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STUDIES ON *FORMICA LUGUBRIS* ZETTERSTEDT IN IRELAND (HYMENOPTERA, FORMICIDAE)

A thesis

presented to the National University of Ireland

for the degree of

DOCTOR OF PHILOSOPHY

by JOHN A.G. BREEN.

FEBRUARY 1976

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Studies on Formica lugubris Zetterstedt in Ireland

(Hymenoptera:Formicidae)

Presented by: John A.G. Breen, February 1976.

Degree: Ph.D.

ABSTRACT

This thesis is based on studies of Formica lugubris from 1972-1975. While this species' range is diminishing in Ireland, the nests are quite common in the State plantations of South Tipperary. It is not certain that the species is indigenous.

Above-ground activity occurs from late-February to the end of October; foraging begins in April. Two territorial "spring-battles" between neighbouring nests are described. Most active nests produced alatae of both sexes and flights were observed on successive June mornings above 17.5°C air temperature. Both polygyny and polycaly seem to be rare.

Where the nests occur commonly, the recorded densities are similar to those reported from the continent. Most nests persisted at the same site since 1973. The nest-sites are described by recording an array of nest, soil, tree, vegetation and location variables at each site. Pinus sylvestris is the most important overhead tree. Nests seem to be the same age as their surrounding plantation and reach a maximum of c. 30 years. Nearest-neighbour analysis suggests the sites are overdispersed.

Forager route-fidelity was studied and long-term absence from the route, anaesthetization and "removal" of an aphid tree had little effect on this fidelity. There were no identifiable groups of workers specifically honeydew or prey-carriers. Size-duty relationships of workers participating in adult transport are described.

Foraging rhythms were studied on representative days: the numbers foraging were linearly related to temperature. Route-traffic passed randomly and an average foraging trip lasted c. four hours. Annual food intake to a nest with 25 000 foragers was estimated at approximately 75 kg honeydew and 2 million prey-items.

Forager-numbers and colony-size were estimated using the capture-mark-recapture method: paint marking was used for the forager estimate and an interval radiophosphorus mark, detected by autoradiography, was used for the colony-size estimate.

The aphids attended by lugubris and the nest myrmecophiles are recorded.

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1.0 INTRODUCTION.

This thesis contains the results of three year's (1973 to 1975) observations on Formica lugubris Zetterstedt in the south of Ireland. The observations encompass a wide spectrum, since no previous long-term study has been made on this species in Ireland.

1.1 NOTE ON THE SYSTEMATIC POSITION OF WOOD ANTS.

Prior to 1955, a total of four species in Britain, two of which occur in Ireland, were confused as the single species "Formica rufa L.", and numerous varieties and sub-specific categories were recognised (cf. Donisthorpe 1927a, p.305). Yarrow (1954, 1955) provided the first acceptable attempt at solving the nomenclatural controversy. He showed that two species of the "Formica rufa-group" occurred in Ireland viz. lugubris, the most widespread in the south of Ireland, and aquilonia Yarrow at a single site in county Armagh. Both these species occur in the north of Britain and two other species, rufa L. s.s. and pratensis Retzius (nigricans Emery sensu Yarrow 1955) occur in the south of England.

The confusion on the European mainland was even greater, where subsequent work (Lange 1958; Betrem 1960) has shown that, in addition to the four British species, the following also occur: uralensis Ruszky, truncorum Fab., polyctena Förster, and nigricans Emery (nec Yarrow 1955). This nomenclature follows Collingwood (1971). An indication that this arrangement of the species in the Formica rufa-group is not entirely satisfactory may be deduced from the conclusions of Ronchetti and Vendegna (1969) working in Italy: these authors "found populations

with intermediate morphological characters, definable as lugubris aut aquilonia and as rufa aut polyctena" and suggested a need for " a revision of the group systematics".

In this thesis the following convention, first used by Sudd (1967,p.80), will be used: whenever there is doubt as to which species earlier work refers, the term wood ant will be used to denote "member of the Formica rufa-group". When quoting work on the closely-related American species of Formica, the nomenclature used will be that of the cited author.

Gösswald et al. (1965) have reviewed the European distribution of wood ants and their distribution map of lugubris is given in figure 1.1 . The species shows a discontinuous distribution: it occurs in the Alps and Pyrenees, in Scandinavia and in Britain and Ireland.

1.2 PREVIOUS WORK.

Previous work on lugubris in Ireland was mainly distributional and will be referred to later. The only major contributions to Irish ant studies are those of O'Rourke (1950a,and references), which were not primarily concerned with lugubris. O'Rourke (1952) provided an ecological classification of ant communities in Ireland, and considered lugubris, with Stenamma westwoodii Westwood as stenotypic species occurring only under conditions of high soil humidity. More recently Collingwood (1959, 1965) has recorded myrmecophiles from both lugubris and aquilonia nests.

In Britain, where the distribution of lugubris is well-documented (Collingwood and Barrett 1964), the species has not been the subject of major long-term study. However Hughes (1975) has recently provided an account of some habitat preferences of lugubris and rufa in Wales. Holt's (1955) major contribution on traffic dynamics was based on aquilonia (Dr I.H.H. Yarrow, in litt.).

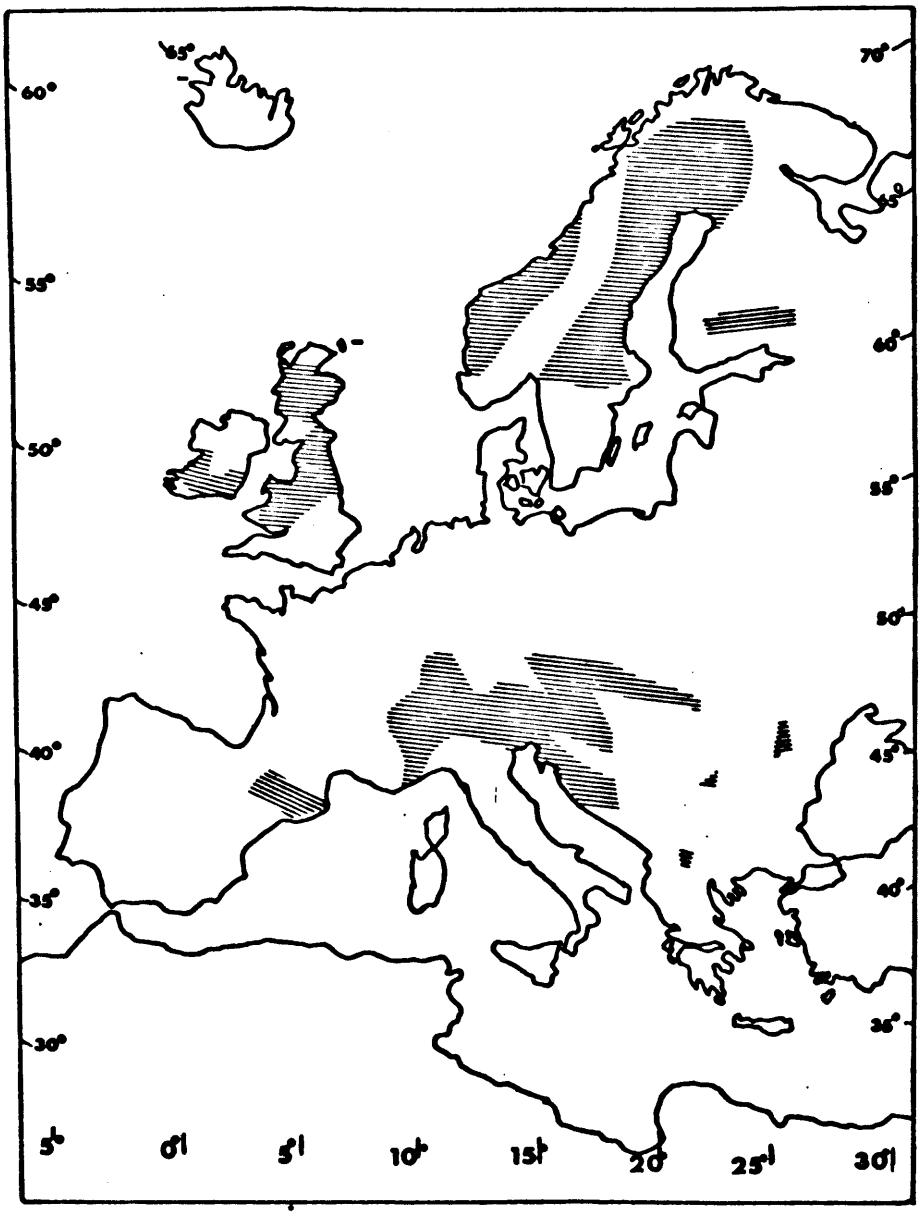


Figure 1.1 The European distribution of lugubris (redrawn from Gösswald et al. 1965).

project. Chapter 2 gives an account of the present and past distribution of lugubris in Ireland, contains an introduction to the study area, and reports the following aspects of lugubris biology in Ireland: annual cycles of activity, occurrence of alatae, flight behaviour and colony-foundation. Chapter 3 records the nest densities observed and their persistence from year to year. The nest site environment is then considered using an array of vegetation, soil, location and forestry-management variables. This chapter also contains information on the effect of shade on the nest environment, and a nearest-neighbour analysis of the nests in one compartment. Chapter 4 gives data on forager route and task fidelity, the results of four days' observations on foraging activity during the daylight hours and the length of foraging times. Estimates are provided of the total colony- and total forager-population in five colonies. Chapter 5 records the myrmecophiles present in the nests, and the aphids which were attended by lugubris.

1.5 TERMS AND ABBREVIATIONS.

The basic unit of social insects is the colony, and this term will be used here, after Brian et al.(1965), to denote "a group that resists the entry of others of the same species". This group resides in one or more nests or mounds (see Pisarski 1972).

Most of the observations described in the subsequent chapters were made in the woods of the state forests. These woods are administered by the Forest and Wildlife Service of the Department of Lands (and will be referred to as Forestry here), and it is necessary to explain some of their terms.

Each woodland unit administered by a Forester-in-charge is termed a "forest", and this may include any number of woods, though two or three woods per forest is the usual. The names of the forests seem to be somewhat arbitrary, however, the names of the woods are usually found on

the 1:10 560 ("six inch") Ordnance Survey maps. For example, Bansha Forest comprises Bansha Wood and Moore's Wood. The woods are laid out in compartments (c. 16 ha) which are enclosed by four 5 m-wide clear spaces, called "ride-lines". Each compartment is allocated a number. Recently there has been a changeover, not yet completed, from an old to a new system of numbering compartments. All the numbers used here follow the "new" system. Details of the tree species and progress of growth in each compartment were obtained from the "1968 Forest Inventory" (unpublished, but described by O'Flanagan 1973), and more recent details were obtained by enquiry to the individual foresters.

The three main study woods are designated as follows: KC = Kilcoran Wood, MW = Moore's Wood, and GG = Glengarra Wood. Nests in these woods will be referred to as follows: the wood abbreviation, followed by the compartment number, followed by an arbitrary alphabetic number; e.g. KC-440a refers to nest a in compartment 440, in Kilcoran Wood.

The tree species which will be frequently mentioned are listed, with their common name, in table 1.1, and abbreviations are used for three of these.

Where possible the units used in this thesis follow the Système Internationale (SI) and table 1.2 gives a list of general and statistical abbreviations used.

Time is reported throughout in Irish summer time, which is equivalent to central European standard time.

1.6 GENERAL METHODS

The methods used in this study will be described at the appropriate place in the text. The following methods are more general in nature and apply throughout.

(a) Temperature measurement:

All field measurements of temperature were made using thermistor

Table 1.1 The tree species in Forestry plantations, with their common name, and abbreviation, if used.

TREE SPECIES	COMMON NAME	ABBREVIATION
Pinus sylvestris	Scots pine	SP
P. contorta	lodgepole pine	PC
Larix decidua	European larch	-
L. kaempferi	Japanese larch	-
Picea sitchensis	Sitka spruce	SS
P. abies	Norway spruce	-
Abies procera	noble fir	-
Pseudotsuga menziesii	Douglas fir	-

Table 1.2 General and statistical abbreviations used in the thesis.

