



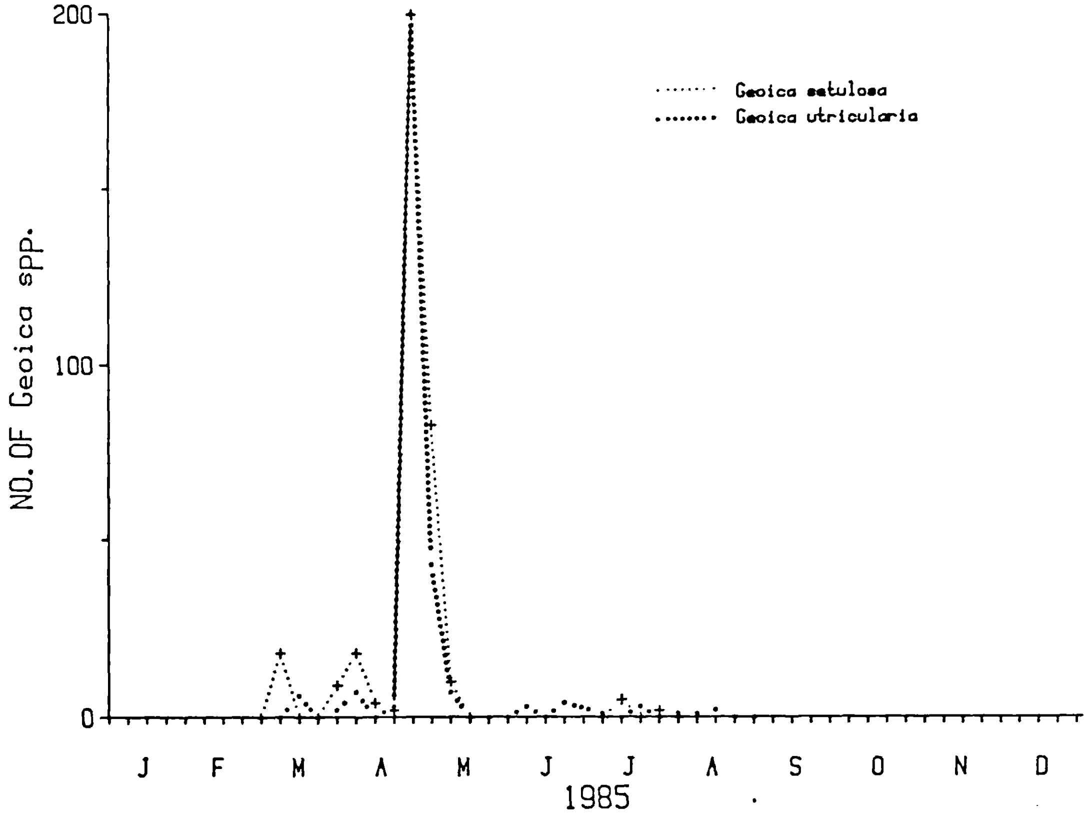
Graph 82. The abundance of Baizongia pistaciae throughout 1985.



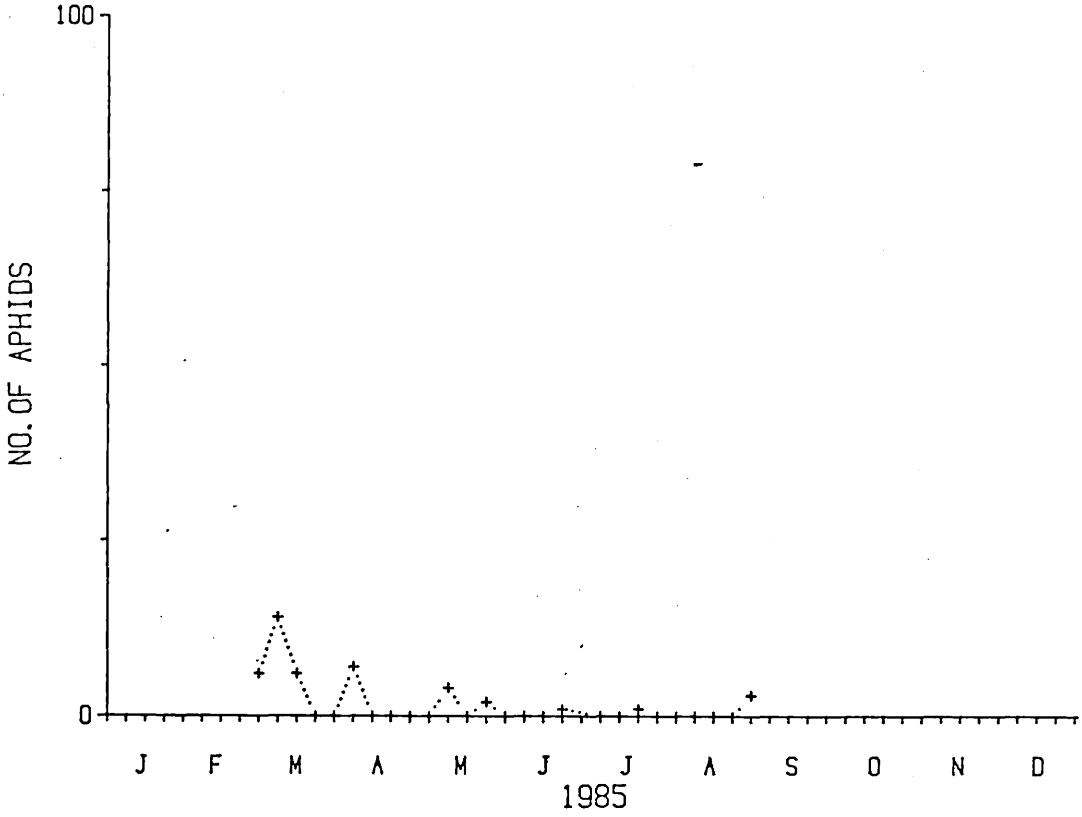
Graph 83. The abundance of <u>Forda formicaria</u> throughout 1985.



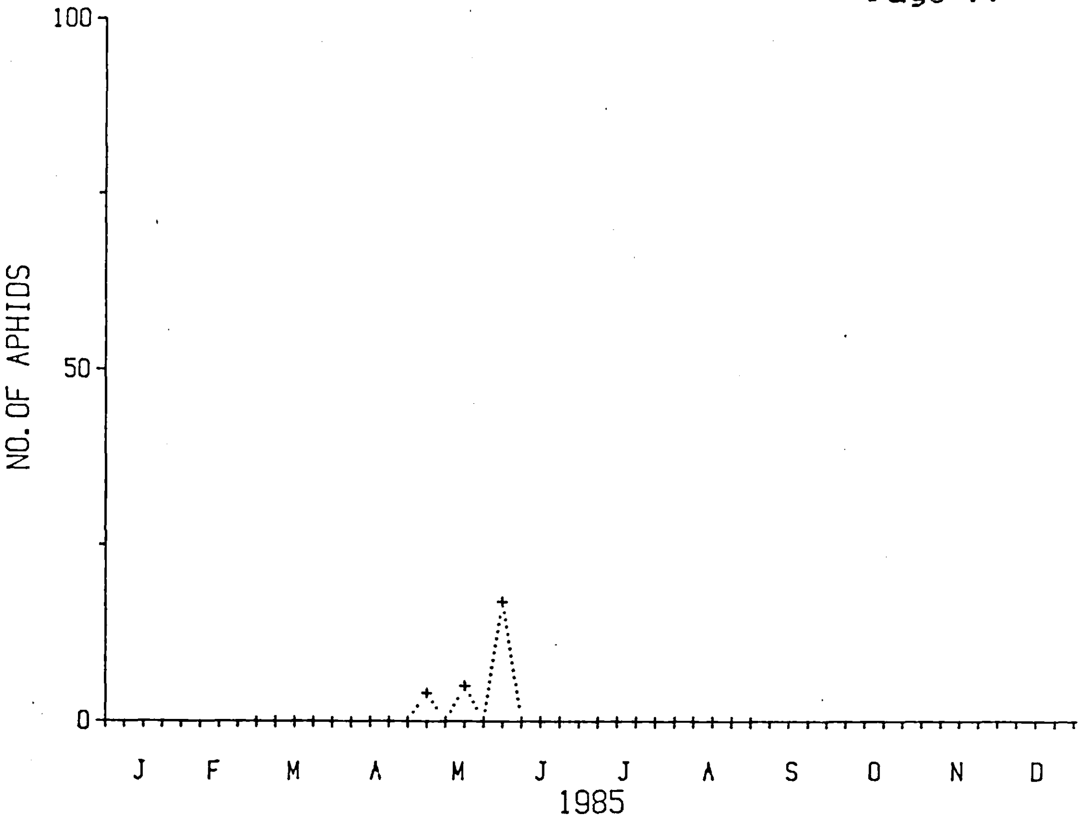
Graph 84. The abundance of <u>Anoecia corni</u> and <u>Anoecia furcata</u> throughout 1985.



Graph 85. The abundance of Geoica setulosa and Geoica utricularia throughout 1985.



Graph 86. The abundance of <u>Trama troglodytes</u> throughout 1985.

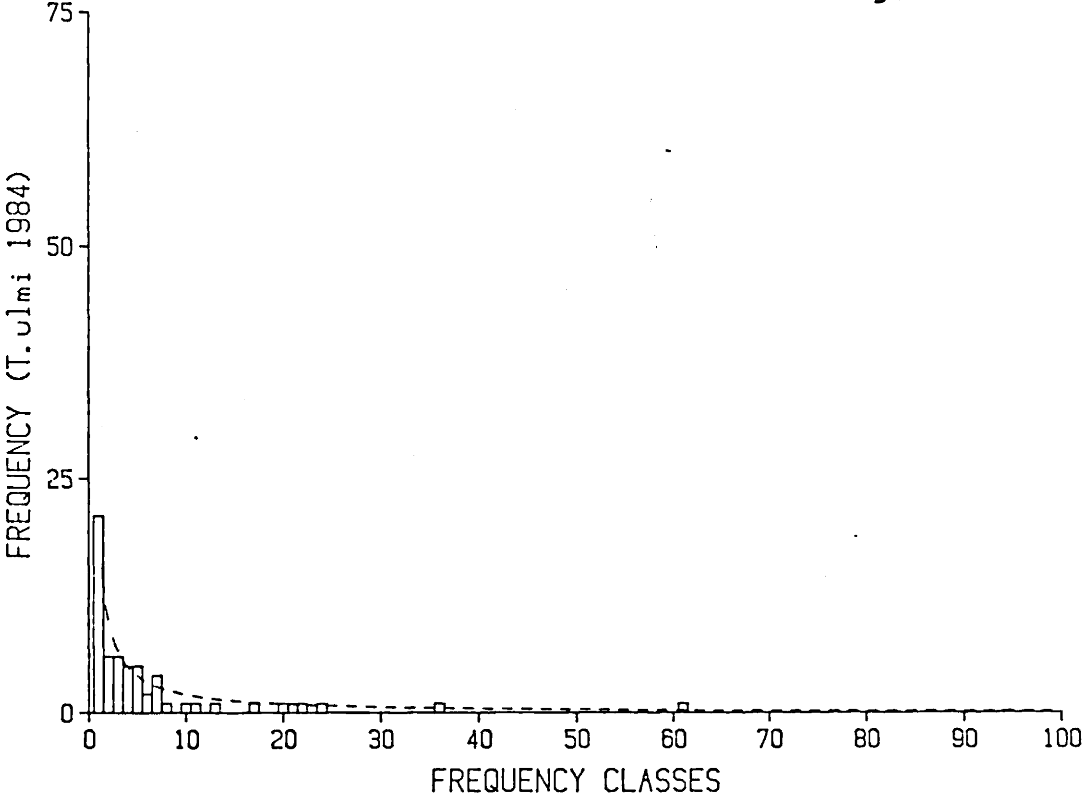


Graph 87. The abundance of Aploneura lentisci throughout 1985.

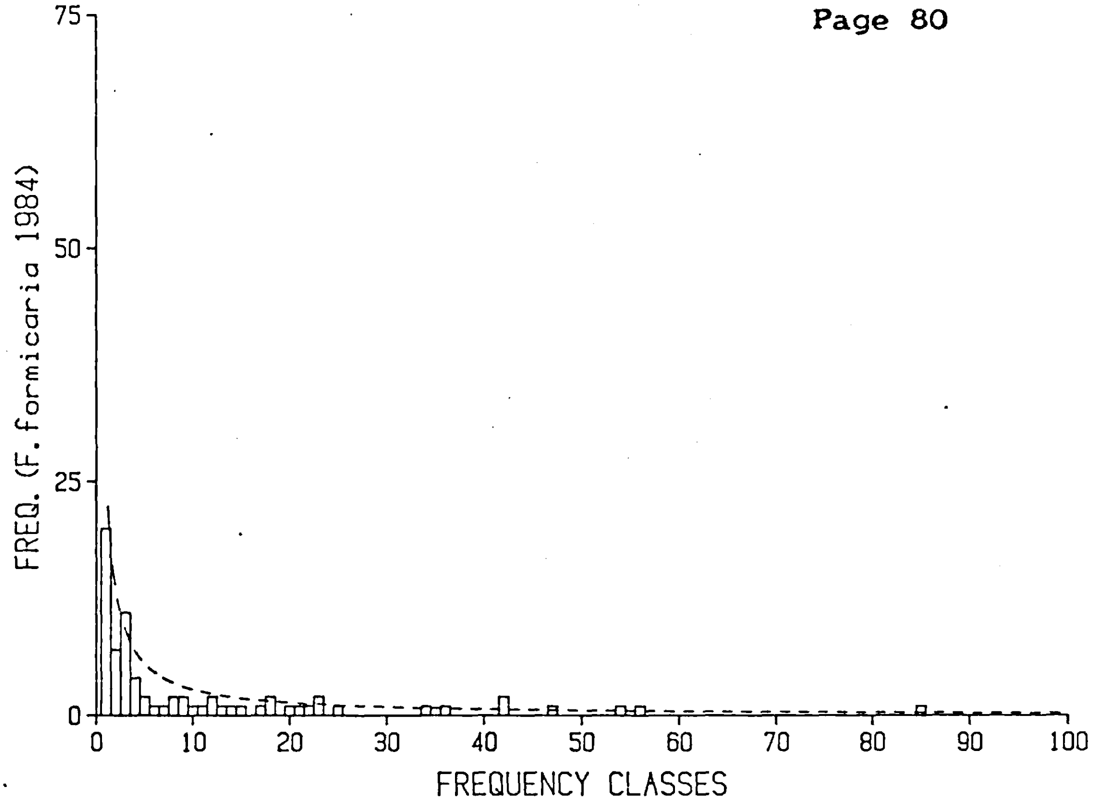
APPENDIX E2

Frequency distribution for aphids 1984

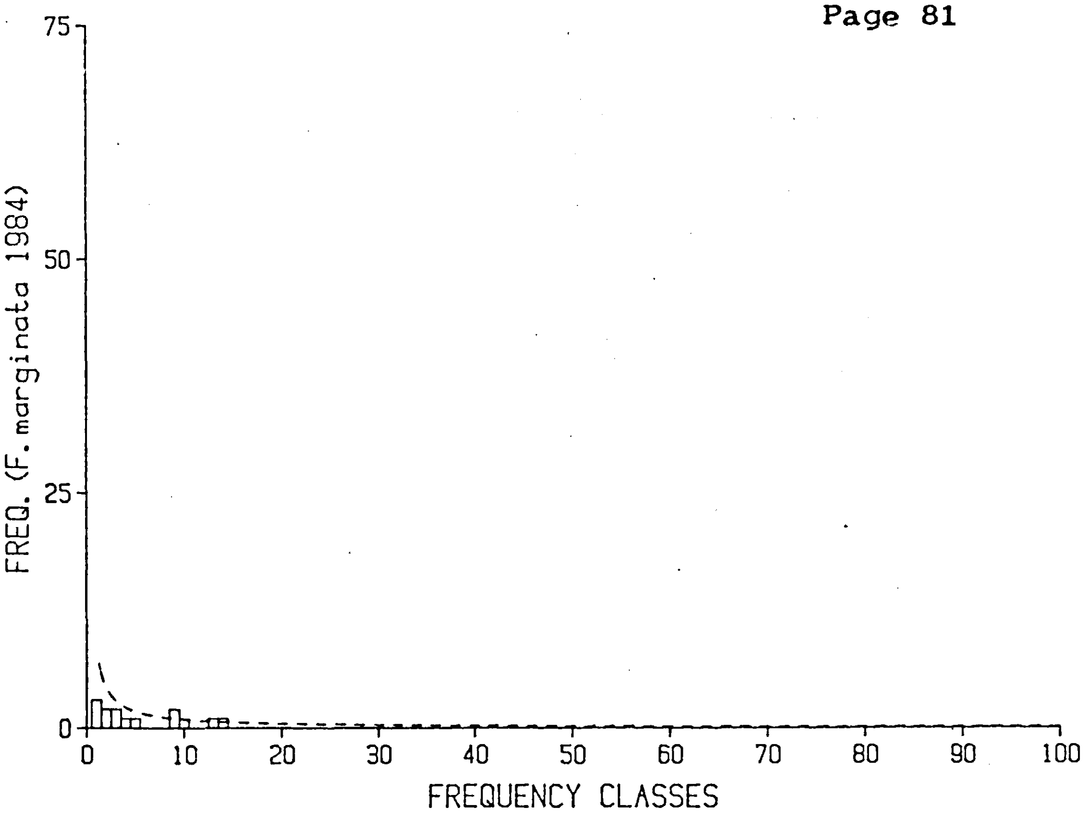
(Graphs 88-96)