GENERAL		STATISTICAL	
^{o}C	degree Celsius	>	greater than
g	gram	<	less than
s	second	S.D.	standard deviation
min	minute	N.S.	not significant
Ci	Curie	P	probability
ct./min	counts per min	t	Student's t
c.	*circa*	r	correlation coefficient
		d.f.	degrees of freedom
		χ^2	chi-squared
		n	number of observations

thermometers supplied by Grant Instruments (Toft, Cambridge). The same thermistor probes (type Bd) were used on either of two instruments: a manual six-point model C, and an automatic nine-point model D, which records temperatures at 15-minute intervals. The manufacturers claim an accuracy of ± 2 percent. Most of the observations consisted of an air- (probe hand-held or suspended 1.25 m above the ground) and ground-temperature (probe lying on ground surface). In both cases the sensing element was shielded from radiation by aluminium cooking-foil (after Wellington 1950). Recently Peacock (1975), using an identical temperature recorder, recommended using hemicylinders of white-painted copper gauze as shields (after Long 1953). A day-long observation showed that both methods gave very similar results; however, the latter method was used in the observations on the effect of temperature on lugubris running speed (4.4).

(b) Confining ants:

Brian (1971) recommended the use of FLUON for confining ants in plastic containers. The method is due to Radinovsky and Krantz (1962), and has been successfully used throughout this study to confine lugubris workers in domestic plastic basins. FLUON is available from Imperial Chemical Industries (Welwyn Garden, England). A single coat of FLUON applied with a small paint-brush sufficed, and it dried at room conditions in five to 10 minutes. The following conditions allowed ants to escape from these basins: mist or rain drops falling on the coating, scratches - especially those caused by stacking a number of basins together, paint-spray when the basins were used to hold ants for mass-marking using aerosol paint.

A second use for FLUON was devised for collecting a number of ants from the same nest into a glass phial (25 x 85 mm): once c. 10 have been collected, it becomes difficult to introduce more without

allowing the others escape. A 30 mm band of FLUON around the neck of the phial allows a large number of ants to be dropped into the container.

(c) Maps.

The maps of the study woods are based on those used by the Forestry Service, which are 1:10 560 Irish Ordnance Survey maps with details of the woods drawn in. The maps included in this thesis are intended to be used in conjunction with either Forestry or 1:10 560 O.S. maps.

Figure 3.7 and figure 4.25 are based on large scale maps produced with the aid of a self-reducing tachymeter. All other maps were produced using a tape-measure and pocket compass. The following symbols have been used in maps of route systems throughout the thesis to denote these tree species: SS (△), SP (○). The symbol is blacked in if the tree is an aphid tree. While an attempt has been made to show all aphid trees in the area mapped, non-aphid trees are not always included.

(d) Statistical treatment.

Student's t-tests, correlation coefficients and linear regressions were calculated using an Olivetti Programma I desk computer, and values of probability (P) read from standard tables (Fisher and Yates 1963). The survey data in chapter 3 was analysed using the Statistical Package for the Social Sciences (S P S S)(Nie et al. 1970). Other calculations were made using desk calculators.

When used in 2x2 contingency tables, χ^2 has been calculated without applying Yates' correction for continuity. This procedure follows the recommendation of a number of recent authors (Grizzle 1967; Conover 1971, p. 146).

Statistical abbreviations used in the thesis are included in table 1.2.

2.0 IRISH DISTRIBUTION, THE STUDY AREA, AND MISCELLANEOUS OBSERVATIONS.

In this chapter, an account is given of the distribution of lugubris in Ireland, and this is discussed. The woods which comprise the study area are then introduced. A number of biological observations on lugubris are reported briefly.

2.1 IRISH DISTRIBUTION.

The first Irish wood ant record is in A.H. Haliday's MS Catalogue of Irish Insects which was "compiled before the middle of the last century" (Stelfox 1927), and is now housed in the National Museum, Dublin. The relevant part of the MS is reproduced in plate 1. Since then, Yarrow (1955) has examined all the available specimens of Irish wood ants, and identified all, except those from Churchill, county Armagh, as lugubris. The Armagh specimens were aquilonia.

The most complete lists of Irish wood ant localities are in Stelfox (1927) and O'Rourke (1950a). Collingwood (1958a, 1965) developed a theme of extinction of lugubris in Ireland - "This ant appears to have totally disappeared from Kerry having last been seen by Mr E.F. Bullock in 1933 near the Upper Lake, Killarney. I have also watched it becoming extinct in a wood in the Glen of Aherlow, Tipperary" (Collingwood 1965).

As part of this study, all the recorded Irish localities were visited and searched for lugubris nests, and the local foresters were contacted. The following account is complete for all the localities mentioned, except, perhaps, for the comments on Wicklow and Wexford, where field-work was confined to three days but all the local foresters were contacted. The distribution account follows the Irish vice-county recording system (an up-to-date vice-county map is given in Scannell and Synnott 1972), and

an Irish Grid 10 km-square map has been compiled. Appendix I lists all the specimens of lugubris from Ireland in the National Museum, Dublin (the Museum), and gives the data-label information.

2.1.1 PRESENT DISTRIBUTION OF LUGUBRIS IN IRELAND.

South Kerry:

Clear's record from "Rossbehy" in the Haliday MS may refer to the nearby woods around Caragh Lake. No nests are known from Rossbeigh Wood. Bouskell (1905) found a nest of the "large wood ant" at Caragh Lake, though no nests are now known from any of the woods in the district. Stelfox (1927) gave "Parknasilla and Valentia" as localities, and cited Saunders (1902). The latter paper did not record wood ants from these localities, but does contain a record of "F. fusca" from "Parknasilla and Valentia", and it seems likely that Stelfox's record should appear under this species. There are no Museum specimens from South Kerry.

North Kerry:

There are Museum specimens collected in Killarney by Halbert in 1905, and published records from Cromaglaun and Long Range, Killarney (Cuthbert 1898; J.N.H(albert) 1908), and nests were "reported to be in existence"by O'Rourke (1950a). Collingwood (1958a) did not find any nests in Kerry.

Three nests are now known from Killarney: two occur in oak at Glena near the Eagle's Nest (discovered by Mr J. Maguire in 1970), and on Cromaglaun Mountain (found in 1973, J.B.), and a third nest is in forestry plantation near Ladies' View (discovered in 1973 by Mr P.J. Bruton). It is evident from the large number of contacts made with people working in these woods, that lugubris is not now common in Killarney.

Waterford:

Nests of lugubris were recorded from "a wooded glen. . . near Clonmel, about two miles south of the town" by Delap (1896). There are specimens

collected in 1927 in Russelstown Wood, in the Museum, and the nests were still there in 1932. No colonies are now known in this wood. Although a number of foresters from other forests were contacted, no lugubris localities are now known within county Waterford.

Wexford:

Moffat (1896) recorded nests from oak woods in Killoughrum Forest, and in nearby Ballyhyland Wood; his specimens are in the Museum. Killoughrum Forest is privately owned and now less than 28 ha in extent. The present owners have never seen wood ant nests there, nor were any nests discovered in Ballyhyland Wood by me.

South Galway:

The first record from this vice-county is due to J.N.H(albert)(1908) who recorded the nests from "close-by Woodford". Specimens from Woodford are in the Museum, collected there in 1901 (Halbert) and 1922 (Phillips). There were "four or five" nests there around 1940 (Mr J. Egan, retired forester, personal communication), and records from O'Rourke (1950a) and Collingwood (1958a, 1965) show a continuity of nests at Woodford. Four nests are now known there, all in a small area of two adjoining woods, Derrycrag (three nests) and Derrygill (one nest), just south of Woodford.

Wicklow:

Recorded from near Clara and Annamoe in the Haliday MS and Stelfox (1924, 1927) reported nests from the Devils Glen. All these sites were searched unsuccessfully, and the foresters and land-owners have not seen any nests in these woods. The most recent Museum specimens are dated 1929.

A nest introduced to Lacken Wood from Moore's Wood (Bansha Forest) by O'Flanagan (1967) was presumably queenless, and has disappeared (Mr L.P. O'Flanagan, personal communication).

Limerick:

Two nests were reported by O'Flanagan and Moloney (1973) and another small nest was found since. All three are just inside the county boundary in Galtee Wood. A local forester remembers seeing nests in this wood around 1946. No nests were found by me in nearby Mahoney's or Cooper's Woods.

South Tipperary (see Map 1 in the map pocket)

The first record for South Tipperary is from Ballinacourty Wood (O'Rourke 1950a). Although Collingwood (1965) reported that all nests had disappeared from this wood, Forestry workers remember nests there until 1970, but none have been seen since. This leaves no known nests in any of the woods on Slievenamuck.

The woods on the Galteymore range contain the greatest number of lugubris nests in Ireland. The nests in two of these woods have been mapped by students from this Department, employed on bursaries from the Forestry and Wildlife Service. The map produced in each census has been updated and included in the map pocket. Considered clockwise from the woods on the north-facing slopes, the following numbers of lugubris nests are known in each wood:

Rossbog Wood: one nest; this wood has not been searched fully, but it probably contains a small number of nests.

Moore's Wood: 43 nests; the nests were mapped by J. Symons, K. Collins, and T. O'Grady during summer 1971. Their map is quite complete, and there were only a few additions since. See map 2.

Ballydavid Wood: Local residents remember nests in this wood about 50 years ago, but none have been seen in recent years.

Kilmoyler Forest: No reports were received of any nests in any of the woods in this Forest, other than Ballydavid (see above).

Cahir Forest: Kilcoran Wood, part of this forest, contains the largest number (93) of nests in this forest, though they become scarce as one progresses eastwards towards Cahir. The nests in part of Kilcoran Wood (west of the main stream flowing through the wood) were mapped during summer 1973 by P. Ahern. Many nests have since been added to his map, and Map 3 is now considered fairly complete. Much nest habitat was destroyed during the study period by fire (155 ha during 1975) and bulldozing, but this wood still maintains the largest number of lugubris nests in Ireland.

Boulakennedy Wood: Three nests.

Glengarra Wood: No formal census has been made in this wood, but Map 4 has been compiled with the help of the forester-in-charge, M. MacGiollaCóda and Mr S. Burke. A small plot (3.3 ha) of privately owned woodland near GG-902 contains six nests. Total 47 nests.

Galtee Wood: Three nests.

Two woods on the north-facing slopes of the Knockmealdowns, Kilballyboy (Clogheen Forest) and Shanrahan (Ballyporeen Forest) contain about 15 nests between them.

This distribution data is summarized in a 10 km-square map in figure 2.1. It is evident that while the number of lugubris localities has fallen, the species is quite common in the woods of South Tipperary. Almost all of the known lugubris nests are located in state-owned woods - only two of the Killarney nests, and the six nests near Glengarra Wood are in privately-owned property. This should facilitate decision-making with a view to maintaining suitable lugubris nest habitat (see chapter 3).

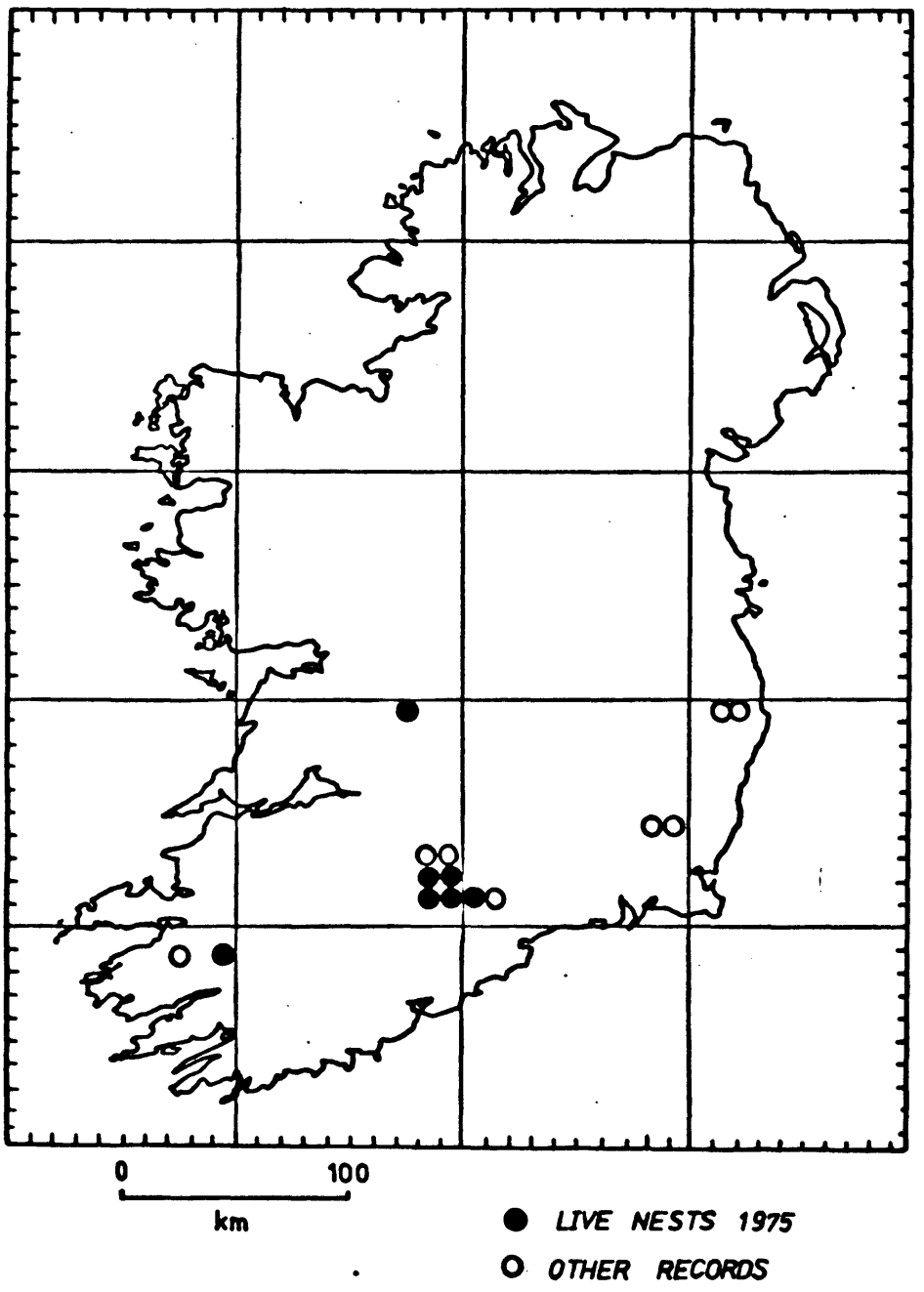


Figure 2.1 The recorded 10-km square distribution of Formica lugubris in Ireland.

2.1.2 A DISCUSSION OF THE DISTRIBUTION.

It is generally assumed in the literature that lugubris is indigenous to Ireland. Haliday considered it "certainly Irish" in his MS Catalogue. Moffat (1896) and Stelfox (1927) also considered the species to be indigenous. J.N.H(albert)(1908) considered Bouskell's (1905) records of myrmecophiles to be strong evidence in support of the claim that lugubris is native to Ireland. However, the alternative has not been discussed, and, while keeping a very open mind on this question, the following points can be made (these apply also to introductions from locality to locality within Ireland):

(1) It is very difficult to account for the scattered range of lugubris in Ireland. The demise of lugubris in Wicklow and Wexford can be ascribed to tree-felling (Moffat 1896 suggested this reason for the decline in Killoughrum Forest). If lugubris was common in native oak, then Moffat's (loc. cit.) maxim, "whatever is in Killoughrum is native", would seem to hold. However, there is no evidence to believe that lugubris was more common in the Killarney oak-woods at the beginning of the century than now. Only three nests were discovered during a week-long excursion of the Irish Field Club Union (Cuthbert 1898), and Bouskell (1905), who was familiar with Kerry woods, commented that the species is "rare in Ireland". It is interesting to note that lugubris has recently been reported in abundance in oak woods in Wales (Hughes 1975).

The Woodford nests seem to have maintained a steady, but low, number for as long as recorded. The Tipperary localities are undoubtedly the main centres of lugubris in Ireland, and will be considered further.

(2) The history of the woods in South Tipperary is of interest but no accurate information was traced prior to the Ordnance Survey maps. Most of the 1:10 560 maps now in use were revised in 1906. Present limits

of the woods largely coincide with the limits of that time. However, reference to the earlier (1840) edition of the O.S. maps gives the following information: On Slievenamuck, Ballinacourty Wood was about half its present size. On the Galteymore Range, the woods mentioned above occupied the following approximate areas:

Rossbog Wood:	16 ha
Moore's Wood:	absent
Kilcoran Wood:	50 ha
Boulakennedy Wood:	absent
Glengarra Wood:	200 ha
Galtee Wood:	as today.

This suggests that the greater part of these woods was planted after 1840, and is supported by the Forestry Inventory for Kilcoran Wood which gives 1858 as the planting date of "old wood". Thus, while there certainly were small woods present, which might have acted as a reservoir of lugubris nests, a large-scale appearance of nests in young plantation during the latter half of the last century must be accounted for. Dispersal of this species is limited by its colony founding behaviour (see 2.3.4) and, while long-distance dispersal by way of temporary social parasitism cannot be ruled out, my observations suggest that this rarely occurs.

(3) A possible motive for introducing lugubris is its use as pheasant food. Although Yarrow (1955) did not consider this likely, Satchell and Collingwood (1955) concluded that "the practice of introducing wood ants into pheasantries was widespread towards the end of last century". All the woods on the Galteymore range were demesne-type woods and gamekeepers were employed in all of them during the last century. Local people

remember that lugubris cocoons were fed to young pheasants. It is said locally that Pernettia mucronata, a berried shrub common in parts of Kilcoran Wood, was introduced as pheasant food and cover. Rhododendron ponticum was also planted as game cover (Dr E. McCracken, personal communication), and is now common in Glengarra and Kilballyboy Woods.

(4) J.N.H(albert)(1908) wrote "When recording it (lugubris) from Wexford, Mr Moffat gave some convincing arguments in favour of this being a native insect as had been suggested (by Johnson, 1896 recording wood ants, now known as aquilonia, in Armagh). The occurrence of these parasitic beetles in nests of the Wood Ant at Caragh Lake (records of Bouskell 1905) is undoubtedly favourable to the same view" (remarks in parentheses are mine). However many of the myrmecophilous beetles recorded from lugubris in Ireland have also been recorded from aquilonia in Armagh (see 5.2). This species was introduced there c. 1840 (Johnson 1896). Furthermore, all the species recorded belong to the group of myrmecophiles which are tolerated by ants (synoeketes) and some of these species are found away from ants' nests. No true guests (symphiles) have been recorded with Irish wood ants.

(5) The fostering of lachnids by lugubris (see 5.1) is more interesting, since one of the species recorded here, Lachnus roboris, is an aphid occurring on native oak. The Cinara spp. recorded are quite host specific, and must have been introduced with their respective host-plants, all of which, with the possible exception of SP are certain introductions. Forbes (1932, 1933) and McCracken (1970) concluded from their investigations that while SP may have survived as a native tree for long enough to have been artificially propagated the evidence suggests that it did not. If so, then the reservoir of Irish lugubris must have been native deciduous woodland with a continuity over the ages between native woods

and introduced conifer plantations. The absence of woods in 1840 at some of the present lugubris sites suggests that the species may have been introduced to these woods.

(6) In the absence of certain evidence, eitherway, it seems better to leave open the question of whether lugubris is native to Ireland.

2.2 THE STUDY AREA

Most of the observations were made in Moore's, Kilcoran, and Glengarra Woods during the three years, 1973 to 1975. Moore's Wood is situated on the north-facing slopes of the Galtee Mountains, and the other two woods are on the southern slopes (see Map 1). Although the first published record for lugubris in South Tipperary is relatively recent (O'Rourke 1950a), there is reason to believe that the species has been equally common in these woods, at least since 1900: a number of local people remember many nests in a wood, which was felled over 50 years ago, and situated between the old Ardane National School and the present-day Moore's Wood.

"One of the most striking characteristics of the Tipperary scene is the way in which the land forms alternate between the slate and sandstone hill-country and the intervening limestone vales" (Whittoe 1974, p.244). The study-woods are located on areas with underlying Old Red Sandstone. The soils are brown podzolics derived from glacial drift (Saale) (Finch 1971), and ironpan is often present, causing stunted growth of species (e.g. SP) whose roots do not penetrate the pan. This problem is now being overcome by deep ploughing prior to planting (Anon. 1972).

Figure 2.2 gives the weekly means of daily max-min dry-bulb temperatures (Stevenson screen) taken by Mr M. Grace at the Waterworks,

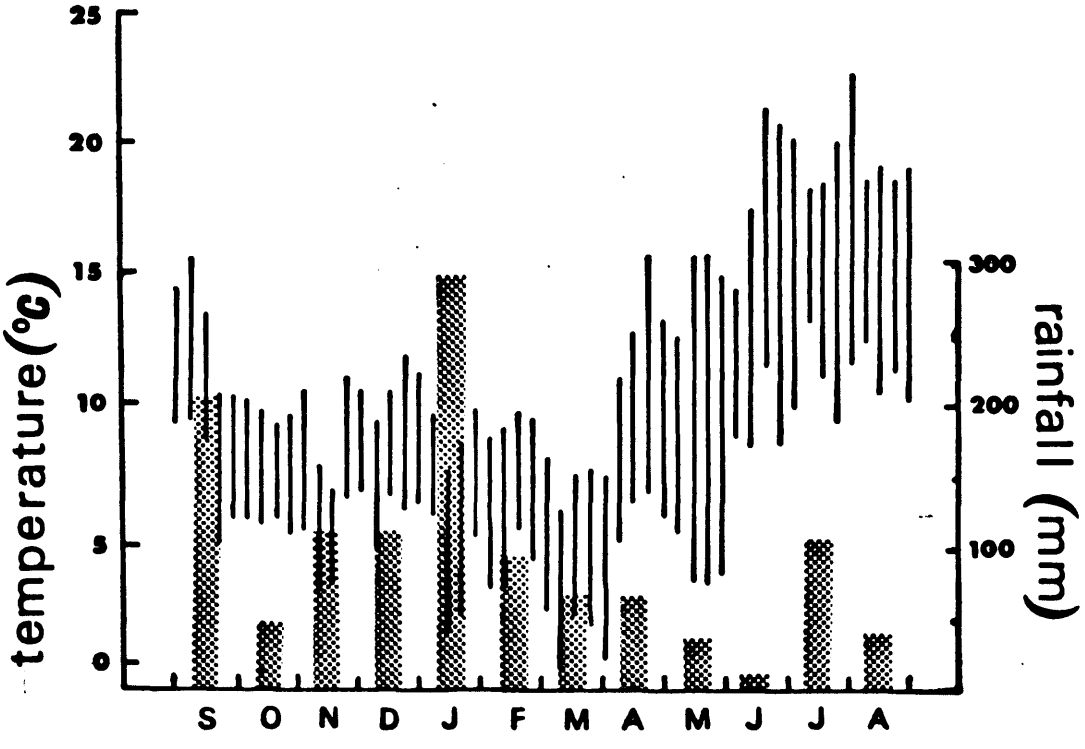


Figure 2.2 Weekly means of daily max-min dry bulb temperatures (Stevenson screen) at the Water-works, Moore's Wood, with total monthly rainfall values (histograms) for the same site; September 1974 to August 1975.

Moore's Wood from September 1974 to August 1975. Monthly rainfall data for the same site are also given.

The following ant species occur in Kilcoran Wood in addition to lugubris:

Myrmica ruginodis Nylander	Lasius niger (L.)
M. rubra (L.)	L. flavus (Fabricius)
M. scabrinodis Nylander	L. fuliginosus (Latreille)
M. sabuleti Meinert	Formica lemani Bondroit
Leptothorax acervorum (Fabricius)	

2.3 MISCELLANEOUS OBSERVATIONS.

These observations are reported briefly here, as the topics are not considered elsewhere in the text.

2.3.1 ANNUAL CYCLES OF ACTIVITY.

The earliest observed above-ground activity was on 26.II.1975. However, there is quite a variation between nests in the time of appearance of ants above ground: activity begins up to six weeks earlier in nests exposed to sunlight than in shaded nests. Workers re-appear above ground at most sites before the third week of March. During the next fortnight, the ants participate in the sunning-cluster behaviour characteristic of wood ants.(PLATE 1) A period of rebuilding the mound follows. Visiting of aphids does not commence until the latter end of April, though large quantities of honeydew are not available until the end of May. The last observed attendance of aphids (Cinara piceae) was on 15.XI.1974, though the end of October is probably a more average date.

The workers of a number of species of Formica develop swollen fat bodies during autumn (Kirchner 1964). Such worker lugubris have been

noted on the routes from the end of September. They have also been seen in the spring sunning-clusters, but workers with swollen abdomens are not present for very long in the spring. These observations are in accordance with Kirchner's study of the changes of the body food-reserves in worker polyctena.

2.3.2 INTER-NEST BATTLES.

Elton(1932) drew attention to the existence of territorial behaviour in wood ants (probably rufa s.s.) and described an attack which took place on 31.III.1929 in which one nest destroyed another. However, he considered that wood ant territories are normally maintained without hostility. The existence of territories without inter-nest hostility has also been reported in wood ants (Dobrzanska 1958), pratensis and uralensis (Stebaev and Reznikova 1972) and pratensis (Reznikova 1974).