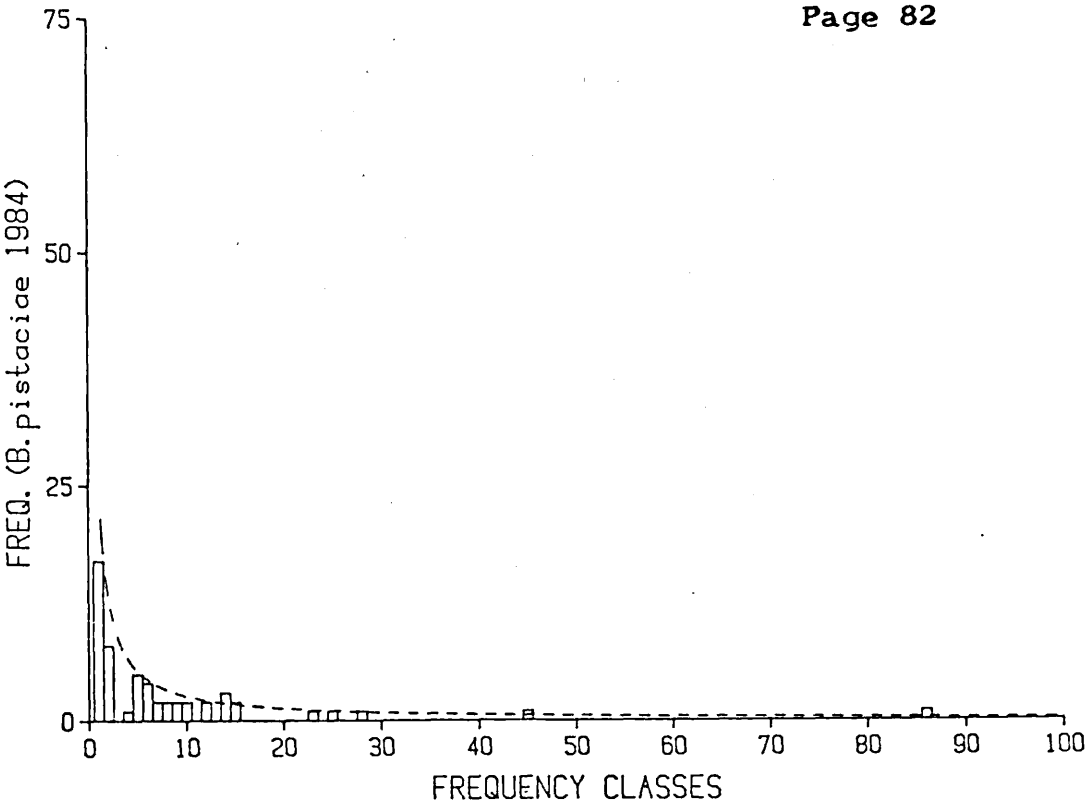
Graph 88. The frequency distribution of Tetraneura ulmi 1984.



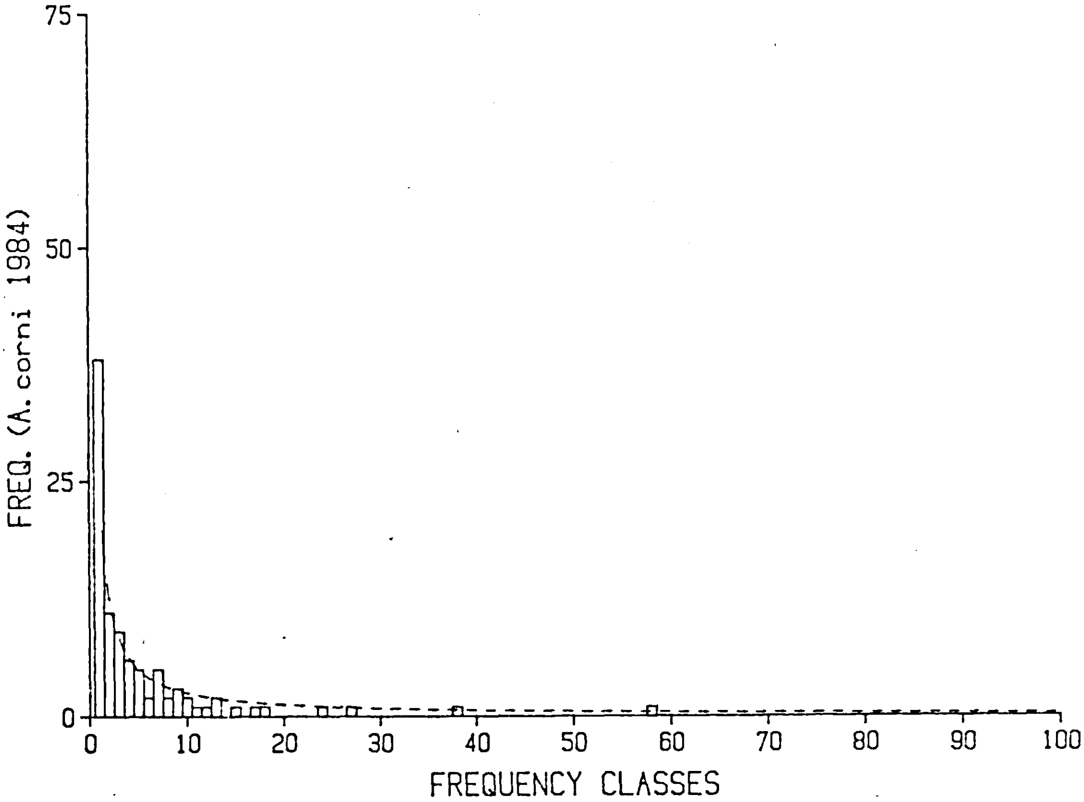
Graph 89. The frequency distribution of Forda formicaria 1984.



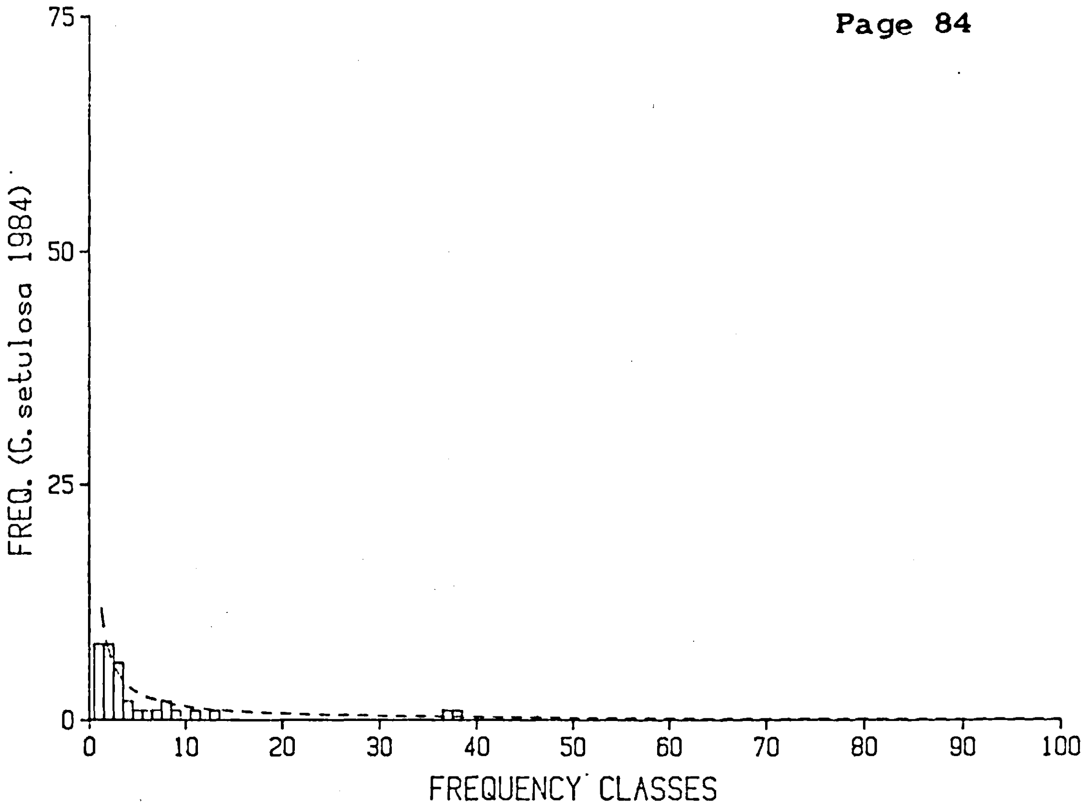
Graph 90. The frequency distribution of <u>Forda marginata</u> 1984.



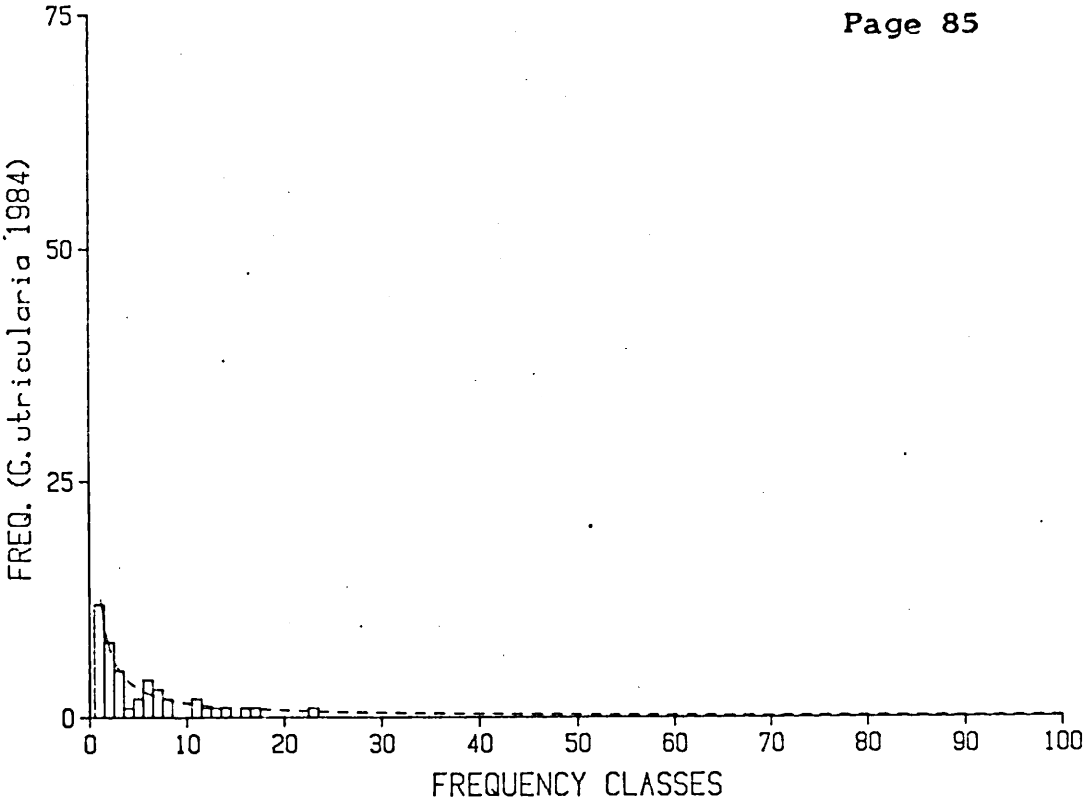
Graph 91. The frequency distribution of <u>Baizongia pistaciae</u> 1984.



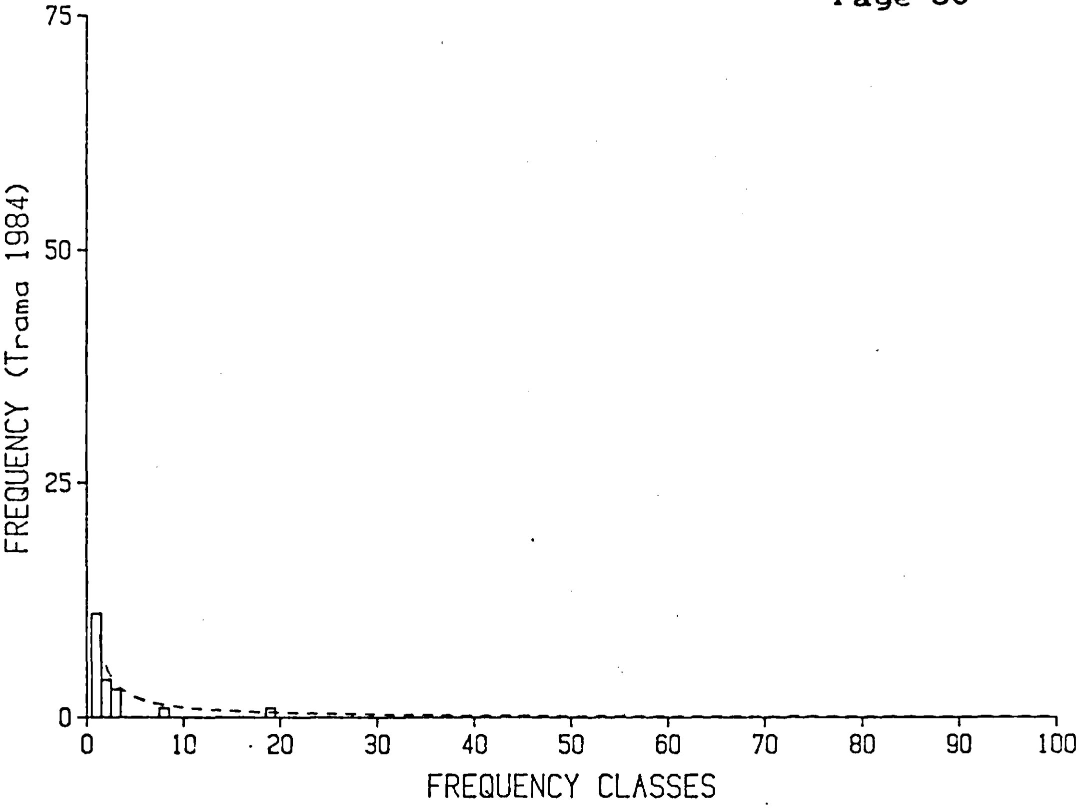
Graph 92. The frequency distribution of <u>Anoecia corni</u> 1984.