Marikovsky (1962) described "savage battles" amongst neighbouring wood ant nests. DeBruyn and Mabelis (1972) studied inter-nest fighting, which they refer to as "spring battles", in polyctena. They suggested that the battles occur due to the increasing encounters between workers from neighbouring nests during the "exploratory phase (April/May)" of foraging. This suggestion seems to run counter to the ideas on fidelity to routes from year to year (see 4.2 and Rosengren 1971).

Two chance observations were made of "spring battles" in different years; both occurred at the same site. A sketch map of the area is given in figure 2.3. Two nests, A and B were located 70 m apart, and their territories were separated by a stream which dries out in summer (nest A = MW-256a; nest B = MW-256b). On 27.V.1973, dead ants were being transported towards each nest from a fighting area 0.04 m^2, located 19 m from nest A. On 1.VI.1973, "normal" foraging was in progress, and the routes from both nests did not approach the fighting area.

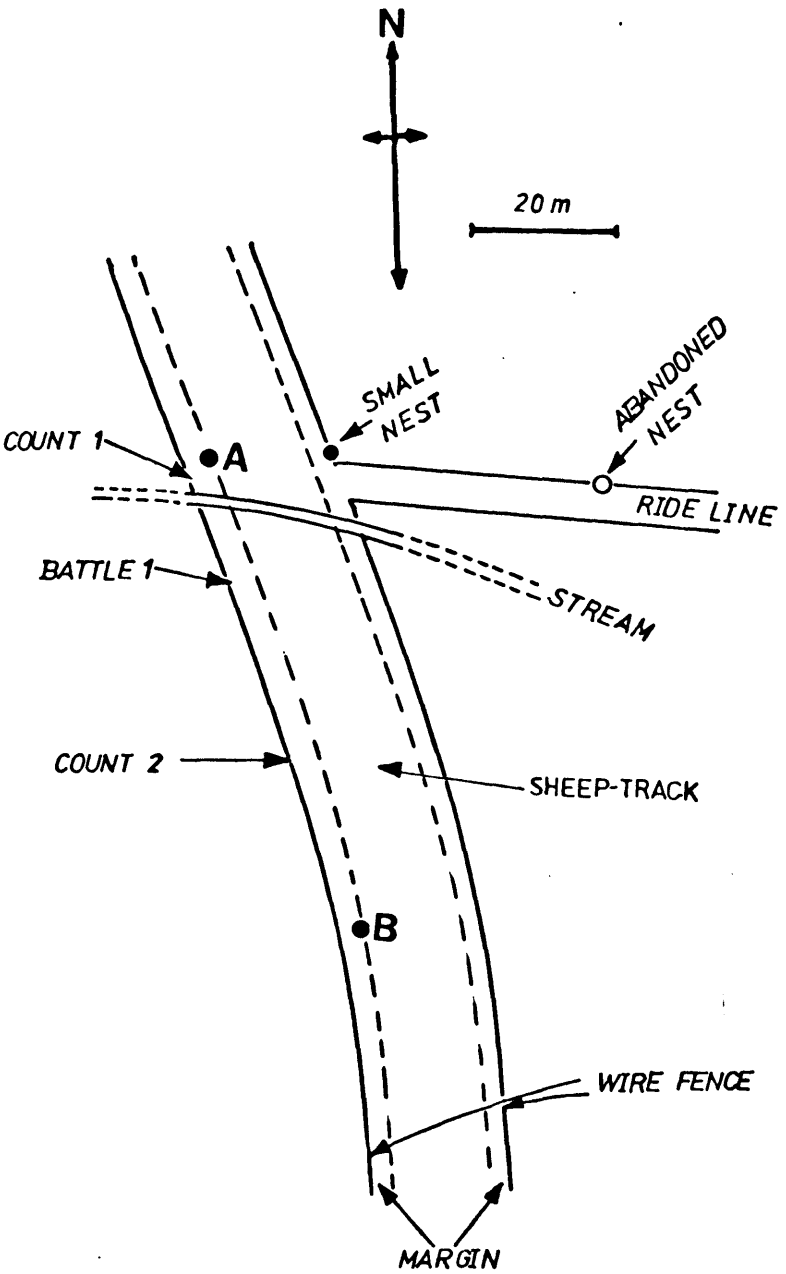


Figure 2.3 Map of the site where "spring battles" were observed in 1973 and 1974. The wood, bounded by the wire fence is 42 years old SP. The "small nest" is the new site of the "abandoned nest", and foragers from this nest and nest A have never been seen crossing the "sheep-track".

On 18.V.1974, both nests were again observed in battle at 17.30 (air temperature with unshielded mercury thermometer, 12.5°C). On this occasion foragers from nest B had reached nest A, which was now the fighting area, and dead ants were being transported back to nest B.

Two counts were made (see figure 2.3). Count 1 (a 10-minute count in each direction) gave this result:

To nest A: 47,

To nest B: 29 + 5 carrying dead ants.

Since observation along the route towards nest B suggested that the result of the count was low, another count was made. Count 2 (a five-minute count in each direction) gave this result:

To nest A: 82 + 2 carrying dead ants,

To nest B: 91 + 16 carrying dead ants.

There were many (c.100) myrmecophiles on the surface of nest A during the attack (the staphylinids Nototheca flavipes, N. anceps, and Thiasophila angulata were most common, and a single specimen of the spider Thyreostenius biovatus was also taken).

Nest A was totally destroyed by the end of May, and a route from nest B continued past nest-site A during 1974 and 1975. Hence, nest B gained additional territory as a direct result of the attack.

2.3.3 FLIGHT ACTIVITIES

The most detailed observations on flight activities in Formica are those of Talbot (1959, 1964, 1971, 1972), while Kannowski (1959a,1963) provided further information and reviewed the literature on formicine flight activity. Additional observations for north American species are provided by Clark and Comanor (1972) and Scherba (1958). Data from these sources have been summarized in table 2.1. This table suggests a pattern of short morning flights of alatae on successive days, with small numbers taking flight each day.

Table 2.1 Details of flights in some *Formica* spp. Time is as given in the original source.

SPECIES	DATE (TIME)	FLIGHT DURATION (min)	MAX. NO. FLYING (no./min)	STARTING TEMP. °C	NO. FLIGHT DAYS	AUTHOR
ulkei	early July (06.30-08.30)	?	?	?	?	Scherba (1958)
ulkei	26.VI-14.VIII (05.20-07.45)	35 - 100	mass flight seen	16.5	11	Talbot (1959)
obscuripes	16-29.VI (05.50-11.35)	5 - 179	82	21.1	10(1959) 5 - 16(1972)	Talbot (1959, 1972)
obscuripes	15.IV-10.V (c.10.20)	c. 40	14	25.0	?	Clark and Comanor (1972)
obscuriventris	27.VII-24.VIII (07.00-08.43)	10 - 96	8	17.2	16	Talbot (1964)
dakotensis	5-11.IX (09.29-11.36)	30-137	13	22.0	7	Talbot (1971)
lugubris	6-20.VI (08.00-10.40)	c. 45	20-30	17.5	at least 5	present study

In contrast, there are few detailed observations on flight activities of European wood ants. Yarrow (1955) commented that "the mating of this, and of the other rufa-group species, remains a mystery", and the reviews of Brian (1965, p.61), Sudd (1967, p.136) and Wilson (1971) do not provide further data comparable to the American work. Marikovsky (1961) recorded mass flights from wood ant nests and has also reported swarms of alatae congregating on mountain-tops. There is also an old record of aquilonia swarming on top of Ben Nevis (Brice, in Collingwood 1958b).

There are no specimens of alatae from Irish lugubris in the Museum, nor are there any published records. Stelfox (personal communication to Collingwood 1958a) never observed alatae in the Devils Glen nests, nor did Collingwood (loc. cit.) ever find alatae in any Irish nests he examined. This led him to speculate that lack of sexual production, perhaps due to unsuitable weather conditions, was a possible reason for the decline of lugubris in Ireland. Observations on production of alatae were made at various times during this study to clarify the situation.

Alatae occurred in most medium to large-sized active nests and were first observed, in the nests, each year on 12.V.1973, 11.V.1974, and 23.IV.1975. Males seemed to appear first in the nests, but most nests produced alatae of both sexes. A small number of nests produced only males, but none were seen with only females. Alatae (males) were last observed in the nests in late September 1973, but no signs of overwintered males were observed the following spring. These notes pertain to the South Tipperary nests, but alatae have also been seen in the three Killarney nests, and in three of the four Woodford nests.

Considerable differences were noted in the time of appearance of alatae in different nests: during 1973, alatae were first observed in Moore's Wood on 12.V and were present in all the active nests during the next few weeks. However in some nests, generally large, non-active, and

located in shaded sites, sexual larvae and pupae, but no alatae were observed as late as the 20.VI, and two callow males and many sexual pupae were seen in MW-284a on 6.VII. (No observations were made to see if these late-emerging alatae ever flew from the nests.) Scherba (1958) made similar observations on the American species, ulkei: "The mound that is shaded or has only a northern exposure to the sun lags in activities such as the development of brood and the initiation of activity in the spring".

Flight behaviour was not observed before 1975. However flight dates can be reasonably inferred from the appearance of large numbers of de-alatae on the ground:

(1) Large numbers of alatae had been present in MW-268a after 12.V.1973, but only very few were found in the nest on 26.V. This coincided with the appearance of de-alatae on the afternoon of the 26.V in Moore's Wood. Large numbers of de-alatae were observed in Kilcoran Wood from 4.VII (regular observations had not been made in this wood prior to this date).

(2) De-alatae were first seen in large numbers in Kilcoran Wood on 13.VI.1974.

(3) Flights of males and females were observed from five nests in Kilcoran Wood on six days during 1975, from 6.VI to 20.VI, and the first and last flights from each nest may not have been witnessed (table 2.2).

Both males and females flew from the vegetation on or near the nest, and females also climbed nearby trees (up to 5 m high) and flew from their highest points. Such differences between males and females have been noted in ulkei (Talbot 1959) and opaciventris (Scherba 1961, quoted by Kannowski 1963). Flights of males only and females only occurred at the same nest (KC-437d) on different days. All the flights lasted 30 to 45 minutes and although 20 to 30 alatae per minute was the highest number to take flight, the usual number was five to 10 per minute. Flights

Table 2.2 Observations of flight activities at five nests in Kilcoran Wood, during June 1975.

DATE:	6	7	9	10	11	20
Nest						
440a	+	+	?	-	-	-
440f	+	+	+	?	+	+
440g	+	-	-	-	-	-
437b	*	+	-	?	-	-
437d	*	+	+	+	+	+
starting time:	08.00	08.30	08.30	10.40	10.40	09.35

Key: - no alatae seen; + flights; ? alatae seen but no flight;
* no observation made.

always took place in the morning, and the actual time of flight varied according to the temperature: each flight started after the first direct sun-rays hit the nest, at air temperature 17.5 to 18.0°C, and was preceded by flapping of wings. One flight started at 16.2°C but the small number of alatae which took flight all landed on nearby trees. These observations are very similar to the published observations on other Formica species (cf. table 2.1).

Alatae were rarely seen on the surface of the nest at other times and this may be suggestive of a circadian rhythm of alate emergence from the nest such as that demonstrated by McCluskey (1965) in alatae of five ant species, including Campanotus clarithorax Emery.

The direction of take-off flight was quite constant at each of these five nests and is shown in figure 2.4. However the directions appeared to bear no relationship either to each other, or to uphill/downhill direction, and may have been dictated by the tree positions at each site.

The "wing flapping" behaviour prior to flight has been noted in other ants (Kannowski 1963), and is interesting in the light of work on pre-flight warm-up behaviour in many insects (e.g. Heinrich 1972). Observations were made at KC-440f to see if the flapping behaviour resulted in higher thoracic temperatures. Each alata was grasped by the wings as it began to fly - if caught by the thorax it was discarded. A type-IM (Grant Instruments) thermistor probe was inserted into the thorax from the ventral side, and the temperature read. The whole observation took less than 15 s for each individual. Males were captured as they flew either from the nest surface or from vegetation. All the females were taken as they took-off from vegetation. The results are given in table 2.3 and suggest that the thoracic temperatures were 2 to 4°C warmer than air temperature.

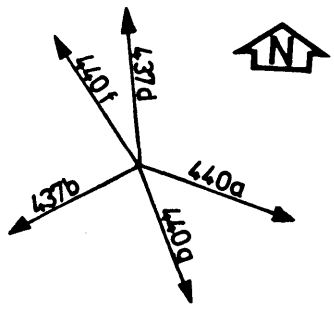


Figure 2.4 Flight take-off directions of alatae at five nests in Kilcoran Wood, during June 1975.

Table 2.3 Internal thoracic temperatures (°C) of 10 male and nine female alatae at time of flight take-off. All the females were taken from vegetation and the males were taken either from the nest surface (N) or vegetation (V). Air and nest surface temperatures are given for comparison.