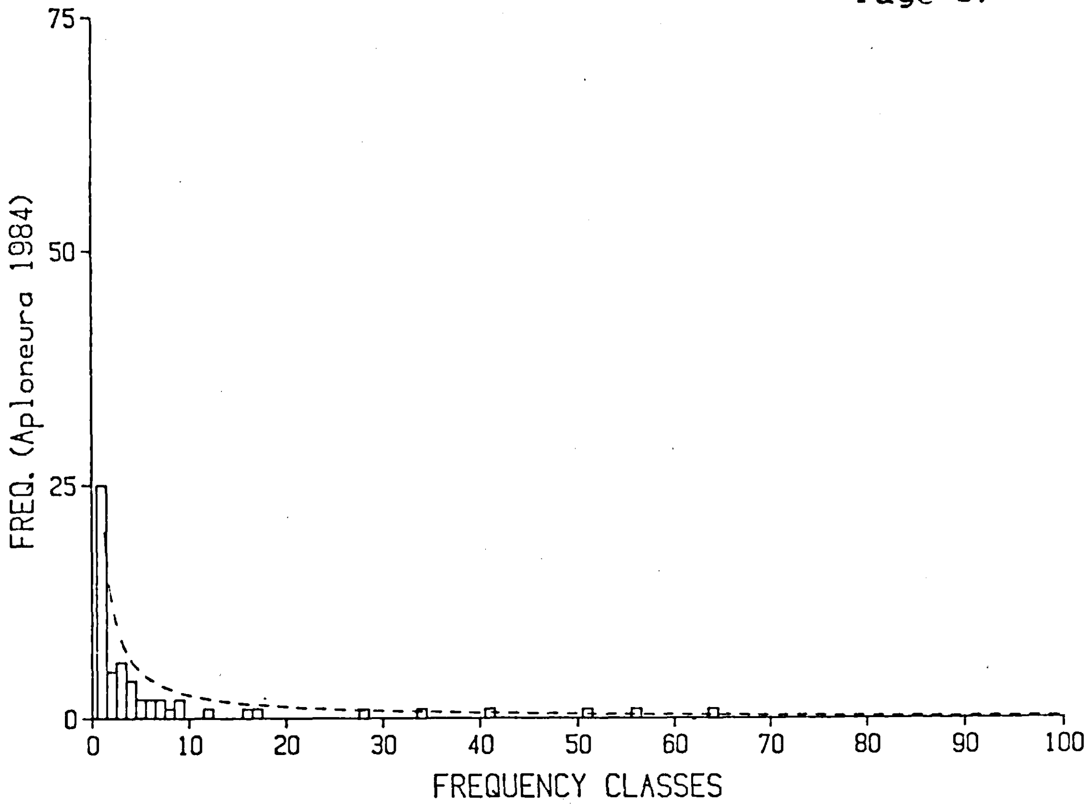
Graph 93. The frequency distribution of <u>Geoica setulosa</u> 1984.



Graph 94. The frequency distribution of <u>Geoica utricularia</u> 1984.



Graph 95. The frequency distribution of _Trama troglodytes_ 1984.

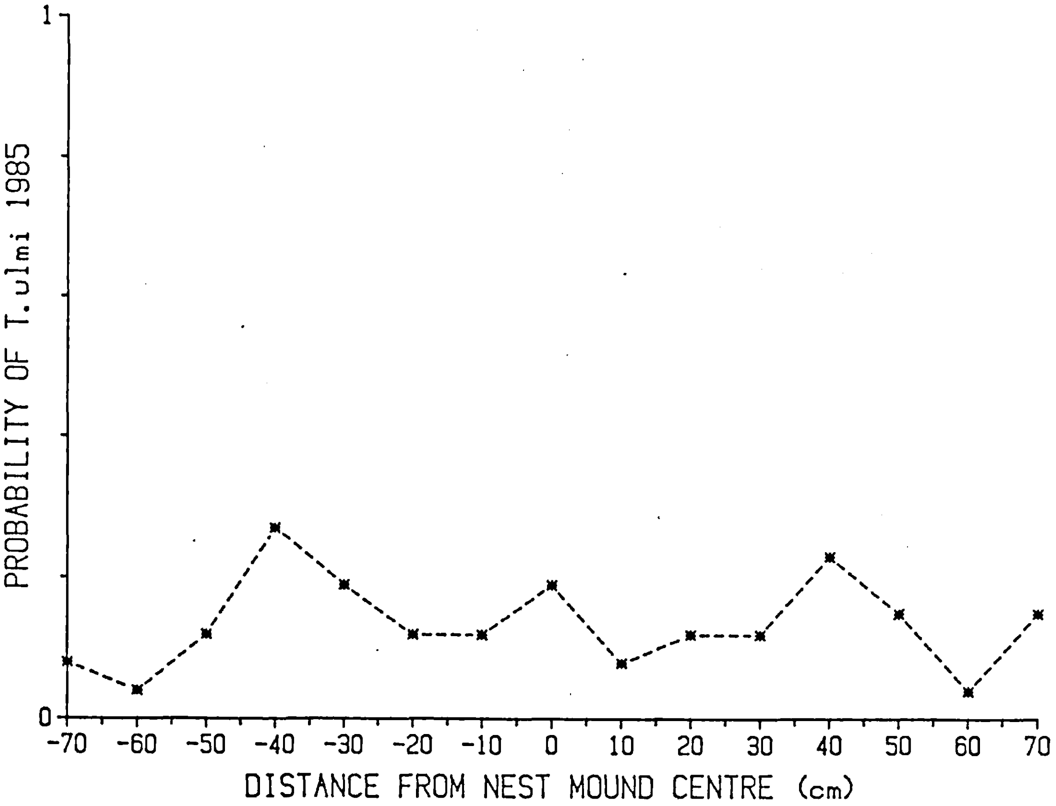


Graph 96. The frequency distribution of Aploneura lentisci 1984.

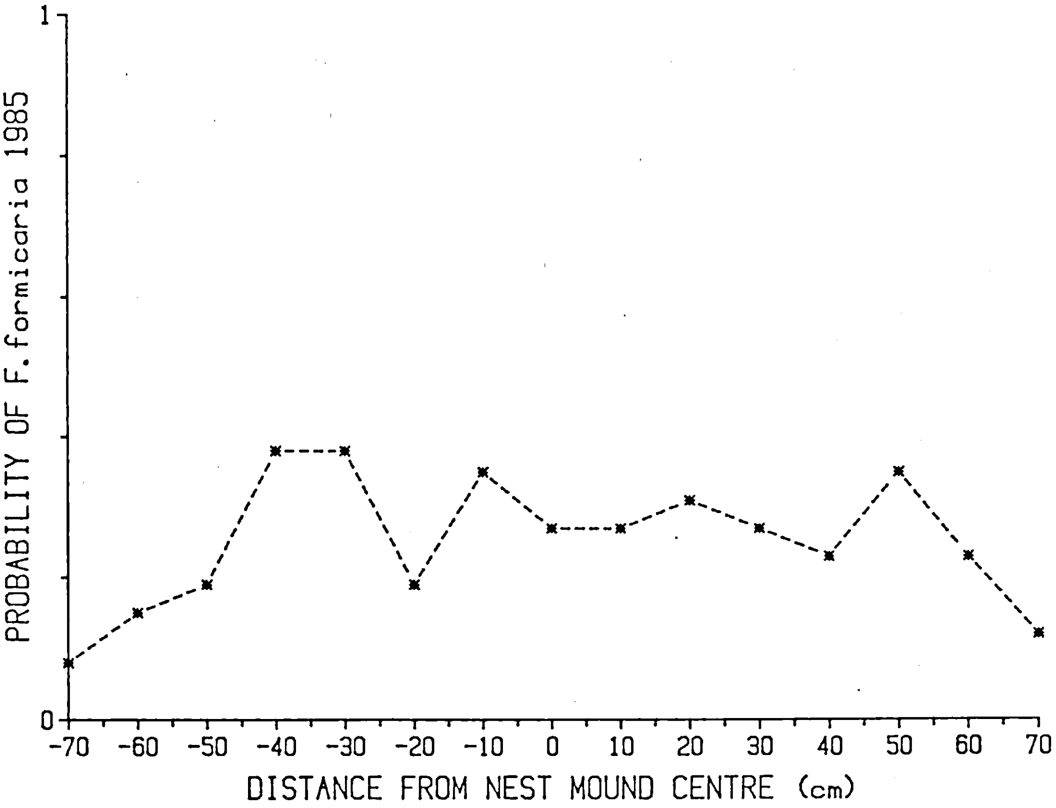
APPENDIX E3

Probabilities of aphid species per nest location

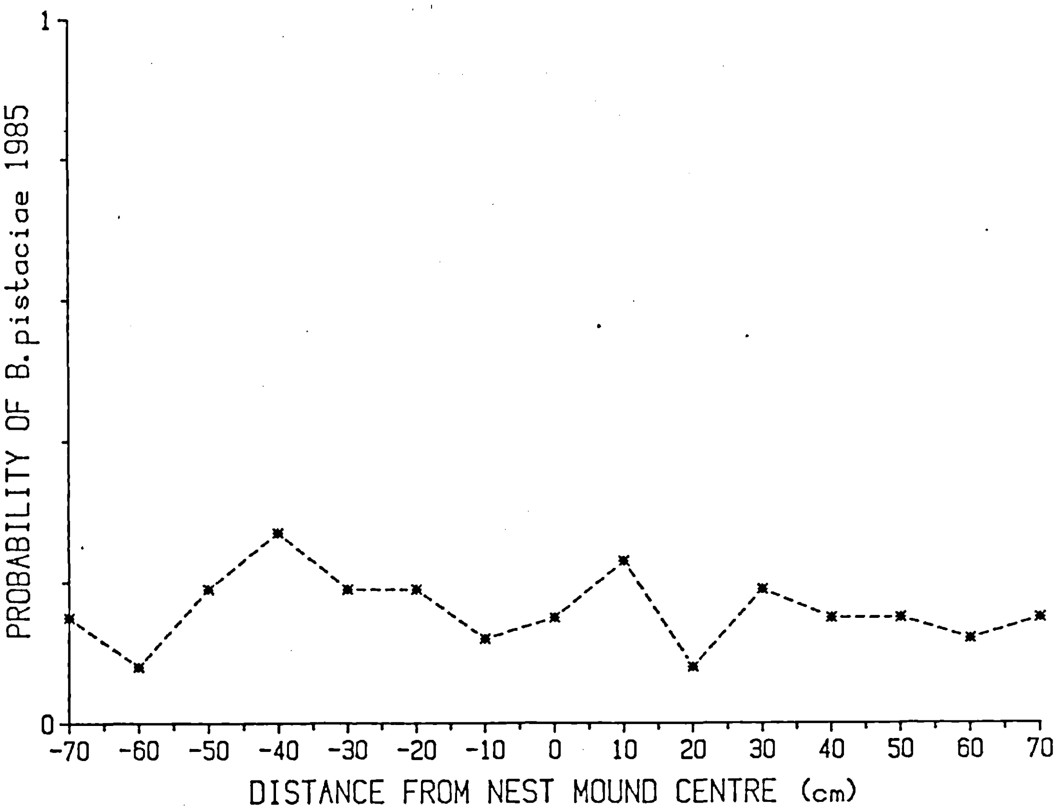
(Graphs 97-105)



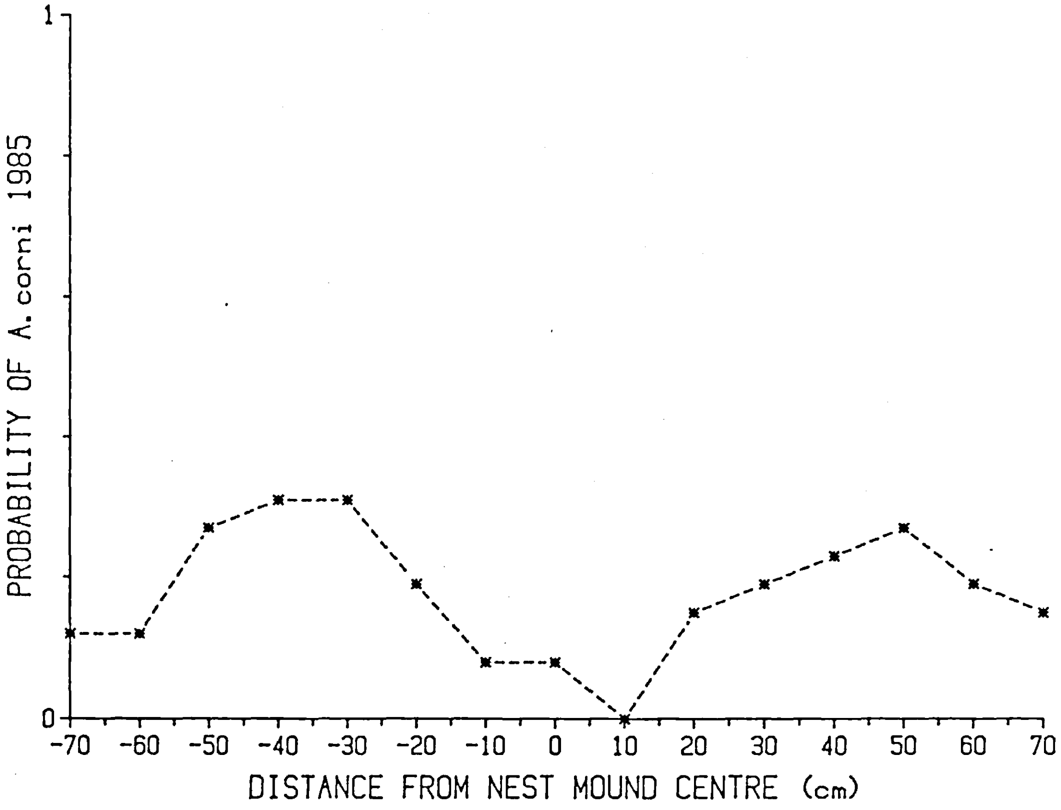
Graph 97. The probability of one or more Tetraneura ulmi per nest location (1985).