MALES		FEMALES	
18.4 (N)	21.4 (N)	16.8	20.1
18.8 (N)	22.2 (V)	18.4	21.0
19.4 (V)	22.2 (V)	18.8	22.8
20.3 (V)	23.5 (N)	19.1	23.4
20.7 (V)	23.5 (V)	20.1	
air: 17.6 - 18.3		air: 17.2 - 19.7	
nest: 26.2 - 29.8			

2.3.4 COLONY FOUNDATION

Colony founding in a number of ant species is by way of temporary social parasitism, where the foundress queen takes over a host nest of a different species. Wheeler (1910, p.441) considered this mode of colony founding of "regular or normal occurrence" and predicted "that it would occur very generally in the rufa and exsecta groups on both continents". There is some evidence that wood ants can found colonies in the nests of Formica fusca-group. Small nests consisting of a wood ant queen and mixed F. fusca-group and wood ant workers are occasionally found (Donisthorpe 1927a, p.299). Collingwood and Satchell 1956) described a small mixed fusca-rufa colony: "The colony consisted of about a dozen large fusca workers, some 30 small rufa workers and one dealate rufa queen". Sudd (1967, p.146) reviewed the literature pertaining to this mode of colony-founding in wood ants and concluded that "the evidence for this is circumstantial. . . all the evidence is that the adoption of a wood ant queen . . . by other ants is rare". Yarrow (1955) reached similar conclusions.

Observations on aspects of colony founding were made at various times during this study. The following points can be noted:

(1) Formica lemani is the common F.fusca-group species throughout the study area.

(2) Although many small (less than 0.25 m diameter) lugubris nests have been opened, mixed colonies were never found.

(3) De-alate lugubris queens were frequently seen near F. lemani nests, apparently trying to gain entry; up to 13 have been observed at one lemani nest at the same time.

(4) These dealatae do not always enter the lemani nest: one queen lugubris was pursued for over 3 m by a lemani worker; at times the pursuer actually attached itself to the queen's leg.

(5) During June 1974, two colonies of lemani were found with a live lugubris queen and unidentified brood in each. Both colonies were located under stones. Queens of lemani may have been present, but were not seen as the nests were not disturbed further. However, lugubris workers did not appear in these nests during 1974 or 1975.

It thus seems that colony-founding by way of temporary social parasitism is rare in Irish lugubris. The more usual mode seems to be colony fragmentation. This can account for the slow dispersal of the species.

2.3.5 POLYGYNY

A number of authors have reported that the colonies of lugubris are polygynous. Yarrow (1955) found nine de-alate queens with "perhaps 300 workers in one small nest", Bolton and Collingwood (1975) mentioned that lugubris nests "may contain many hundreds of laying queens", and the legend of a plate reproduced in Cotti (1963) of an Italian nest reads: "searching for queens". The actual number of queens in large wood ant nests has not been recorded, but Cory and Haviland (1938) reported 1407 queens in one nest of the American species exsectoides. The following observations suggest that Irish lugubris nests are not polygynous:

(1) Although numerous nests have been opened at all times of the active season, the colony queen(s) has not been seen. It is unlikely that a large number of queens could be continuously overlooked.

(2) Queens of polyctena have been reported (Chauvin 1970, p.46) to take part in the sunning-cluster behaviour. Although the clusters of lugubris have been frequently disturbed (more than 40 times in 1975 alone), no queens were seen amongst the workers.

(3) Rosengren (1971) was able to conclude that his study-nest of rufa

was polygynous from observations of several queens being transported simultaneously between constituent mounds of a polycalous colony. This behaviour has not been seen in Irish lugubris nests.

2.3.6 FLOWER VISITING BY FORAGERS

O'Rourke (1950b) drew attention to the fact that ants visit flowers and are responsible for some pollination. He quoted Posnette who showed that Crematogaster spp. pollinate 50 percent of the cocoa (Theobroma leiocarpa) in Ghana. Sudd (1967, p.98) assembled records of flower visiting by ants but reported no observations on wood ants.

Flower visiting by lugubris workers was frequently noted during this project. The behaviour occurred most often during the early part of the year and was rarely seen after June, when honeydew sources were attended. The following plants were visited by lugubris:

Rhododendron ponticum	Hieracium sp.
Vaccinium myrtillus	Rubus fructicosus
Ulex europaeus	Taraxacum officinale
Cirsium sp.	

Of the plants in this list, Rhododendron is an important source of food when it occurs near the nests, and distinct routes were formed to this shrub during 1974. Vaccinium is also frequently visited, but the other plants were only visited in small numbers.

3.0 NEST SITES IN RE-AFFORESTATED WOODLANDS.

A knowledge of the nest-site requirements of lugubris under Irish conditions is an obvious prerequisite to the drafting of any proposals on the conservation of the species. This chapter contains data relating the observed density of lugubris nests and their persistence from year to year to similar published data from Europe. The nest sites are then considered by analysis of a series of vegetative, soil, physical and forestry management variables. Finally, spatial distribution of the nest sites is studied by applying the nearest-neighbour technique to the nests in one compartment.

3.1 NEST DENSITY.

Elton (1932) drew attention to the necessity of clearly defining what is meant by density, and proposed these terms: "lowest density, which is the number of animals divided by the total area of the census", "economic density, which is the number of animals divided into the area of territory which they actually visit or live in", and "greatest density, which includes all local (often temporary) aggregations within the territory". It is of interest to compare the observed density of lugubris obtained under plantation conditions in Ireland, with published results for related species. Since some published results correspond to "lowest density", and others to "economic density", both will be considered here.

Klimetzek and Wellenstein (1970) assembled a table of lowest densities of wood ant nests in Europe, which they expressed as numbers of nests per 100 ha. Table 3.1 contains some of these data, together with the results obtained for three woods during the present study. The observed lugubris densities are quite similar to those observed on the continent, but it must be remembered that these woods contain, together, 87 percent of the Irish lugubris nests known at present.

Table 3.1 Lowest densities of wood ant nests.

SPECIES	CENSUS AREA (ha)	NO. NESTS	DENSITY (no./100 ha)	AUTHOR
wood ants	562	214	38.1	Eckstein (1937)
wood ants*	1 640	258	15.7	Klimetzek (1970)
wood ants	935 681	15 106	1.6	Klimetzek and Wellenstein (1970)
lugubris	594 (MW)	43	7.2	present study
lugubris	290 (KC)	93	32.1	present study
lugubris	514 (GG)	51	9.9	present study

* = 63% rufa, 20% polyctena, 12% pratensis, 5% lugubris.

Economic densities are more difficult to deduce, since precise information is required on territory area. However, an approximate figure for economic density can be deduced from small areas within the the census area where large numbers of nests occur close together. Under these conditions, lowest density approximates to economic density. Compartment KC-450, 15.2 ha in area, contained 33 live nests (= 2.2 nests per ha) (see 3.5). This represents 4609 m^2 to each nest, or 0.0002 nests per m^2, and corresponds to an average foraging territory of radius 38.3 m per nest, if we assume circular territories. Brian (1965, p.7) reviewed the literature on economic densities of European wood ants, and gave figures ranging from 1-2 nests per ha in the Alps, to 6-8 per ha in German oak woods. The Irish lugubris nests fit on the lower end of this scale.

3.2 NEST PERSISTENCE.

Data on the persistence of ant mounds at the same site were provided for the American species ulkei (Dreyer and Park 1932; Dreyer 1942), exsectoides (Cory and Haviland 1938) and opaciventris (Scherba 1963). Klimetzek (1970, 1972, 1973) made three total inventories of wood ant nests (63 percent rufa, 20 percent polyctena, 12 percent pratensis) in a 1640 ha wood at three-year intervals. His results showed that while the actual nest numbers did not vary much, this apparent stability masked a large turnover of nest-sites: new nests appeared at a rate of 15 percent per annum and 22 percent of nest sites were abandoned each year.

In the course of the present study all nests were recorded each year as live, dead or abandoned. "Live" nests are those still occupied by ants. Unoccupied nests were classified as abandoned when either known previous history, or strong circumstantial evidence (i.e. a live nest located nearby) indicated the site was vacated in favour of another site.

All other unoccupied nests were classified as dead. The nests considered here are all the nests known prior to the end of 1973, including those at Woodford and Killarney. Nests were not considered if they were subsequently affected by bulldozing or fire.

The results are given in table 3.2. Most (87 percent) of the live nests remained at the same site during the period of observation. The overall annual rate of abandoning nests was eight percent. Annual mortality was nine percent when all nest sites are considered, though it was highest (18 percent) in Moore's Wood. It is difficult to give a precise rate of appearance of new nests in such a large study area, though it is in the order of five percent per annum in Kilcoran Wood. These observations suggest a more stable year-to-year nest structure than that described by Klimetzek (loc. cit.).

Further observations on abandoning of nest sites were made during 1975. A total of 10 out of 142 (seven percent) live nests under observation abandoned their old nest site. All but one of these moved during April and May, while the single exception, KC-440h, changed site during August. The behaviour of nest moving was almost confined to small nests. The nest diameters (cm) of the abandoned mounds were as follows: 21, 22, 24, 28, 37, 37, 97, 105, and 114. One nest moved c. 20 m whereas the remainder moved to a new site less than 5 m from the old site. Seven of these nests were young immature nests which did not produce alatae in 1975. The other three were mature nests and produced alatae. The observations suggest a pattern of young nests in young plantation changing nest site early in the year. Most of the large nests have not moved during the period of observation. Many abandoned lugubris nests are subsequently recolonised by F. lemani or Myrmica ruginodis.

Table 3.2 The state in 1975 of nests recorded as live in 1973.

	WOODS			
	MOORE'S	KILCORAN	OTHERS	TOTALS
1973: live nests	45	55	12	112
1975: live nests				
(a) at same site	25	45	9	79
(b) abandoned	4	5	3	12
(total live nests)	(29)	(50)	(12)	(91)
dead nests				
(a) at same site	12	5	0	17
(b) abandoned	4	0	0	4
(total dead nests)	(16)	(5)	(0)	(21)

3.3 THE NEST ENVIRONMENT.

Reference to the maps contained in the map pocket shows that the nests of lugubris tend to be more common in some compartments than others. A possible reason for this pattern is a limited availability of suitable nest sites. This section gives results of an attempt to characterize the nest site of lugubris in re-afforestated plantation in South Tipperary.

There have been many studies on ant nest environments. Talbot (1934) studied the distribution of ant species in various habitats around Chicago, and Talbot (1953) described the ants of an old-field community in Michigan. Brian and Brian (1951) studied the effect of insolation on ant nest environments (mainly Myrmica ruginodis) in the west of Scotland. Brian (1964), Brian et al.(1965) and Brian et al.(1966) described the nest environment and the distribution of heathland ants in Dorset. Stradling (1968) studied the ant community of a Welsh coastal sand-dune.

Previous work on the habitats of Formica spp. include those of Dreyer and Park (1932) who showed that the mounds of the American species ulkei were confined to wood margins and that this was due to more light penetration to the nest surfaces at these sites. Klimetzek (1970, 1973) studied the distribution of wood ant nests (mostly polyctena, rufa and pratensis) in a German wood. The nests occurred most frequently at 300 to 400 m and 600 to 700 m altitude, on forest roads (75 percent of all nests) or on the forest margins (18 percent of all nests). Abies alba, Picea abies (Norway spruce), and Fagus sylvatica (Beech) were the most important overhead trees. Hughes (1975) provided data on habitat preferences of rufa and lugubris in Wales. High densities of lugubris (actual figures not given) were found in oakwood, under 30 to 50 year old larch, and the species has spread into young plantation. The nests were found up to 305 m altitude, the artificial tree line.

3.3.1 MATERIALS AND METHODS.

The study was based on all the nest sites of lugubris (live, dead or abandoned) located in South Tipperary, which were known and mapped prior to the end of 1974 (these nests are all allocated an alphabetic character in maps 2, 3, and 4), with the following exceptions: any nests whose immediate nest environment was interfered with either by bulldozing or by fire, and also a small number (7) of nests for which any data was missing when the analyses were made. This left a total of 184 nest sites for which all the data were available.

A series of variables was measured at each nest site. This differs from Brian's (1964) work where it was possible to use a relatively small area (8 ha) to study the distribution of four species of ants in relation to a series of variables measured at randomly chosen points. The approach followed here limits the form of analysis, but overcomes the problem of a large study area with a low nest density. The field observations were made at various times during 1974 and early 1975, though the end of 1974 has been taken as datum for the nest characters.