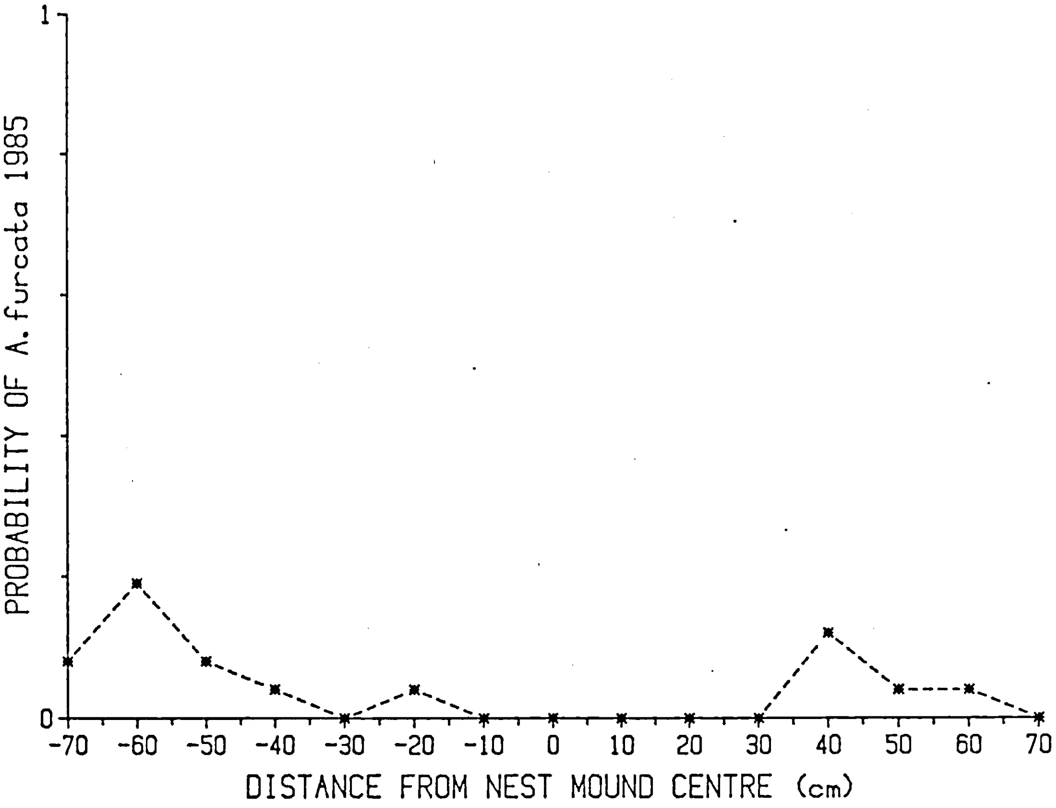
Graph 98. The probability of one or more <u>Forda formicaria</u> per nest location (1985).



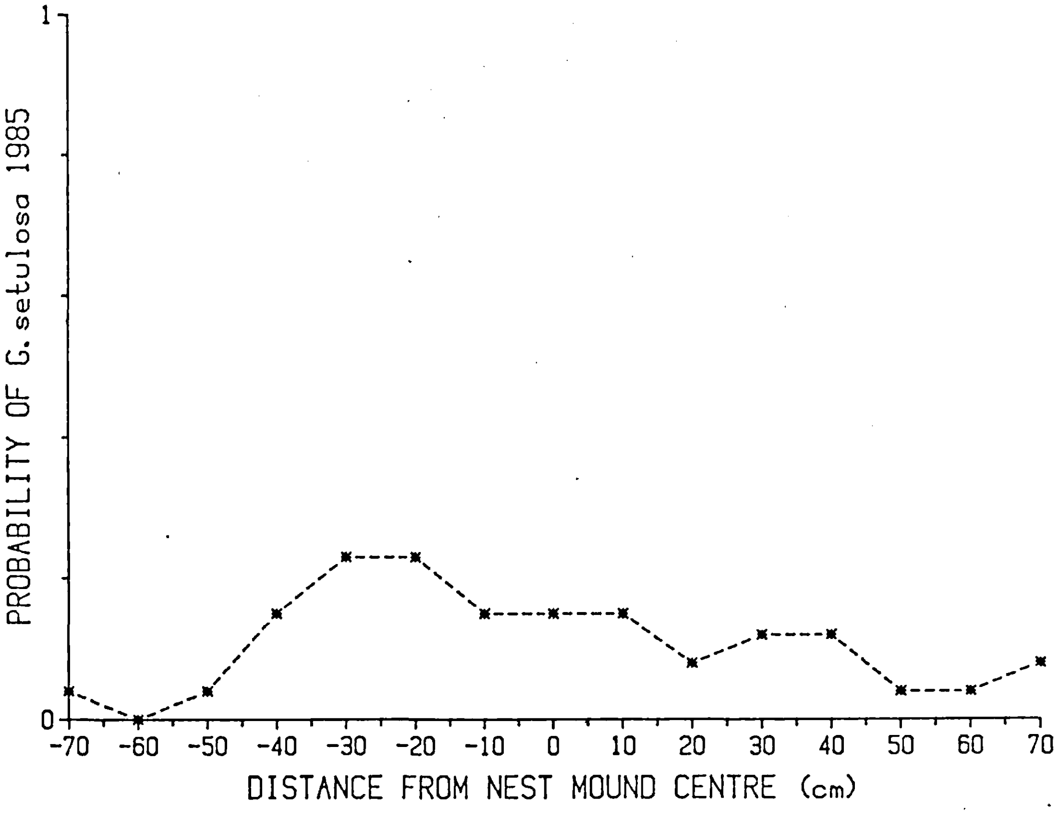
Graph 99. The probability of one or more Baizongia pistaciae per nest location (1985).



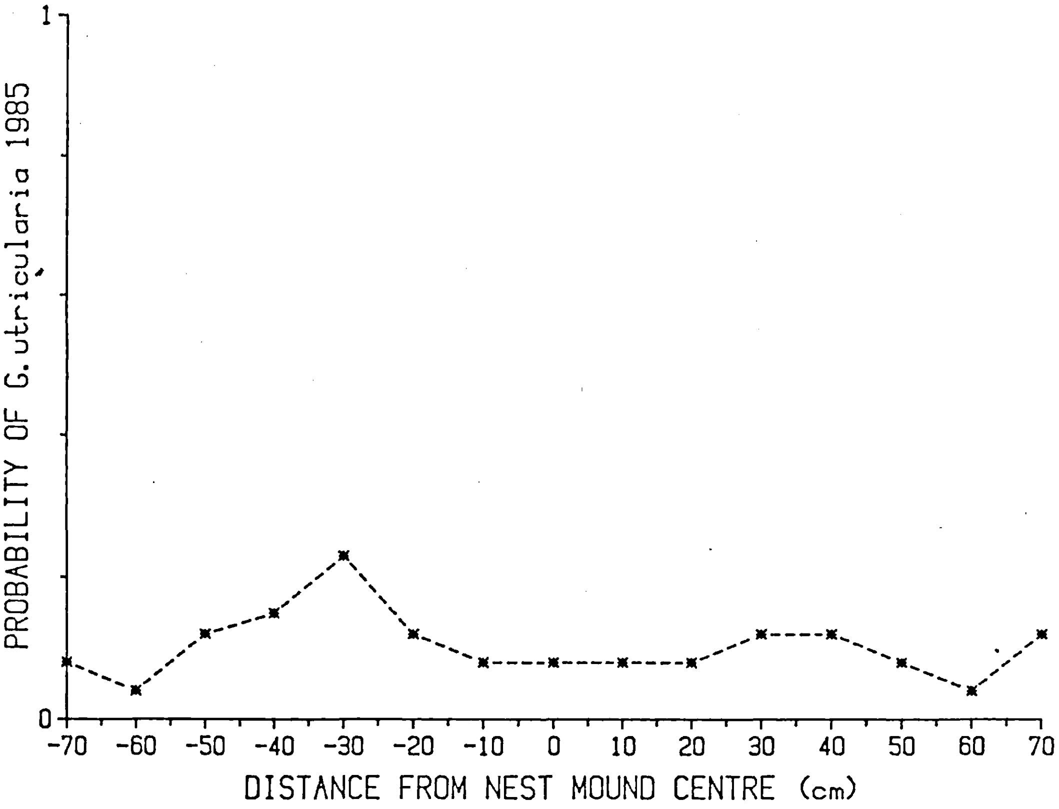
Graph 100. The probability of one or more Anoecia corni per nest location (1985).



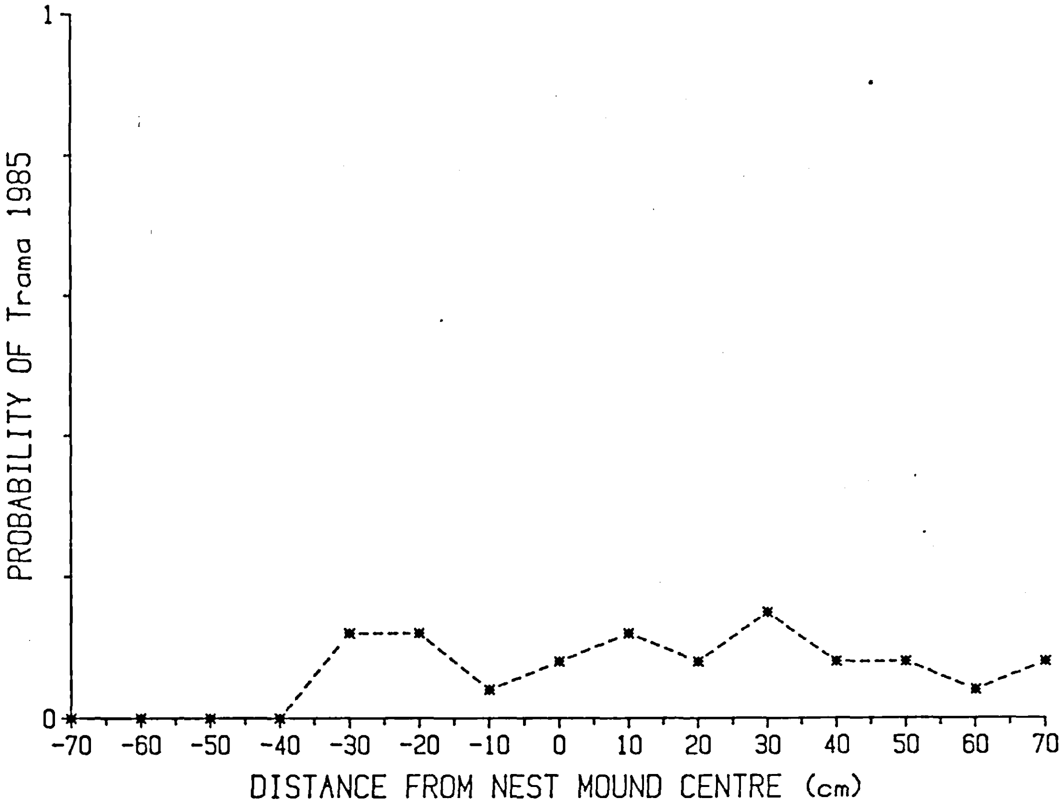
Graph 101. The probability of one or more Anoecia furcata per nest location (1985).



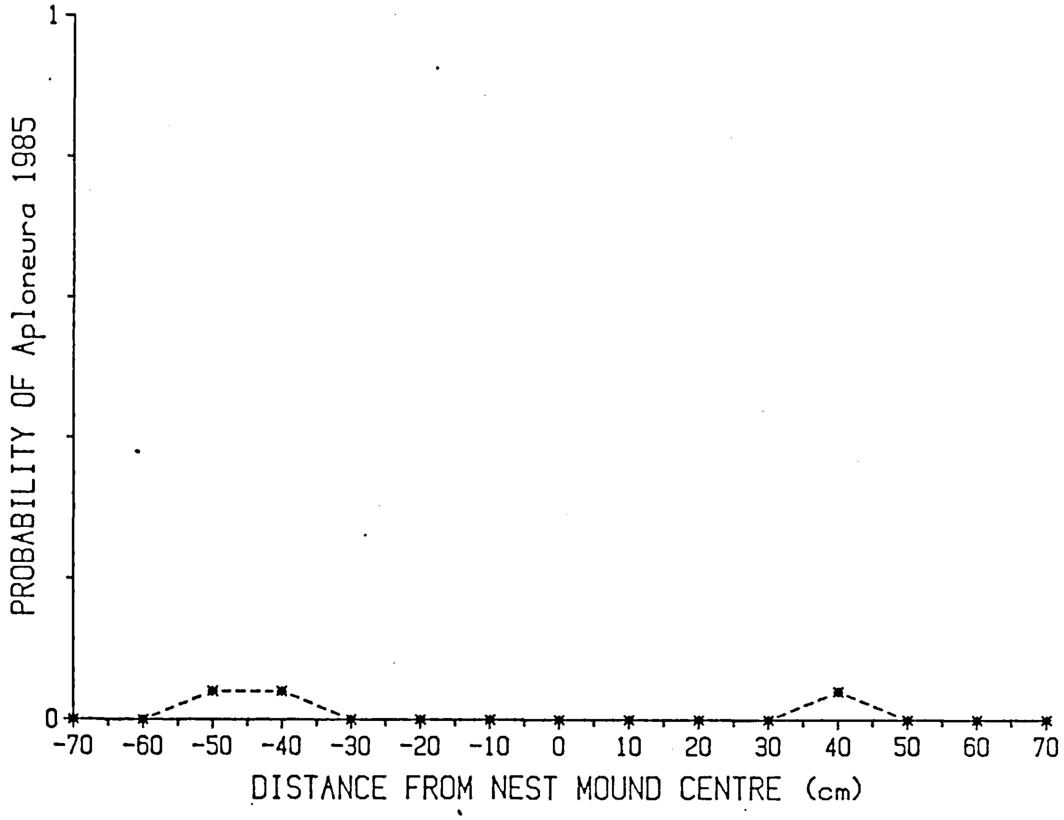
Graph 102. The probability of one or more Geoica setulosa per nest location (1985).



Graph 103. The probability of one or more Geoica utricularia per nest location (1985).



Graph 104. The probability of one or more Trama troglodytes per nest location (1985).

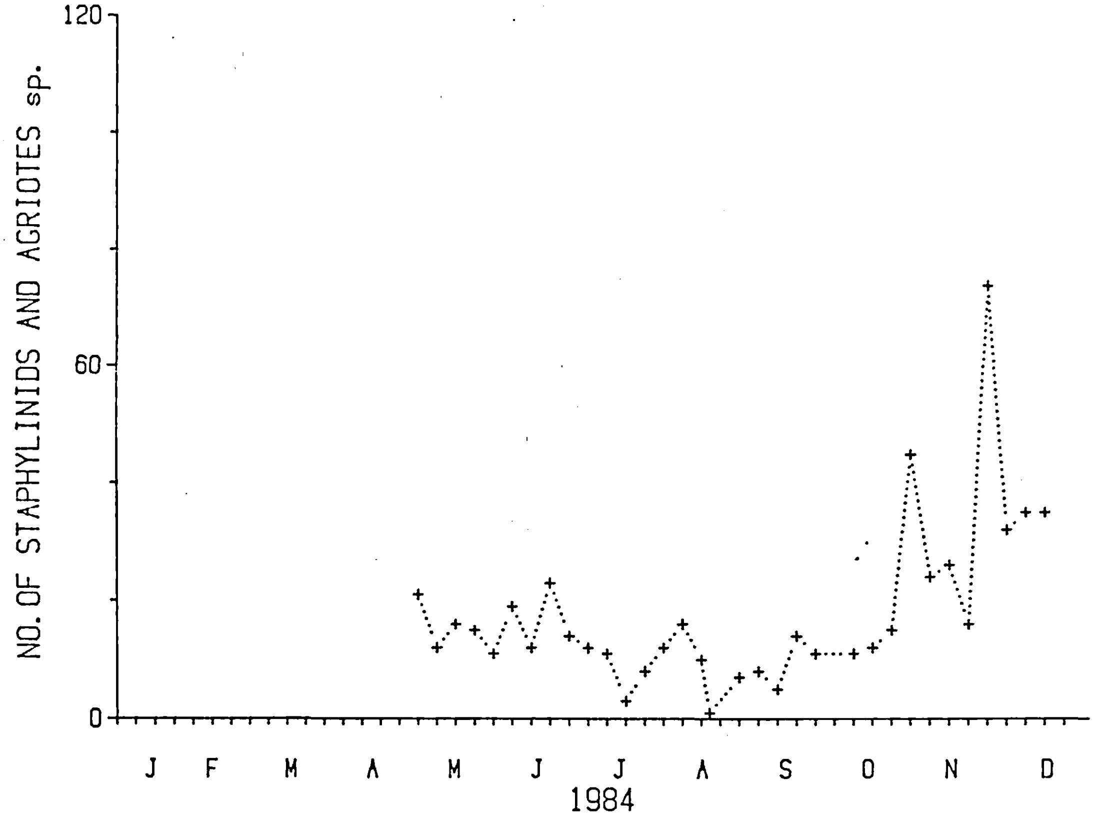


Graph 105. The probability of one or more Aploneura lentisci per nest location (1985).

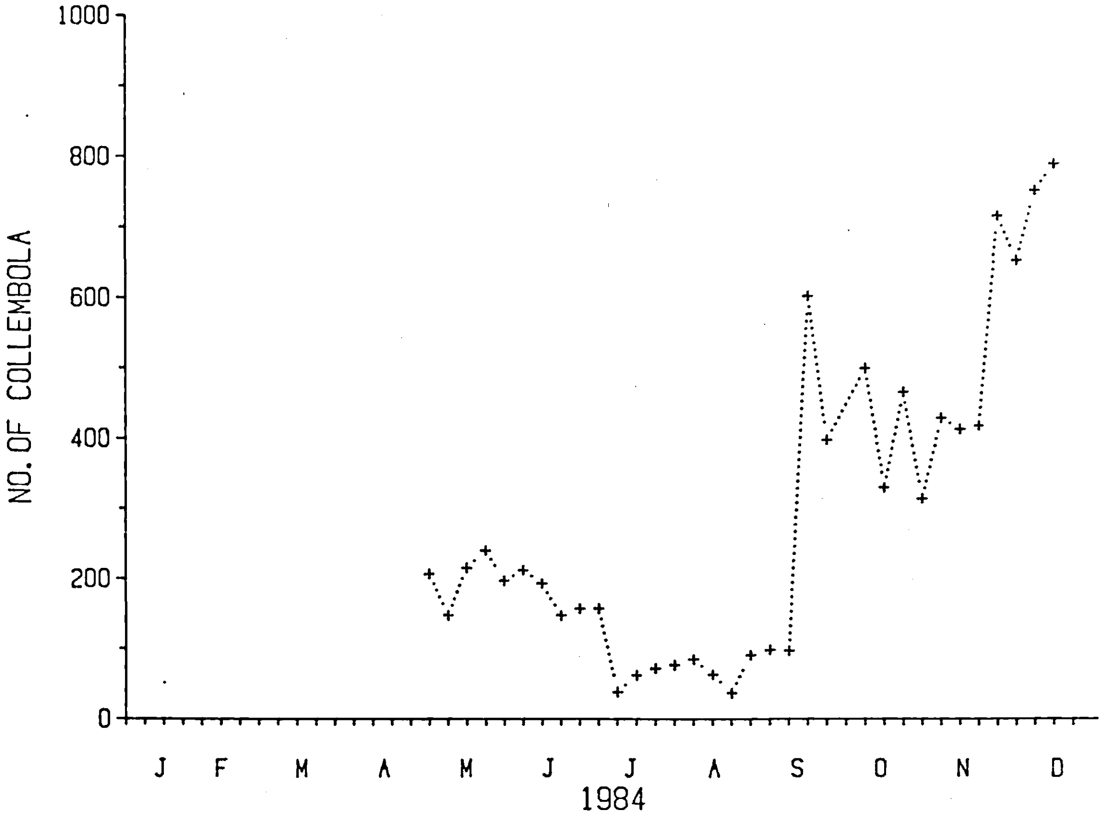
APPENDIX E4

Abundance of soil organisms throughout 1984 and 1985

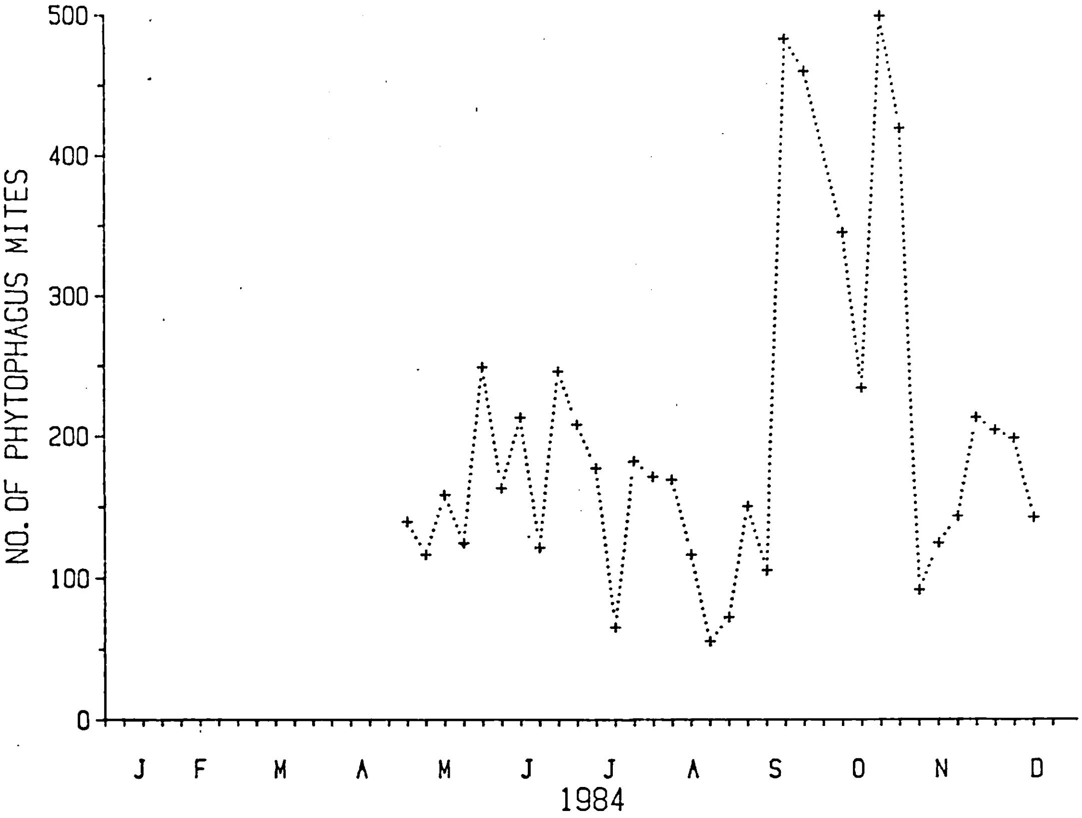
(Graphs 106-121)



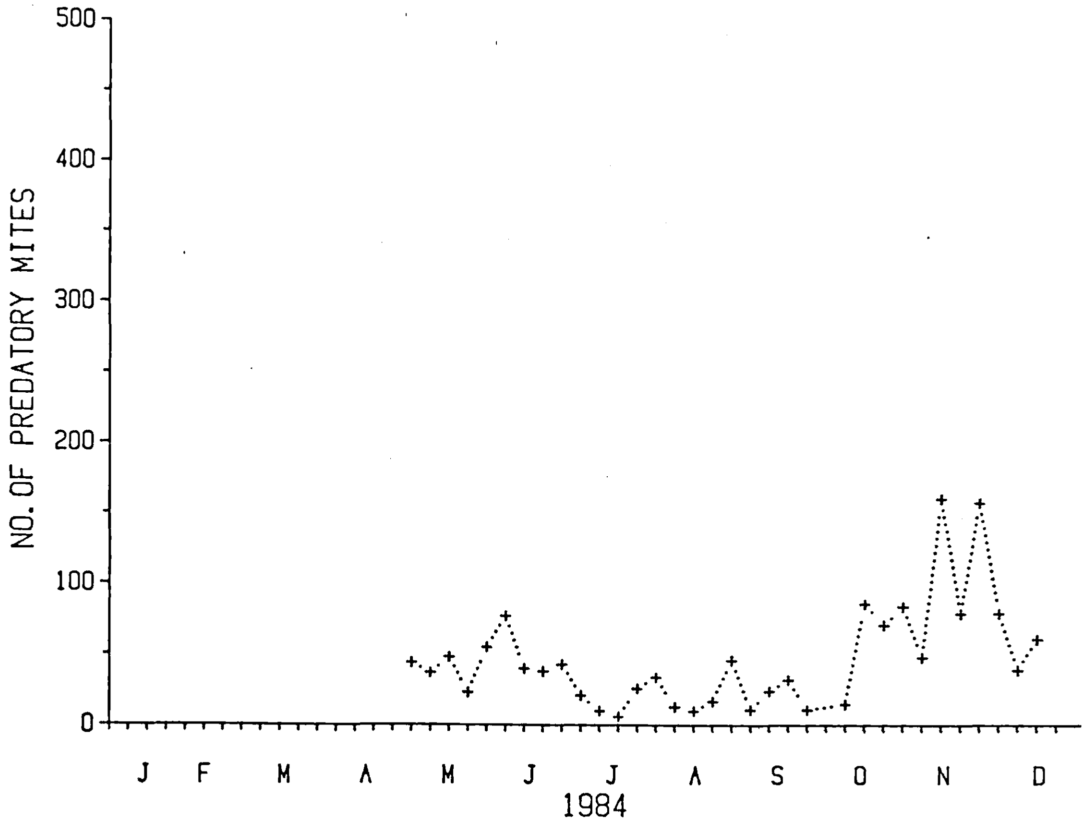
Graph 106. The abundance of staphylinids and <u>Agriotes</u> sp. in 1984.



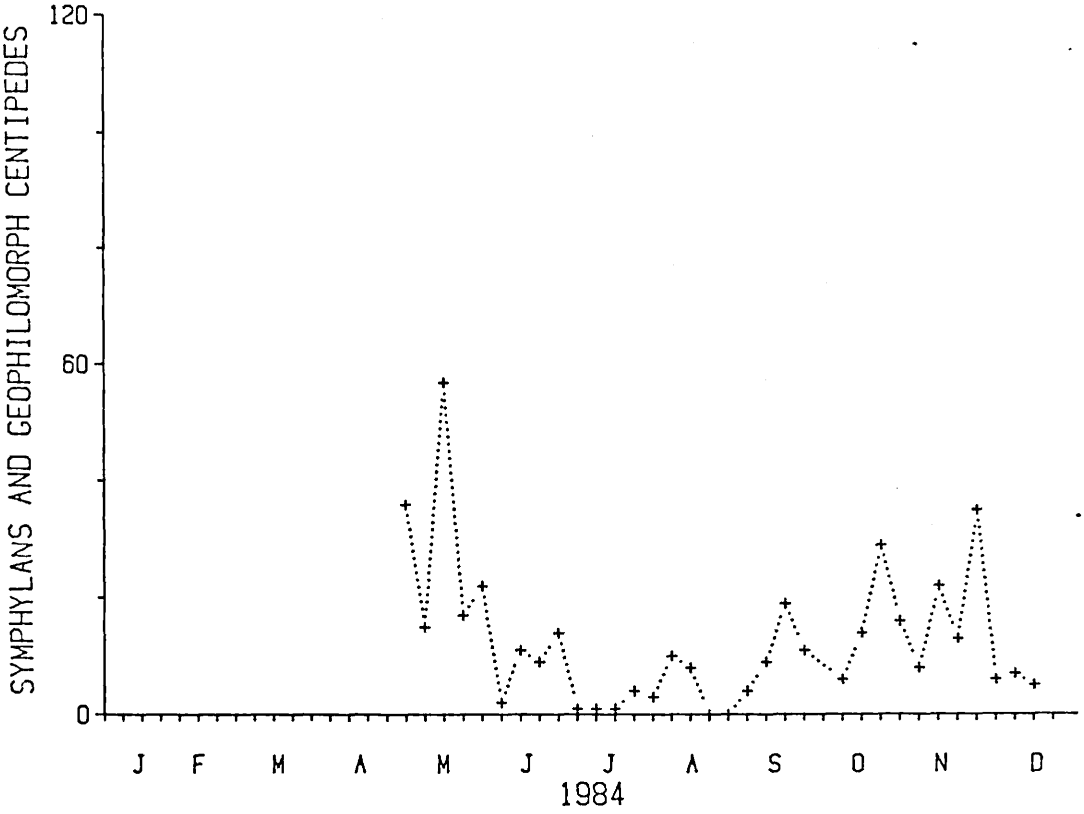
Graph 107. The abundance of soil collembola in 1984.



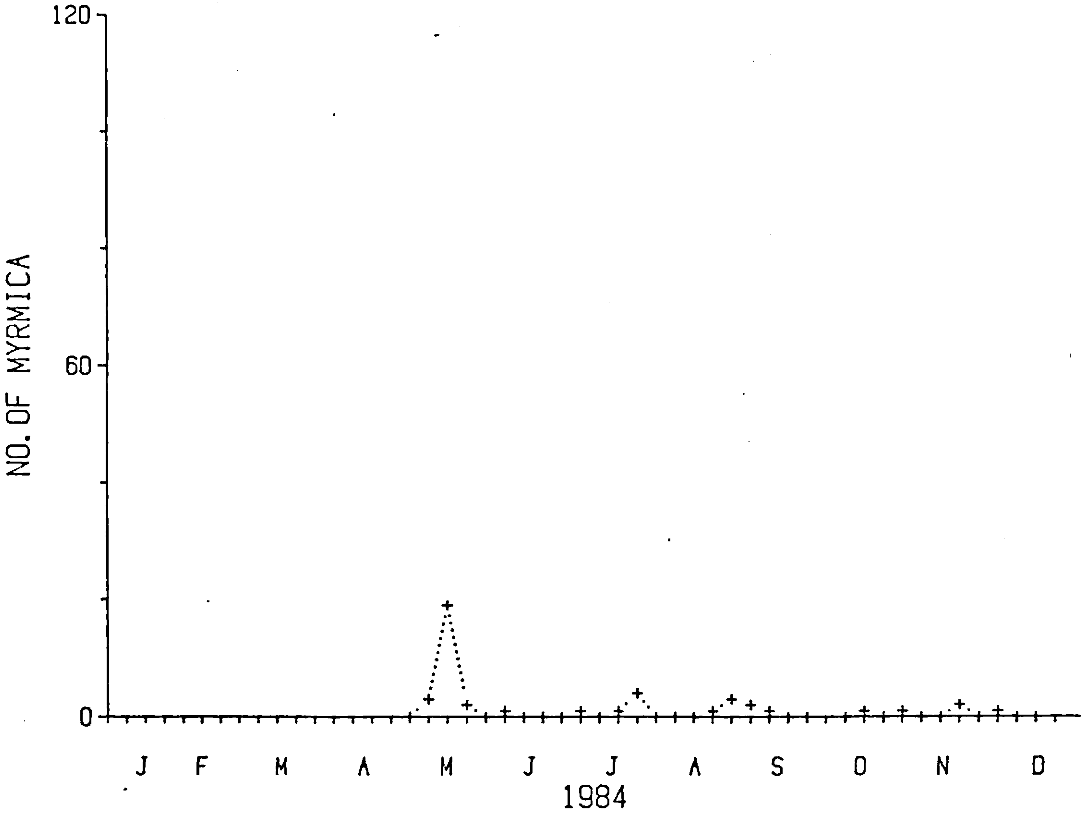
Graph 108. The abundance of phytophagus mites in 1984.