Nest characters:

Nest diameter is the largest basal diameter in cm. Definitions of live/dead/abandoned nest sites were given on page 36. In the present survey, live nests were classified subjectively as either active or non-active. Active nests were those with freshly thatched mounds, with little or no vegetation growing on the mound, with many ants on the nest surface, and with large traffic on the routes. Non-active nests were the opposite on all these points. Since each nest was visited at least six times during 1974 and 1975, it is felt that nests were assigned to these classes consistently.

Tree characters:

The species of tree adjacent to the nest site were recorded, and

the height of the stand was estimated using a foresters' altimeter (Blume-Leiss). Canopy was recorded on a subjective 1 to 5 scale:

1 = < 2 m trees - very open.
2 = c. 2 - 3 m trees - open.
3 = c. 3 - 5 m trees - lower branches closing.
4 = >5 m trees - upper branches meeting.
5 = >5 m trees - upper branches densely closed.

Tree age was taken from the Forestry Inventory, more recent planting dates were obtained by enquiry to the forester.

Location characters:

Aspect was measured using a pocket compass. Slope was measured over 10 m using a stake marked at the observer's eye-level and the angle scale of the altimeter. Altitude (in m) was estimated from the 1:10560 scale Ordnance Survey maps.

Soil characters:

Soil samples were taken on three successive rainless days (18-20.III.1975), 0.5 m from each nest at each of the cardinal points. A laboratory cork-borer (diameter 25 mm) was used to sample the top 10 cm of soil. Since the three days remained rainless, data collected on different days are compared directly.

Soil pH was measured, after Peech (1965) on a 1:1 soil:water mixture (20 g fresh soil, 20 ml distilled water) using a Radiometer 28 pH meter.

Soil water was measured gravimetrically, by loss of weight on drying at 40°C for 15 days, and is expressed as a percent of wet weight.

Soil organic carbon was estimated using the Walkley and Black technique (details are given in Holme and McIntyre 1971, p.49). In this method, organic matter is oxidised by a chromic acid-sulphuric acid mixture and the excess chromic acid is determined by titration with a standard ferrous salt. The determination was made on a soil sample of

0.25 g, except at 62 sites where a sample of 0.1 g was used due to the high organic content. (This has been allowed for in the calculations.)

Vegetation characters:

The percent cover of the various plants at each site was estimated using a 0.25 m^2 quadrat placed at each of the cardinal points of the nest and adding the results to give cover per 1 m^2. Ulex was not identified to specific level, but is mainly U. europaeus. The vegetation characters used here are the cover of the six most common species (Molinia caerulea, Calluna vulgaris, Erica cinerea, Ulex spp., Pteridium aquilinum, and Vaccinium myrtillus), all mosses and liverworts considered together as "moss", and the percent of area not covered by any vegetation, "bare".

3.3.2 ANALYSIS.

All the data were punched on computer cards. The aims of the analysis were to discover if there was any trend relating nest environment to nest size and activity. The analyses were carried out on the college IBM-370 computer, using the Statistical Package for the Social Sciences (S P S S; Nie et al. 1970), a flexible programme package designed for the analysis of surveys. Analysis has been carried out at (1) all sites, (2) non-abandoned sites, or (3) occupied sites only, as appropriate. For example, a frequency distribution analysis of nests on different slopes can be made meaningfully on all sites, whereas a similar analysis of nests occurring under different tree heights would not consider possible change in tree height since some nests had died.

3.3.3 COMMENT ON THE DATA MATRIX.

A comment on some aspects of the data to be considered is appropriate before any generalizations are made from the results of these observations.

An immediate question is how representative are the nest sites chosen for study. The nests in Moore's Wood and Kilcoran Wood have been mapped (see 2.1.1). Few additional nests have been found in subsequent observations in these woods, and it seems justified to consider all the nest sites known in 1974 as representative. Most of the Glengarra Wood nest sites were not known before 1974 and were discovered by forestry workers in the course of their normal duties. However, since many small nests in an almost impenetratable habitat (tall Ulex and Rubus amongst young SS, e.g. in compartments GG-931, 933 and 936) were found (see Appendix II), it seems fair to consider the Glengarra nest-sites as an unbiassed sample of the nests in that wood. A different problem is that of discovering abandoned and dead nests, though a reasonable sample of these classes has been studied to justify drawing some conclusions from them.

3.3.4 RESULTS: CONSIDERING ALL SITES.

The numbers of nests in the different classes are given in table 3.3 for each of the study woods. It can be seen that while the relative proportion of nests in each class is similar in Kilcoran and Glengarra Woods, there are more dead and abandoned nests in Moore's Wood.

The diameters of nests in different nest-classes are given in table 3.4, and the ages of their associated trees are given in table 3.5. Nests classified as "dead" tend to be large and associated with older trees, whereas those classified as "abandoned" occur over a wide range of nest sizes and tree ages. "Live" nests are well-distributed over the size and tree-age categories.

A value of 48.99 is obtained for χ^2 when the diameters of all live nests are tabulated in a contingency table with tree age (table 3.6)(with 25 d.f. $P<0.01$). It is evident from the table that there is a good relationship between diameter of nest and the age of the associated trees. This is

Table 3.3 The number of nests of different classes in each of the study woods, and in other woods.

NEST CLASS	WOOD				TOTALS
	KILCORAN	GLENGARRA	MOORE'S	OTHERS	
live-active	48	33	35	8	124
live non-active	6	2	8	2	18
dead	4	1	12	1	18
abandoned	7	4	11	2	24
TOTALS	65	40	66	13	184

Table 3.4 Nest diameters (cm) of nests classified as live, abandoned and dead; data from all woods.

NEST DIAMETER	NEST CLASS			TOTAL
	LIVE	ABANDONED	DEAD	
0 - 25	11	1	1	13
26 - 50	24	6	0	30
51 - 75	21	8	1	30
76 - 100	43	6	4	53
101 - 125	28	2	6	36
126 - 150	14	1	2	17
>151	1	0	4	5
TOTAL :	142	24	18	184

Table 3.5 The tree age at nest sites classified as live, abandoned and dead; data from all woods.

TREE AGE (years)	NEST CLASS			
	LIVE	ABANDONED	DEAD	TOTAL
0 - 10	30	5	0	35
11 - 20	9	2	1	12
21 - 30	32	2	4	38
31 - 40	47	10	8	65
41 - 50	20	4	5	29
>50	4	1	0	5
TOTAL:	142	24	18	184

Table 3.6 Cross-tabulation of the diameters of all live-active nests by the age of the overhead trees.

DIAMETER (cm)	TREE AGE (years)						
	0 - 10	11 - 20	21 - 30	31 - 40	41 - 50	>50	TOTAL
0 - 25	6	0	2	1	1	0	10
26 - 50	12	1	6	2	1	1	23
51 - 75	3	2	3	7	4	1	20
76 -100	6	2	11	14	5	0	38
101 -125	1	3	7	8	3	0	22
126 -150	0	0	1	6	2	2	11
>150	0	0	0	0	0	0	0
TOTALS:	28	8	30	38	16	4	124

$\chi^2 = 48.99$, 25 d.f. $P<0.01$.

consistent with general field observations and it seems that a reasonable simplification is possible by considering that, under plantation conditions, the age of the nest is approximately that of the trees overhead, though there is a lag of a few years between planting and colonization. Thus a fire destroyed a part of Boulakennedy Wood in March 1973. This area was bulldozed and replanted during 1974. A few very small nests were discovered by forestry workers during late 1975. As a further example the nests in compartments GG-936 and GG-937 can be mentioned. These nests are all uniformly small to medium sized, and are located in an area which was destroyed by fire in 1967. The generalization relating age of nest to tree age is not always true in older stands (> 40 years), usually of SP. In these stands, the canopy has re-opened, and ground vegetation re-appears. Small, immature nests are sometimes found under these "semi-natural" conditions.

The tree-species associated with the nest sites are given in table 3.7. Both species of spruce, Sitka and Norway, have been treated together as "spruce" for two reasons, Norway spruce only occurred at a few sites, and the same aphids occur on both species. Similarly, both Japanese and European larch were treated together as "larch". Scots pine (SP) and contorta (PC) were treated separately for two important reasons: aphids have not been observed on PC but always on SP, and secondly, because of the emphasis on planting PC by the Forestry Service.

It is evident from the table that SP is numerically the most important overhead tree; it occurs at 71 percent of the sites and is the only species at 29 percent. In contrast, while PC occurs at 55 percent of sites, it is the only species at four percent of sites. Spruce occurs at 29 percent of sites and is the only species at five percent. Larch is the least important overhead tree, occurring at three percent of sites, and is the only species at only one site.

Table 3.7 The tree species at all nest sites. (+ = present, and - = absent).

TREE SPECIES				NO. NESTS IN EACH WOOD				
SPRUCE	PC	SP	LARCH	KC	GG	MW	OTHERS	TOTAL
-	-	-	-	0	3	0	0	3
+	-	-	-	3	4	3	0	10
-	+	-	-	2	0	5	1	8
+	+	-	-	2	24	3	1	30
-	-	+	-	16	4	27	7	54
+	-	+	-	4	2	3	1	10
-	+	+	-	34	3	22	3	62
+	+	+	-	0	0	1	0	1
-	-	-	+	1	0	0	0	1
+	-	-	+	2	0	0	0	2
-	-	+	+	1	0	1	0	2
-	+	+	+	0	0	1	0	1

The trees at the nest site are important both as providers of suitable overhead canopy and as hosts of aphids. It can be seen from table 3.7 that the presence of PC does not exclude the occurrence of nests. However the low number of nests under PC alone (at all these sites either SP or SS was nearby) does suggest that pure stands of PC exclude nest sites, presumably because aphid trees are lacking. It can be noted that older plantations of PC (those over 20 years old) usually contain a small number of SP (cf. figure 4.4 where the aphid trees are the only SP present in an otherwise pure PC stand), whereas recent plantings of PC tend to be more "efficient" with no SP amongst them. This trend will drastically reduce the number of available nest sites.

Figure 3.1 gives the frequency of nests on different slopes, soil pH, and altitude. There is a large variation with slope; one nest has persisted on a slope of 34° since 1973 in Kilcoran Wood. Most of the nests occur on soil pH under 4.5 units, though the observed values ranged up to 7.7. Satchell and Collingwood (1955) also reported lugubris nests at high pH, and this is contrary to an earlier view (Nelmes 1938) that wood ant nests were confined to acid soils. (The higher pH values were always at roadside sites where gravel of a higher pH has been spread.) The distribution at different altitudes is largely a reflection of the altitudinal distribution of the woods, and the nests have been found right up to the artificial tree-line. However, these altitudes contrast with those at which lugubris occurs at in Italy: 1300 to 2200 m (Pavan et al. 1971).

Figure 3.2a gives the nest-site aspects for all live nests and it can be seen that nests occur commonly over a range of aspects; their rarity on westerly sites is due to the absence of west-facing habitats. A total of 78 (55 percent) of these nests had "long slopes" oriented towards the direction of the greatest solar intensity (figure 3.2b). Similar observations on nest orientation have been reported by Scherba (1958)