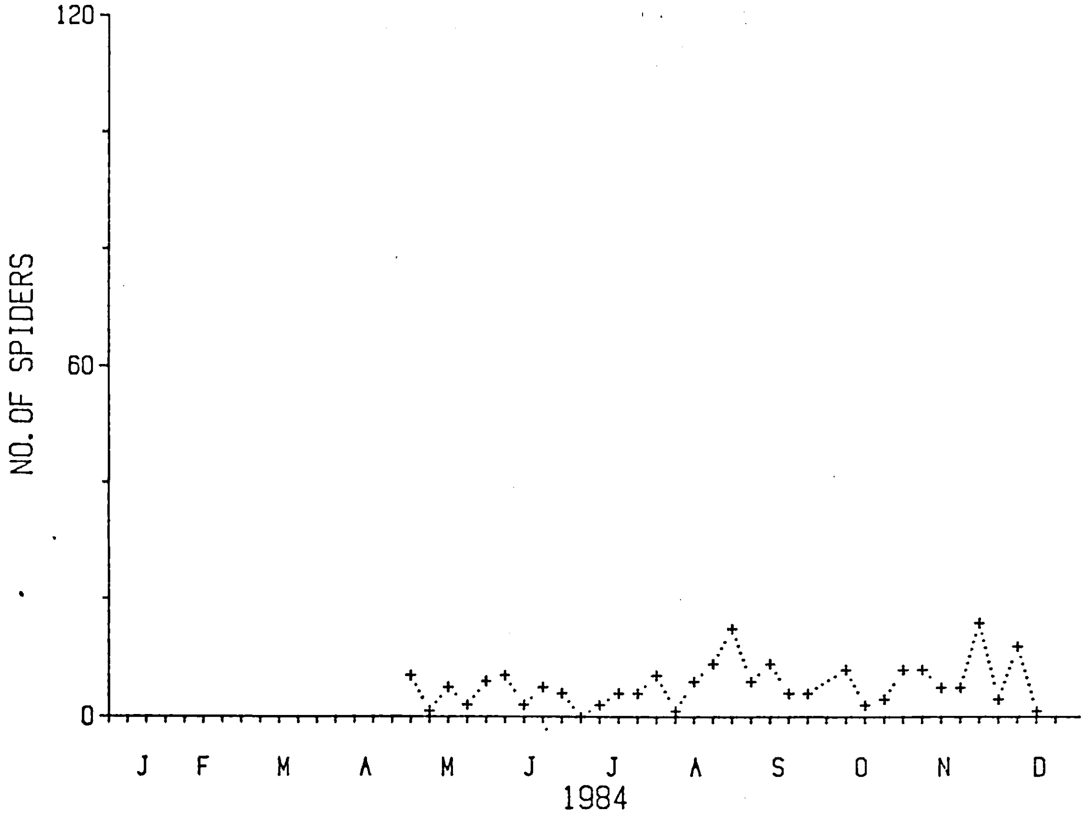
Graph 109. The abundance of predatory mites in 1984.



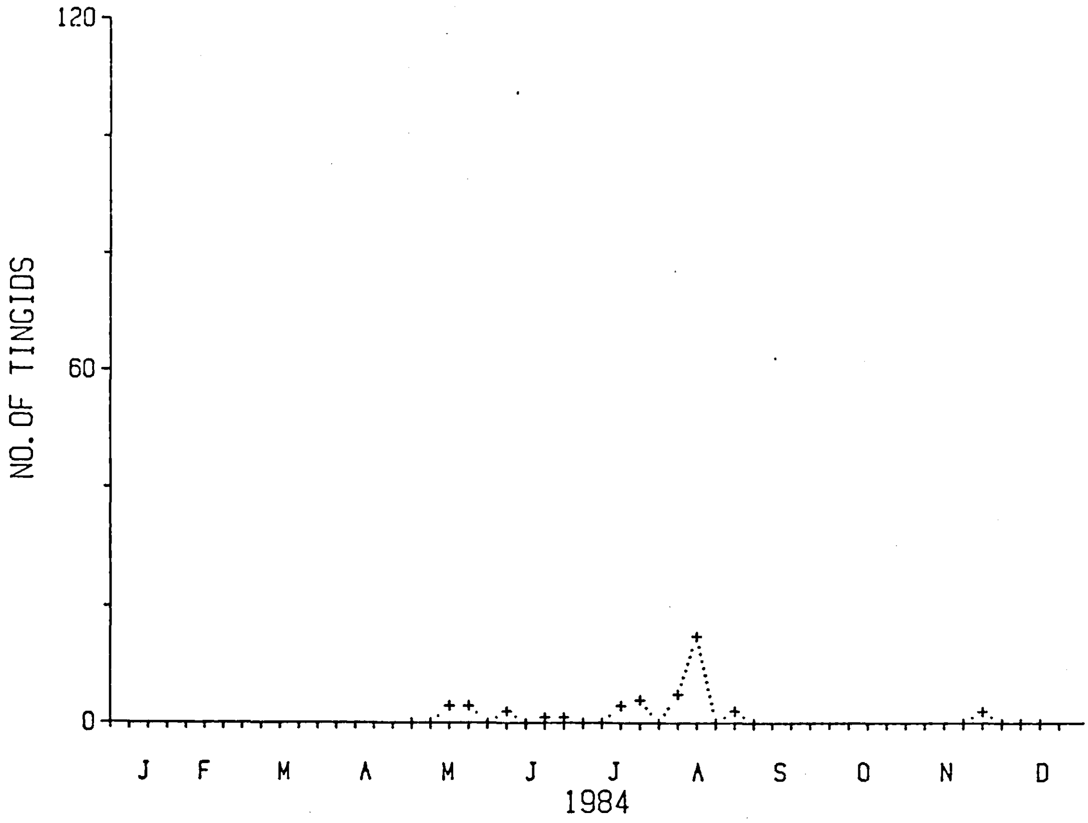
Graph 110. The abundance of symphilids and geophilomorph centipedes in 1984.



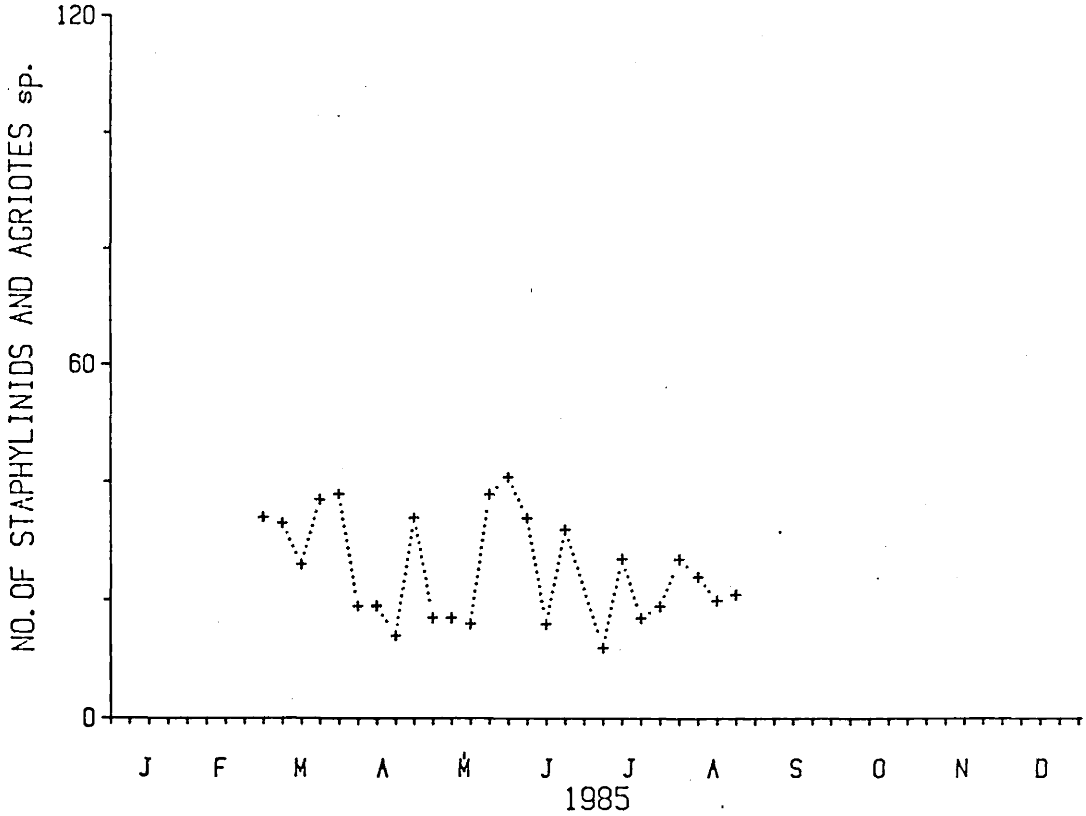
Graph 111. The abundance of Myrmica scabrinodis in 1984.



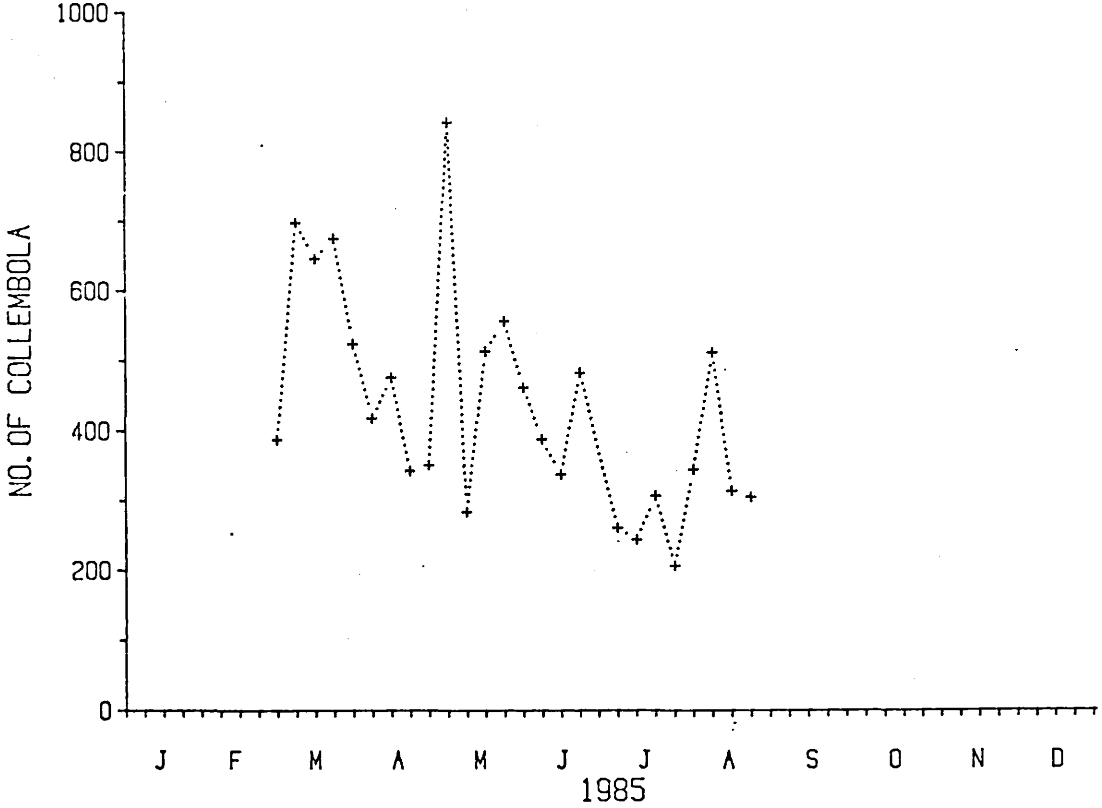
Graph 112. The abundance of spiders in 1984.



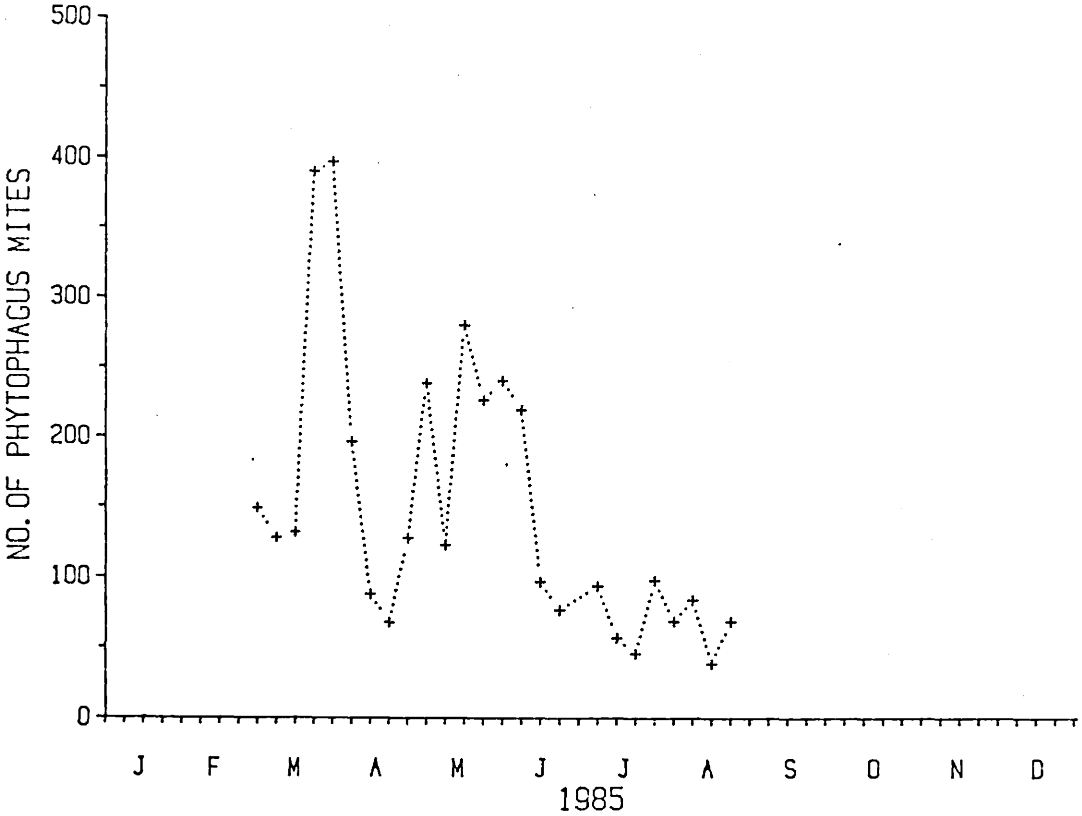
Graph 113. The abundance of Acalypta platychila in 1984.



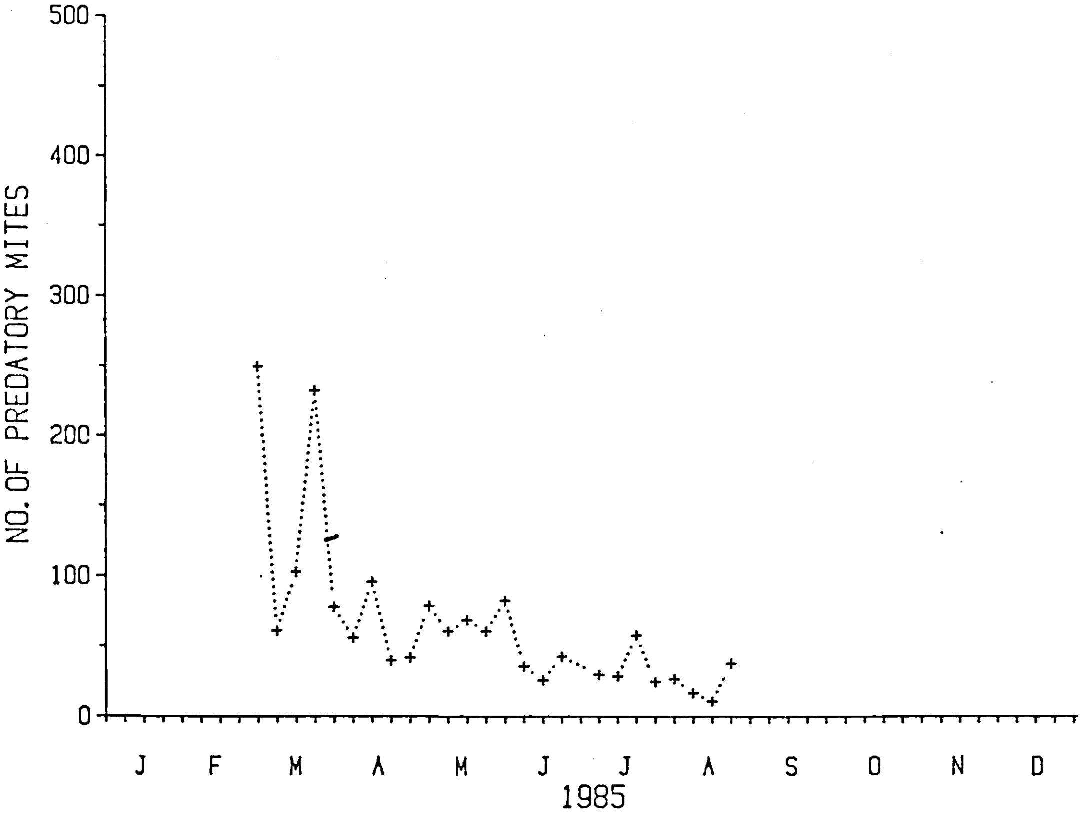
Graph 114. The abundance of staphylinids and <u>Agriotes</u> sp. in 1985.



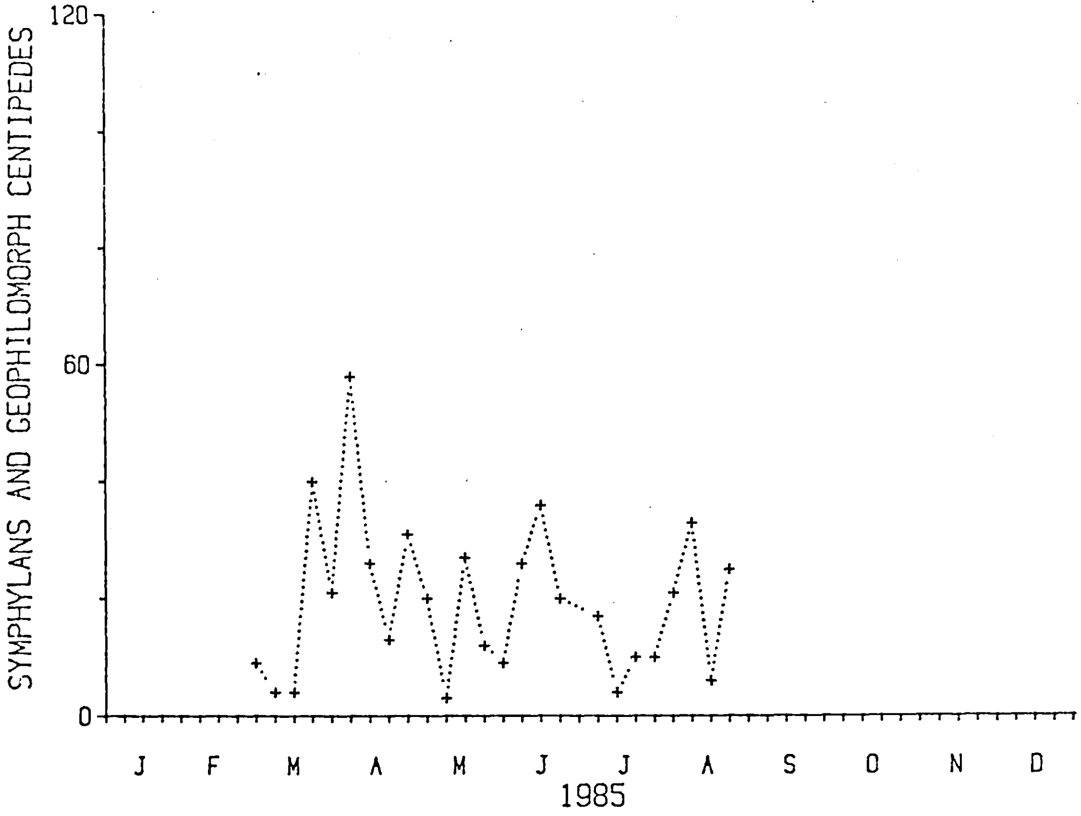
Graph 115. The abundance of soil collembola in 1985.



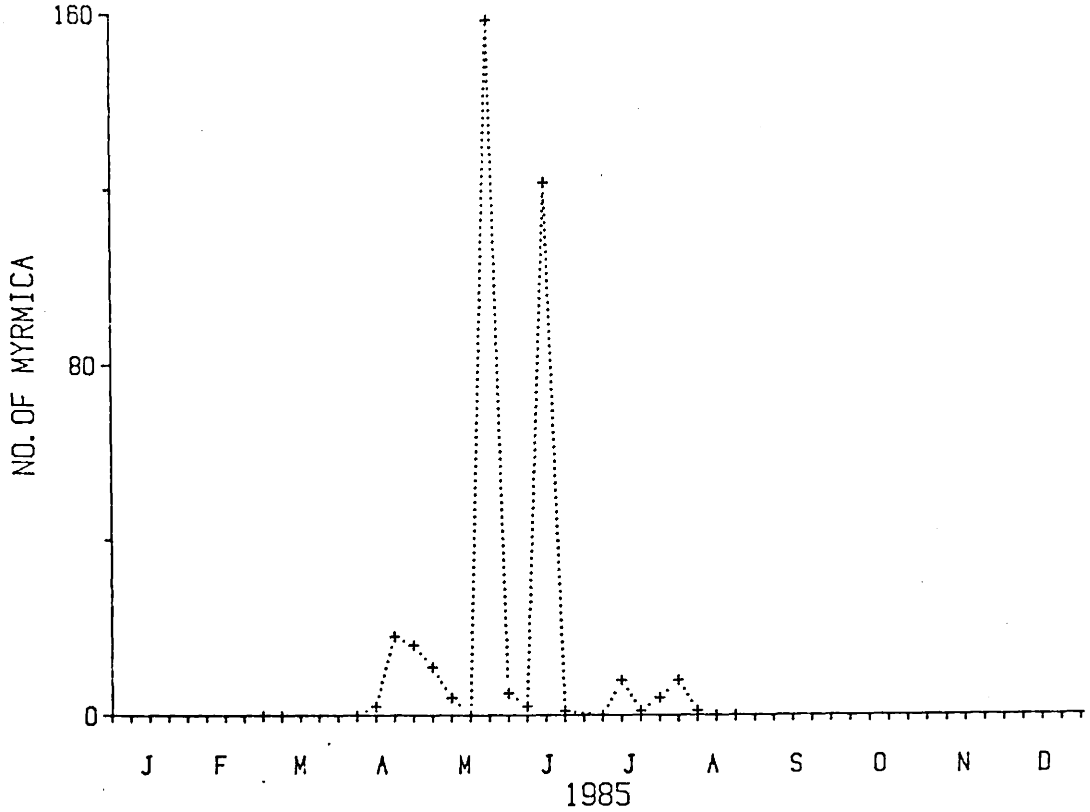
Graph 116. The abundance of phytophagus mites in 1985.



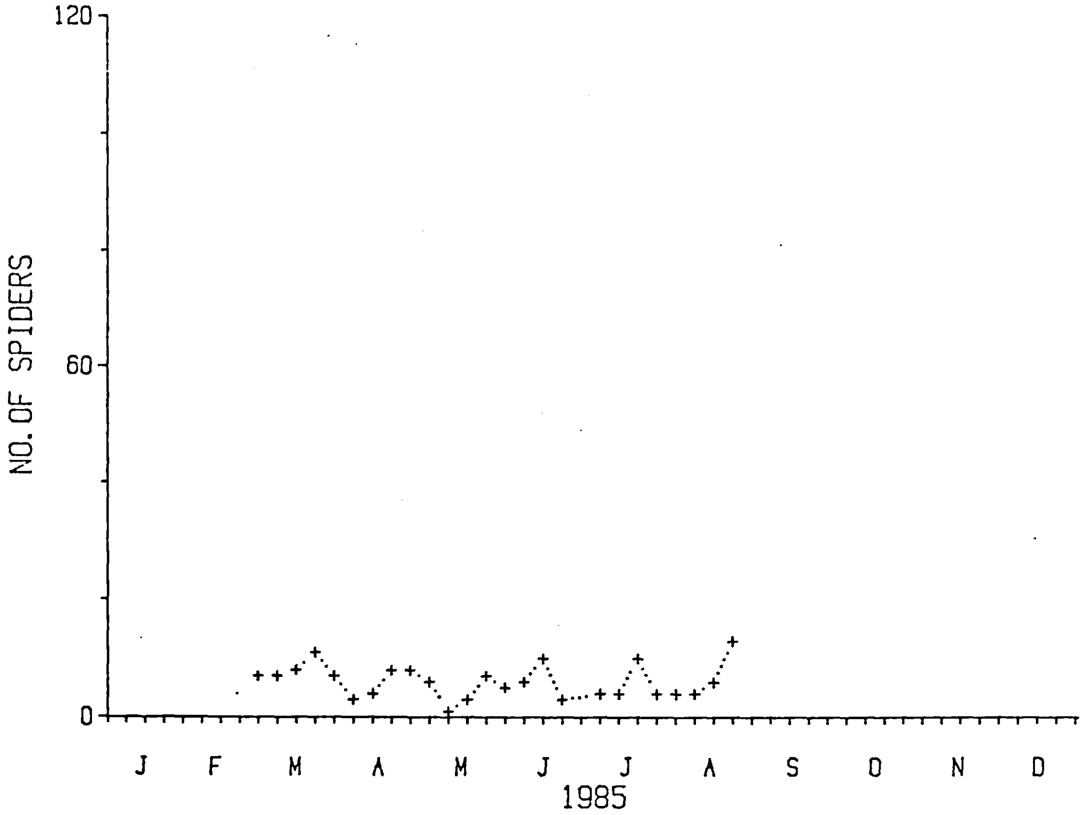
Graph 117. The abundance of predatory mites in 1985.



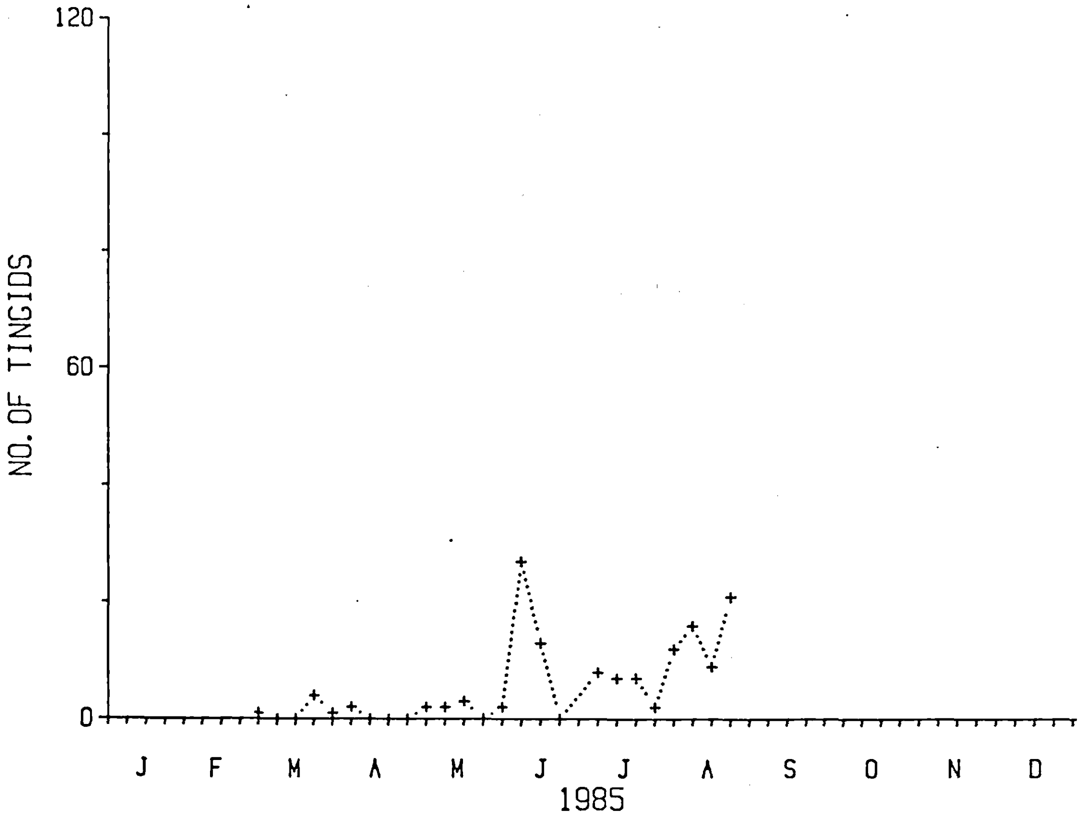
Graph 118. The abundance of symphilids and geophilomorph centipedes in 1985.



Graph 119. The abundance of Myrmica scabrinodis in 1985.



Graph 120. The abundance of spiders in 1985.



Graph 121. The abundance of Acalypta platychila in 1985.

APPENDIX E5

Monthly totals for ant, aphid and soil organism captures, 1983-1985.