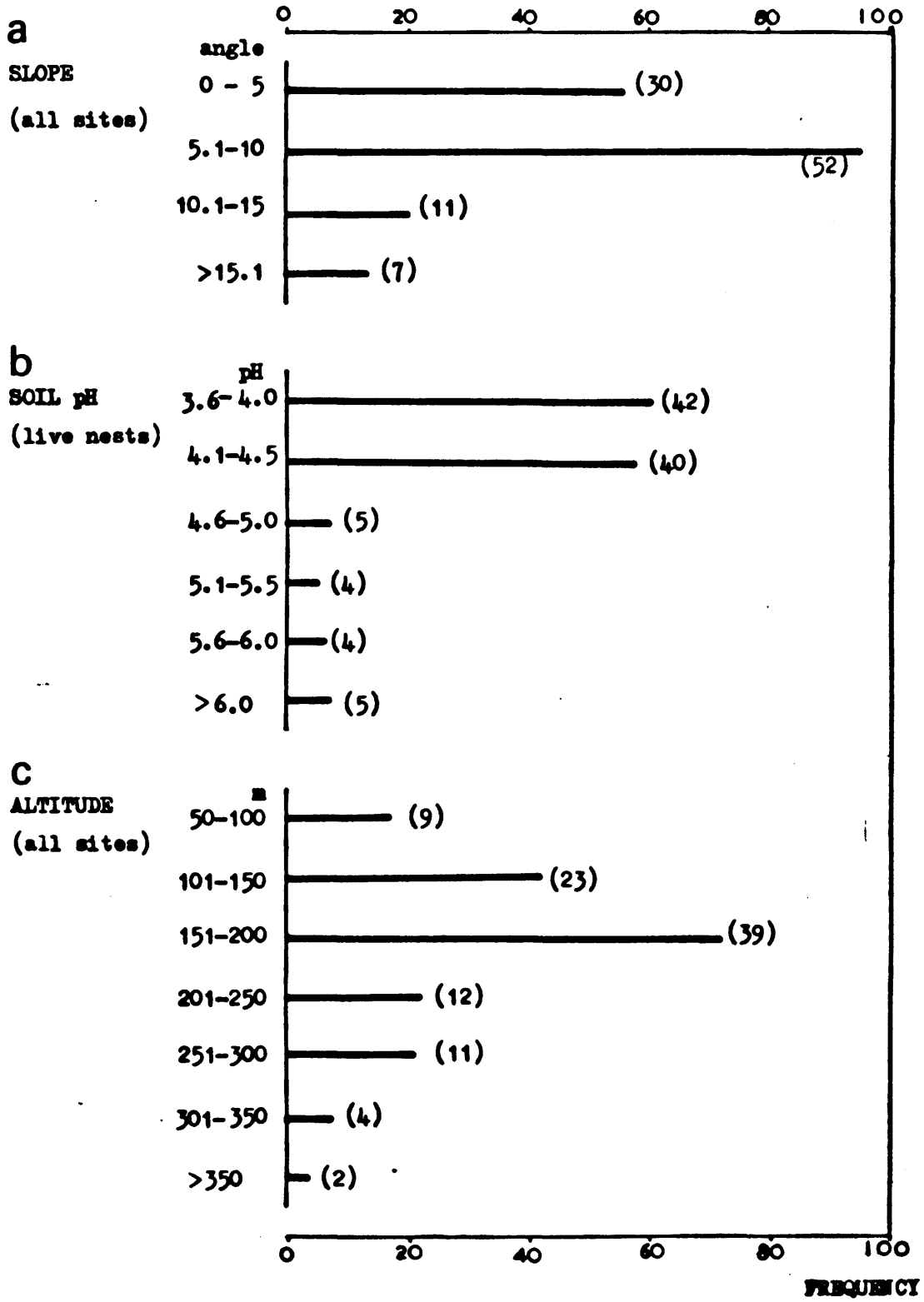


Figure 3.1 The frequency of nest sites on different (a) slopes, (b) soil pH, and (c) altitudes. Percentages are indicated in parentheses.

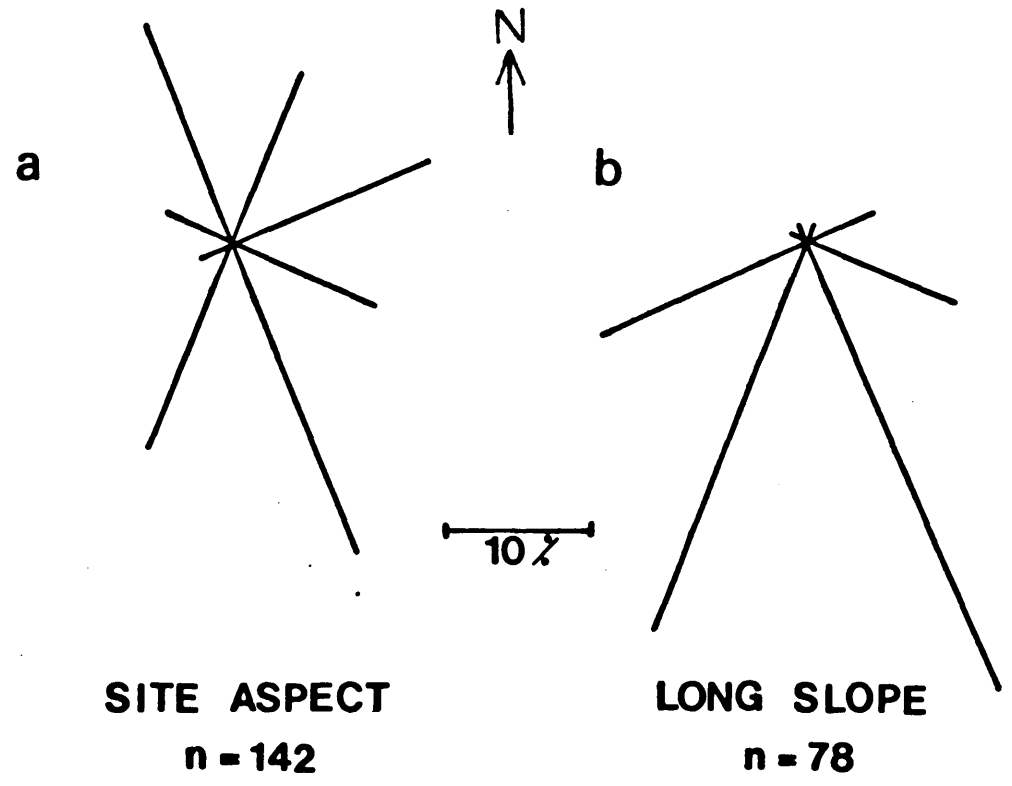


Figure 3.2 The site aspect and direction of long slope of live nests.

for the American species ulkei.

While making the field observations, it was noticed that there seemed to be a tendency for (a) nests to occur on road-sides or ride-lines when the trees overhead were old and to be scattered in the wood when the plantation was young, and (b) nests of smaller diameter seemed to occur scattered in woods, while larger nests tended to be on road-sides or ride-lines. Both these observations have been tested in 2x2 contingency tables where the nests are classified as occurring on road-sides or ride-lines ("margins") or "in wood", on the one hand, and according to the mean of tree age (29.8 years) (table 3.8) or mean of nest diameter (81.1 cm) (table 3.9) on the other. In both cases a significant result was obtained for χ^2, thus confirming the field observations.

3.3.5 RESULTS: DIFFERENCES BETWEEN WOODS.

The diameters of all the live nests in Kilcoran, Glengarra and Moore's Woods are arranged in a contingency table (table 3.10) where it can be seen that there is a preponderance of small nests in Glengarra, when compared to the other two woods ($\chi^2 = 22.95$, with 10 d.f. $P < 0.05$).

Nine contingency tables similar to table 3.6 were constructed, in which nest sites were classified according to nest diameter and tree-age, and using the same intervals. The data were drawn from live-active, live non-active and dead nests for the three major study woods, Kilcoran, Glengarra, and Moore's. There were no significant results for dead and live non-active nests in any wood. The results for live-active nests were:

Kilcoran Wood: $\chi^2 = 22.83$, 12 d.f., $P < 0.05$,
Glengarra Wood: $\chi^2 = 29.22$, 15 d.f., $P < 0.05$,
Moore's Wood: $\chi^2 = 17.44$, 20 d.f., $P = 0.62$.

While the tables for dead and live non-active nests were based on small numbers, it does seem that nests in these categories do not show a clear

Table 3.8 The numbers of live nests occurring on roadsides and ride-lines ("margins") or within the wood, when the tree age is greater and less than the mean tree age (29.8 years).

	MARGINS	IN WOOD
Tree age < 29.8 years	29	40
Tree age > 29.8 years	53	20

X^2 = 13.59, 1 d.f., P< 0.001.

Table 3.9 The numbers of live nests occurring on roadsides and ride-lines ("margins") or within the wood, when their diameter is less than, or greater than the mean nest diameter (81.1 cm).

	MARGINS	IN WOOD
Nest diameter < 81.1 cm	29	35
Nest diameter > 81.1 cm	52	26

X^2 = 6.54, 1 d.f., P< 0.05.

Table 3.10 The diameters of all live active nests in Kilcoran, Glengarra, and Moore's Woods.

NEST DIAMETER (cm)	NO. NESTS IN EACH WOOD			
	KILCORAN	GLENGARRA	MOORE'S	TOTAL
0 - 25	0	6	4	10
26 - 50	7	12	4	23
51 - 75	7	5	7	19
76 - 100	19	7	10	36
101 - 125	12	1	7	20
126 - 150	3	2	3	8
> 151	0	0	0	0

relationship between nest diameter and tree age. In two of the three woods, however, there were significant patterns relating diameter of live-active nests to tree age. The relationship did not hold in Moore's Wood, and this suggests differences between the woods.

Three tree variables for each wood are plotted in figure 3.3 on a percent scale. It can be clearly seen that when considered from the point of view of tree age, tree height and overhead canopy, that the nest sites in Moore's Wood occupy the oldest sites, with the highest trees and most dense canopy. The nest sites in Glengarra are on the other end of the scale, while those in Kilcoran lie in between.

It seems reasonable to suggest that the absence of relationship between nest diameter and tree age is due to the preponderance of older habitats, where, as was mentioned in 3.3.4, small young nests sometimes occur.

Reference back to table 3.6 suggests that the largest nests occur under trees of 30 to 50 years, though mostly under those of 30 to 40 years. The observations on recolonization of burned areas suggest that there is a time lag of from two to four years between replanting and occurrence of young nests. This allows an estimate of 28 to 38 years be made for the maximum age of nests. Comparable estimates of 25 and 30 years were given for nests of the American species ulkei (Dreyer 1942) and exsectoides (Andrews 1925, quoted by Scherba 1958).

The data also suggest that, under plantation conditions, the lugubris nests are in equilibrium with the man-made environment. Local people frequently comment that the nests were more vigorous and numerous in Moore's Wood 20 to 50 years ago. In contrast, local people near Glengarra Wood were aware of very few nests.

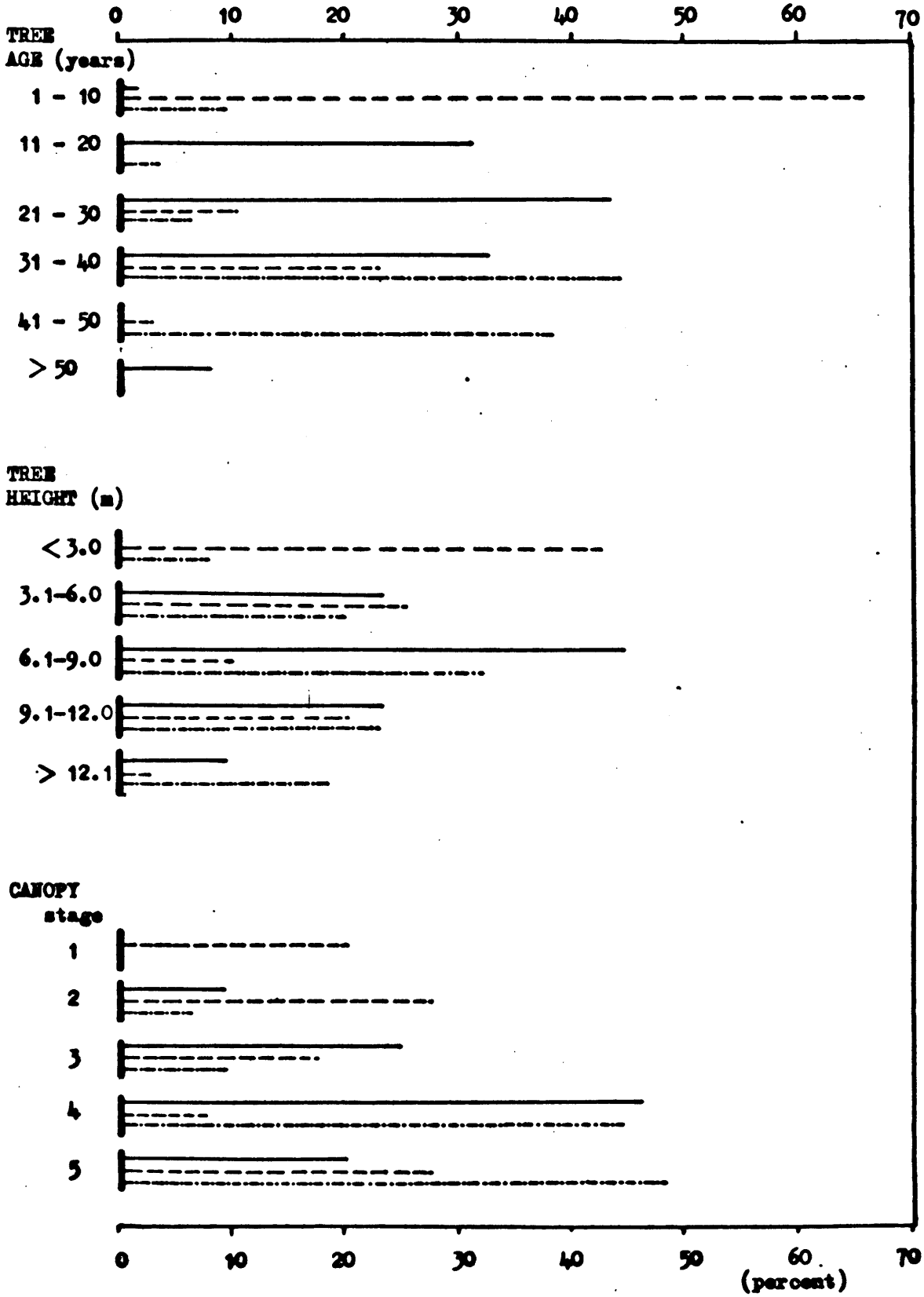


Figure 3.3 Tree age, tree height and canopy stage at all live nests in Kilcoran, Glengarra and Moore's Wood.