(Tables 62-70)

Month	Number of samples	*Lasius flavus* workers	*Myrmica scabrinodes*	Biomass of larvae (g)	Biomass of pupae (g)	Biomass of alates (g)	Number of males	Number of females	Number of new workers
		Mean per nest							
January	36	171	1	0	0	0	0	0	0
February	48	110	0	0	0	0	0	0	0
March	36	410	2	0	0	0	0	0	0
April	48	1382	26	0.05	0	0	0	0	0
May	48	2178	1	0.07	0	0	0	0	0
June	60	989	23	0.04	0.04	0	0	0	0
July	48	729	0	0.01	0.15	0.06	93	7	33
August	48	688	2	0	0	0	8	0	0
September	60	427	9	0	0	0	1	0	0
October	48	385	0	0	0	0	0	0	0
November	60	179	0	0	0	0	0	0	0
December	48	172	0	0	0	0	0	0	0
Total	588	32701	292						
Mean per year		654	6						
Standard Error		201	6						
Maximum number per nest		4060	113	0.13	0.42	0.22	372	24	107

Table 62. The monthly abundance of Ants 1983

		Mean per nest							
Month	Number of samples	*Lasius flavus* workers	*Myrmica scabrinodes*	Biomass of larvae (g)	Biomass of pupae (g)	Biomass of alates (g)	Number of males	Number of females	Number of new workers
January									
February									
March									
April	12	878	0	0.001	0	0	0	0	0
May	60	1468	5	0.056	0	0	0	0	0
June	48	571	0	0.024	0.024	0.031	0	8	0
July	48	786	1	0.015	0.163	0.294	188	55	99
August	60	636	1	0	0.010	0.068	80	9	41
September	36	206	0	0	0	0.005	13	0	0
October	48	300	1	0	0	0	0	0	0
November	60	111	1	0	0	0	0	0	0
December	24	717	0	0	0	0	0	0	0
Total	396	20627	43						
Mean per year		625	1						
Standard Error		162	1						
Maximum number per nest		2032	19	0.090	0.118	0.744	381	183	49

Table 63. The monthly abundance of Ants 1984

Mean per nest

Month	Number of samples	Lasius flavus workers	Myrmica scabrinodes	Biomass of larvae (g)	Biomass of pupae (g)	Biomass of alates (g)	Number of males	Number of females	Number of new workers
January									
February	15	71	0	0	0	0	0	0	0
March	60	378	0	0	0	0	0	0	0
April	60	1318	9	0.023	0	0	0	0	0
May	75	1659	36	0.032	0.002	0	0	0	0
June	45	1766	42	0.083	0.105	0	0	0	0
July	75	2612	4	0.044	0.408	0.279	188	73	27
August	60	1817	0	0.010	0.0542	0.130	126	29	51
September									
October									
November									
December									
Total	390	40779	362						
Mean per year		1568	14						
Standard Error		344	15						
Maximum number per nest		3486	159	0.2082	0.858	0.904	489	253	108

Table 64. The monthly abundance of Ants 1985

Month	Number of samples	Mean number of Aphids per nest									
		Anoecia corni	Anoecia furcata	Baizongia pistaciae	Forda formicaria	Forda marginata	Geoica setulosa	Geoica utricularia	Tetraneura ulmi	Trama troglodytes	Aploneura lentisci
January	36		5	17	115.7		0.3	1	75	3.7	89
February	48		14.5	9	102.3		5	4.75	27	0.25	418.5
March	36		1	28	46.6			0.6	38	2.3	32.7
April	48		0.75	33.5	87	4.75	33.8	27.3	55.5	1.25	15
May	48	3.5		71.5	68.3	2.25	6.25	56.0	135		74
June	60	23.6	16.25	4.8	36.8		8.4	8.6	71.6	0.4	0.6
July	48	18.5		6.8	12.5			0.8	37.3		
August	48	38.5		0.8	6	0.8	1.5	1	28.3	0.5	0.25
September	60	39.8		9.6	3.2	1	1.4	2.8	34.4	2	2.6
October	48	21.0	8.5	0.5		1	1.5	1.3	43.8	3.8	3
November	60	4.4	64.8		25.4	4.2	4	3.4	170.6	3.6	53
December	48		20.8	0.3	146.8	0.3	17	8.3	39	8.0	32.3
Total	588	647	571	788	2819	62	343	502	3274	112	3124
Mean per year		12.4	11.0	15.2	54.2	1.2	6.6	9.7	63	2.2	60
Standard Error		1.3	1.5	1.7	4.1	0.1	0.8	1.4	3.8	0.2	9.7
Maximum number per nest		96	154	260	482	17	97	122	332	30	1230

Table 65. The monthly abundance of root aphids 1983

		Mean number of Aphids per nest									
Month	Number of samples	*Anoecia corni*	*Anoecia furcata*	*Baizongia pistaciae*	*Forda formicaria*	*Forda marginata*	*Geoica setulosa*	*Geoica utricularia*	*Tetraneura ulmi*	*Trama troglodytes*	*Aploneura lentisci*
January											
February											
March											
April	12	0		0	56	1	3	0	93	0	0
May	60	3		68	113	2	32	28	16	0	1
June	48	18		1	23	0	2	3	59	0	56
July	48	9		7	1	0	1	4	3	0	5
August	60	11		0	0	0	0	0	3	0	6
September	36	6		0	0	0	1	0	0	2	1
October	48	26		3	0	8	0	0	10	2	1
November	60	23		4	18	7	0	2	8	2	34
December	24	34		20	10	0	7	29	13	17	16
Total		480		445	827	77	192	237	543	55	487
Mean per nest		15		13.5	25	2	6	7	16	2	15
Standard Error		7		11	18	2	5	4	11.6	2	11
Maximum number per nest		74		142	258	33	55	57	169	33	126

Table 66. The monthly abundance of root aphids 1984

Month	Number of samples	Mean number of Aphids per nest									
		Anoecia corni	*Anoecia furcata*	*Baizongia pistaciae*	*Forda formicaria*	*Forda marginata*	*Geoica setulosa*	*Geoica utricularia*	*Tetraneura ulmi*	*Trama troglodytes*	*Aploneura lentisci*
January											
February	15	0	0	39	15	0	0	0	1	6	0
March	60	0	1	23	119	0	7	2	4	5	0
April	60	0	5	24	59	0	57	80	3	1	0
May	75	9	2	21	57	0	19	10	18	1	5
June	45	10	0	13	6	0	0	2	6	0	0
July	75	16	0	4	2	0	2	1	20	0	0
August	60	44	12	9	1	0	0	1	16	1	0
September											
October											
November											
December											
Total	390	333	77	423	1037	0	356	394	406	44	26
Mean per nest		13	3	16	40	0	14	15	16	2	1
Standard Error		8	3	7	31	0	16	23	10	1	1
Maximum number per nest		87	31	59	340	0	205	311	102	14	17

Table 67. The monthly abundance of root aphids 1985

Mean number of Soil Organisms per nest

Month	Number of samples	Hymenoptera *Lasius flavus* workers	Coleoptera Staphylinids + *Agriotes* sp.	Collembola	Hemiptera			Others	Spiders	Acarina		Myriapoda Symphilids + Geophilomorphs
					Aphids	Coccids	*Acalypta platychila*			Predatory	Phytophagus	
January	36	171	70	846	307	6	0	0	9	205	638	26
February	48	110	64	467	581	5	1	0	6	165	383	31
March	36	410	81	432	112	29	5	1	11	132	483	32
April	48	1382	45	354	259	7	1	0	8	77	305	24
May	48	2178	29	290	417	1	1	0	3	67	200	20
June	60	989	29	253	170	8	3	1	2	74	180	19
July	48	729	12	187	76	0	5	1	3	53	176	4
August	48	688	16	350	78	3	4	1	7	51	175	6
September	60	427	27	402	97	2	2	3	13	31	169	12
October	48	385	16	265	84	1	4	1	10	45	218	14
November	60	179	24	433	335	2	6	4	12	57	343	7
December	48	172	39	320	273	9	5	12	18	59	304	11
Total	588	32701	1765	18441	11500	295	158	102	417	4017	14345	835
Mean per nest		654	35	369	229	6	3	2	8	80	287	17
Standard Error		201	7	24	74	2	1	1	1	16	44	4
Maximum number per nest		4060	118	909	1342	109	24	32	23	279	745	46

Table 68. The monthly abundance of Soil Organisms 1983

Month	Number of samples	Mean number of Soil Organisms per nest										
		Hymenoptera	Coleoptera	Collembola	Hemiptera					Acarina		Myriapoda
		Lasius flavus workers	Staphylinids + *Agriotes* sp.		Aphids	Coccids	*Acalypta platychila*	Others	Spiders	Predatory	Phytophagus	Symphilids + Geophilomorphs
January												
February												
March												
April	12	878	21	201	152	2	0	10	7	44	140	36
May	60	1468	15	203	262	1	2	6	4	48	163	23
June	48	571	15	165	162	22	1	3	3	36	198	9
July	48	786	9	64	29	2	2	1	4	17	148	2
August	60	636	8	75	21	5	4	0	5	19	113	4
September	36	206	10	367	9	12	0	0	12	24	356	13
October	48	300	21	408	42	8	0	0	6	65	387	16
November	60	111	34	534	91	4	1	0	7	104	158	17
December	24	717	35	772	143	2	0	0	7	51	181	6
Total	396	20627	586	9442	3264	208	41	55	181	1547	6673	415
Mean per nest		625	18	286	99	6	1	2	5	47	202	13
Standard Error		162	4	77	38	5	1	1	1	13	42	4
Maximum number per nest		2032	45	790	268	87	15	12	16	159	548	57

Table 69. The monthly abundance of Soil Organisms 1984

Mean number of Soil Organisms per nest

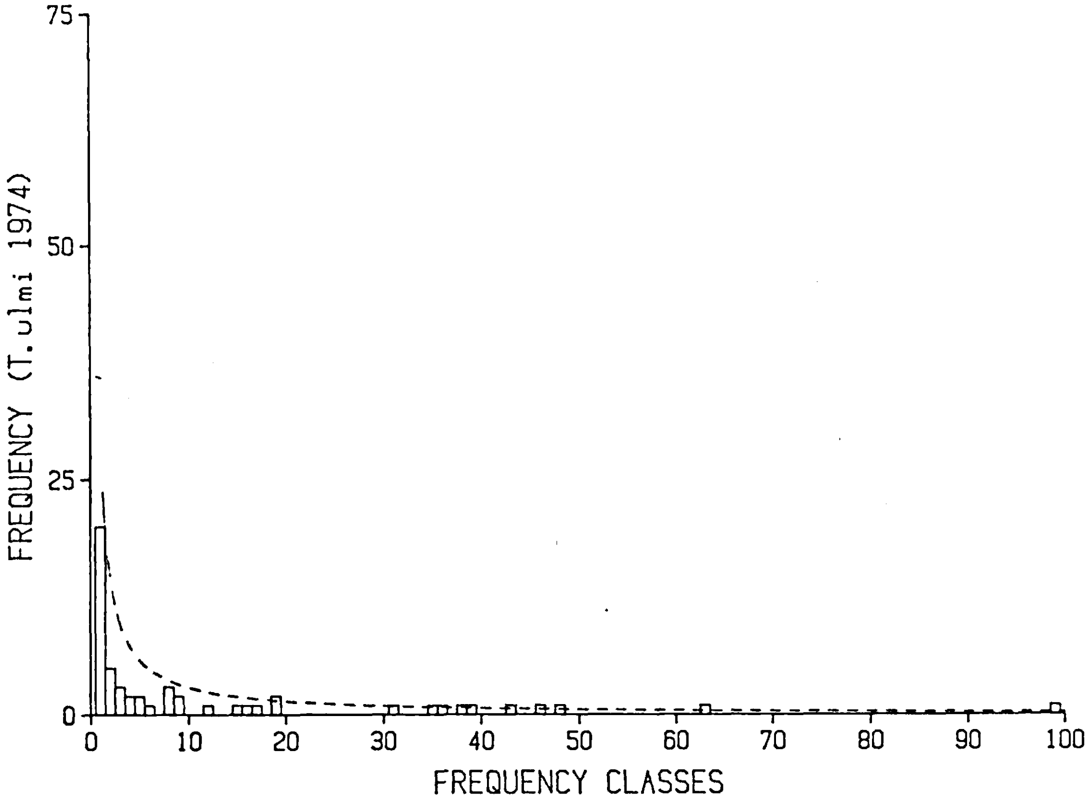
Month	Number of samples	Hymenoptera	Coleoptera	Collembola	Hemiptera			Others	Spiders	Acarina		Myriapoda
		Lasius flavus workers	Staphylinids + *Agriotes* sp.		Aphids	Coccids	*Acalypta platychila*			Predatory	Phytophagus	Symphilids + Geophilomorphs
January												
February	15	71	34	388	61	4	1	0	7	250	149	9
March	60	378	34	637	159	12	1	2	8	119	262	17
April	60	1318	22	398	256	1	1	2	6	59	120	32
May	75	1659	26	533	141	5	2	3	4	71	222	14
June	45	1766	27	404	39	20	13	2	6	35	131	27
July	75	2612	20	274	44	14	7	5	5	34	73	12
August	60	1817	21	359	82	8	16	3	10	22	64	20
September												
October												
November												
December												
Total	390	40779	652	11206	3095	222	156	54	169	1674	3804	501
Mean per nest		1568	25	431	119	9	6	2	7	64	146	19
Standard Error		344	3	61	29	6	3	1	1	11	38	5
Maximum number per nest		3486	41	844	633	59	21	7	16	250	398	58

Table 70. The monthly abundance of Soil Organisms 1985

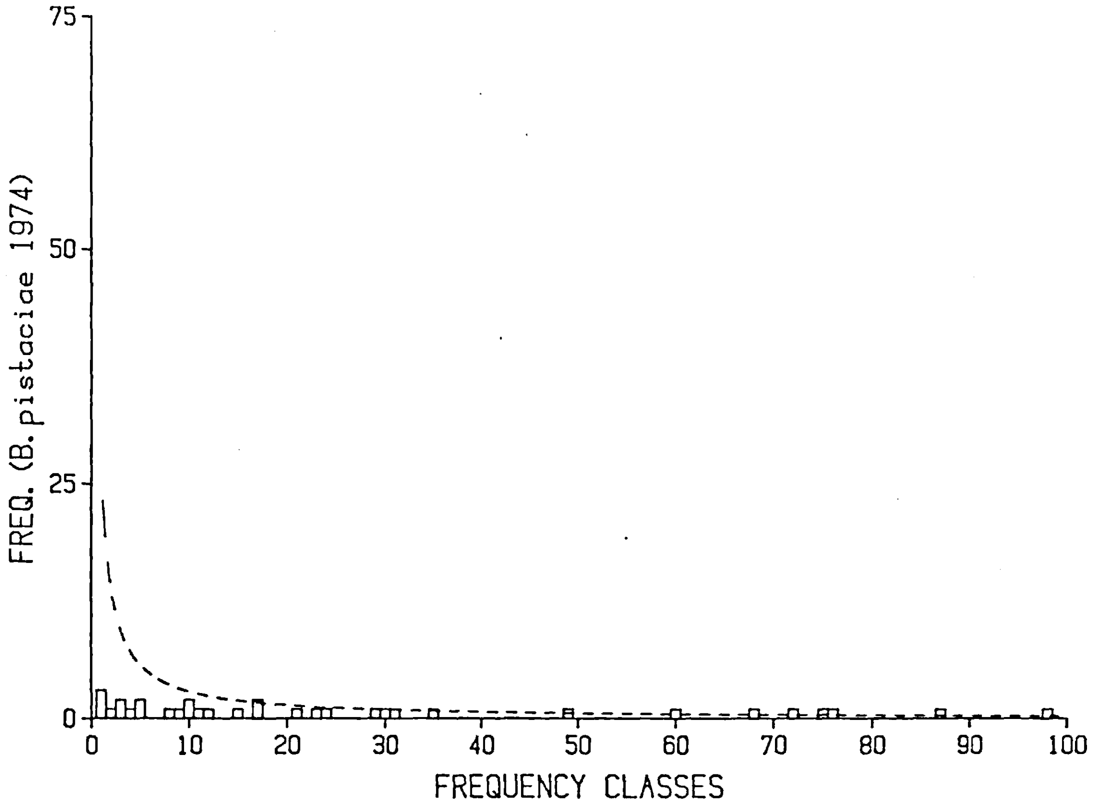
APPENDIX F

Re-analysis of results from Pontin 1974

(Graphs 122-123)



Graph 122. The frequency distribution of <u>Tetraneura ulmi</u> 1974.



Graph 123. The frequency distribution of <u>Baizongia pistaciae</u> 1974.