3.3.6 RESULTS: CONSIDERING ALL THE VARIABLES.

The correlation coefficients between the variables at all live nest sites are given in table 3.11. The following non-numeric variables were excluded from this analysis: nest classes, tree species, canopy and aspect. The significance levels of the coefficients are also indicated, and it can be seen that nest diameter is positively correlated with tree height, tree age, soil organic matter, soil water content, area of bare surface and Vaccinium. High values for these variables can be considered representative of the ageing process in woods. Nest diameter was negatively correlated with Molinia, Calluna, and Erica cinerea, indicating the absence of these plants at sites where the nest diameters were greatest.

There is a possibility that some of these relationships are spurious: for example, the relationship indicated by the correlation coefficients between two of these variables and nest diameter may really be caused by a strong correlation between both of these variables and another variable. Thus, in this case, all the observed relationships may be due to each of the variables being individually correlated to tree age or tree height and not to nest diameter. The technique of partial correlation analysis allows the calculation of the correlation coefficients between pairs of variables while removing the effect of one or more variables on the analysis.

Partial correlation coefficients were calculated between nest diameter and all the variables that gave significant relationships in table 3.11. The effect of the variables tree age and tree height was removed ("controlled") singly and together. The results are given in table 3.12.

The table indicates that the positive correlation between nest diameter and soil organic, soil water, bare ground are independent of tree age and tree height. However, when the effects of tree height and tree age are removed, the significance levels of the relationships with

Table 3.11 The correlation coefficients (x 100) between the nest site variables.
(* = P< 0.05; ** = P< 0.01; *** = P< 0.001)

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
nest diameter	1	-	47***	30***	10	-7	-13	25**	26**	-25**	-31***	5	-32***	14	-6	44***	25**	1
tree height	2		-	61***	-1	-11	15	12	5	-13	-37***	-2	-27***	0	5	34***	16	2
tree age	3			-	-2	-1	18*	1	1	-22**	-6	-13	-10	-6	9	12	30***	3
slope	4				-	21*	-7	18*	12	-25**	1	-3	-4	9	12	11	13	4
altitude	5					-	-10	4	9	-6	12	-27***	12	-12	15	-4	12	5
soil pH	6						-	-42***	-47***	-7	-7	-14	-2	16	-4	7	-13	6
soil organic	7							-	83***	-5	-8	2	-27***	12	14	5	26**	7
soil water	8								-	-8	-3	-1	-18*	9	26**	-3	29***	8
Molinia	9									-	-20*	-3	-7	-22**	-23**	-50***	-24**	9
Calluna	10										-	-7	16	-19*	6	-35***	-13	10
Ulex	11											-	1	-6	-6	-11	-14	11
Erica cinerea	12												-	-18*	-6	-22**	-12	12
Pteridium	13													-	-8	2	16	13
Moss	14														-	-12	4	14
Bare	15															-	4	15
Vaccinium	16																-	16

Table 3.12 The simple and partial correlation coefficients (x 100), relating nest diameter and some of the nest site variables.

CONTROLLING VARIABLE	TREE HEIGHT	TREE AGE	SOIL ORGANIC	SOIL WATER	Molinia	Calluna	Erica	Bare	Vaccinium
none	47***	30***	25**	26**	-25**	-31***	-32***	44***	25**
tree height	-	01	22**	27***	-21*	-17*	-22**	34***	20*
tree age	38***	-	25**	27***	-20*	-31***	-30***	43***	17*
tree height and tree age	-	-	22*	27***	-21*	-18*	-23***	35***	20*

* = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$.

Molinia, Calluna, Erica cinerea, and Vaccinium have been reduced. It is interesting that by controlling for tree height, the linear relationship between nest diameter and tree age becomes non-significant, whereas tree height remains significantly correlated with nest diameter when controlled for tree age. Since both are inter-related, this indicates a complex relationship between nest diameter and tree age.

3.4 THE EFFECT OF SHADE

The importance of nest insolation has already been noted: the timing of nest activity in the spring, the development of brood and flight activities are all governed by the degree of insolation (cf. the work of Brian and Brian, 1951, on Myrmica ruginodis). The position of nests on roadsides or within woods is largely due to the availability of sites exposed to sunlight, and it is reasonable to suggest that the importance of nest-abandoning behaviour in small nests is due to the changing environment provided by younger plantations. The existence of long slopes on the mounds, independent of aspect is an adaptation which makes maximal use of available radiation.

Two series of observations were made to study the effect of different vegetation on ground insolation. Temperature profiles during 24 hours were obtained for shade plants, and light penetration was studied using photosensitive-paper integrators (Friend 1961).

3.4.1 TEMPERATURE PROFILES OF SHADE PLANTS.

Newly abandoned nests are sometimes overgrown with luxuriant Calluna growth, and few live nests have been discovered in tall Vaccinium. It is possible that the shade from these shrubs is detrimental to nest sites. The importance of Pteridium as a shade plant was stressed by Satchell and Collingwood (1955) who suggested that the spread of Pteridium might explain the decline of rufa in Windermere woods.

Temperature profiles of Calluna vulgaris, Pteridium aquilinum, and Vaccinium myrtillus were measured on successive days during a spell of fine weather in early June 1975 at sites in Kilcoran Wood. In each case, thermistor probes, with cooking-foil anti-radiation shields, were suspended at ground level, 0.5, 1.0, and 1.5 m from the ground (figure 3.4). The profiles recorded at three-hourly intervals are given in figure 3.5, where the height of the vegetation is also indicated. The results for Calluna are similar to those obtained by Delany (1953) and Gimingham (1972, p. 49).

The graphs for Calluna and Vaccinium show the same trends, and demonstrate that these shrubs exert a considerable shading effect at the hottest time of the day, while ground temperatures are actually warmer than ambient at night. The temperatures at different levels in Pteridium, on the other hand, were remarkably uniform except at 12.00. However, ground temperatures at a nearby site without Pteridium were up to 8°C higher during the early afternoon. This indicates that while Pteridium shade is not as complete as Vaccinium and Calluna shade, it considerably reduces ground insolation.

Field observation suggested that few nests occurred in tall bushy Calluna and Vaccinium. However, many live-active nests have persisted at sites overgrown with Pteridium throughout this study (one of these, KC-458a is shown in figure 3.4). The shade exerted by Pteridium - and by larch, is seasonal and both do not exert full shade until June. This suggests a seasonal response leading to nest abandoning, as otherwise sites with strong Pteridium shade should be abandoned immediately the shade appears in June. It can be noted that Carlson and Gentry (1973) induced nest moving in Pogonomyrmex badius (Latreille) from August to October by applying artificial shade to the nests.



Figure 3.4 Temperature probes (arrowed) in position at 0.25 m intervals through Pteridium aquilinum near nest KC-458a on 8.VI.1975.

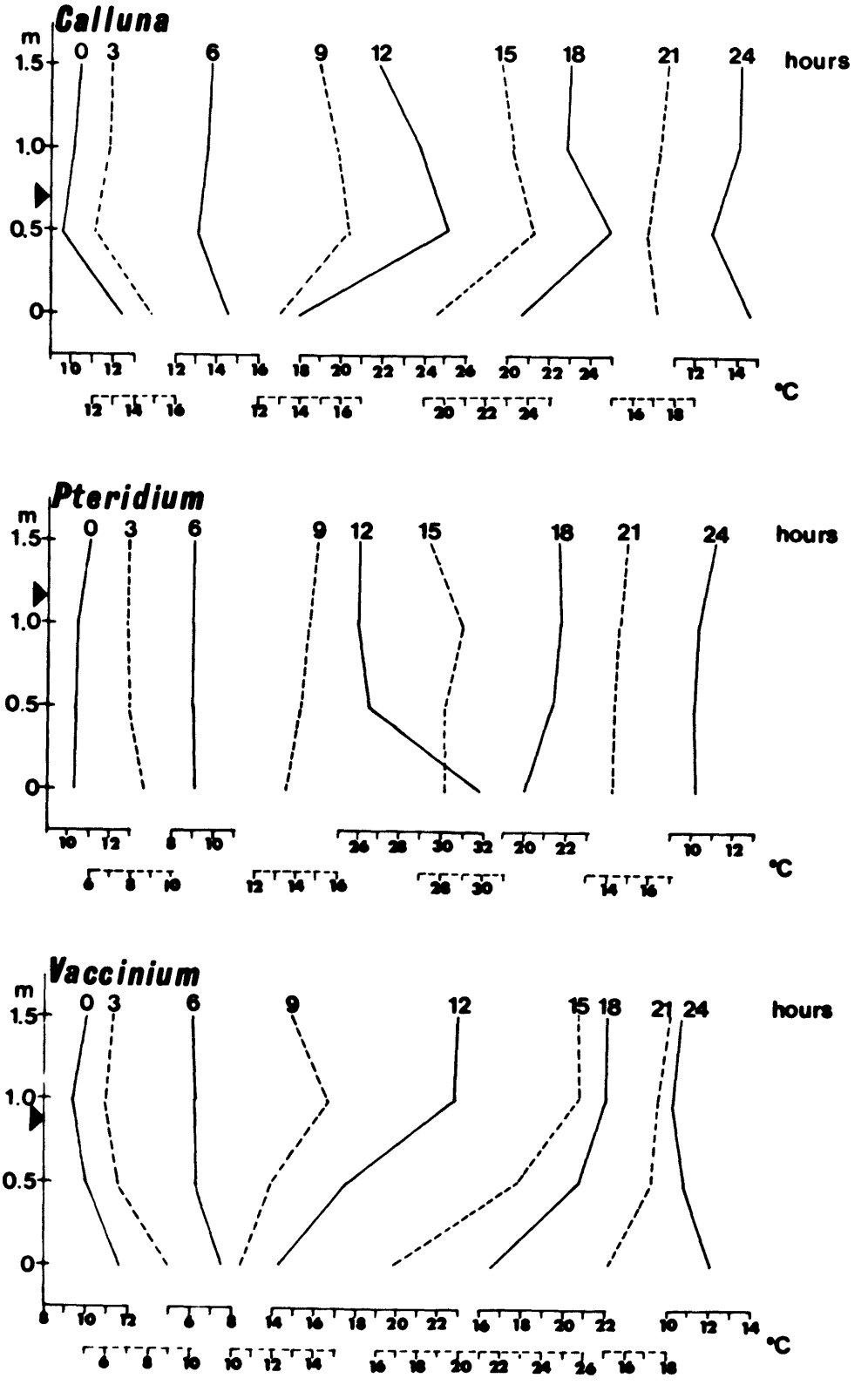


Figure 3.5 Temperature profiles during 24 hours of Calluna vulgaris, Pteridium aquilinum and Vaccinium myrtillus in Kilcoran Wood during early June 1975. Height of vegetation is indicated by a black triangle.

3.4.2 LIGHT PENETRATION.

Observations on light penetration were made in Moore's Wood on 27.V.1974, a dry cloudy day. Estimates of the percent light penetration were obtained using the photosensitive-paper light integrator method described by Friend (1961): 15-page booklets (c. 30 mm square) of photosensitive paper (Nig Banda paper for dryline copying - "blue-prints") are placed in disposable plastic dishes (diameter 90 mm). After exposure for a standard length of time, the booklets are developed in ammonia vapour. The number of pages bleached serves as a measure of the amount of light falling on the booklet during that time.

The plastic dishes were placed in position by night (26.V.1974), and removed the following night, thus overcoming the problem of exposing integrators simultaneously at a large number of sites. Integrators were placed on five 50 m-transects through different stands of wood, and on all the nest sites (60) then known in Moore's Wood. Five integrators were exposed at an unshaded site nearby and percent light was calculated by reference to these.

The five transects were located as follows:

A - Compartment 284, 8 m thicket-stage SS, 25 years old;
B - Compartment 284, 14 m high-forest stage SS, 39 years old;
C - Compartment 267, 7 m retarded SP, 39 years old;
D - Compartment 285, 13 m high-forest stage SP, 40 years old;
E - Compartment 259, 4 m young plantation PC, 8 years old.

The results are given in figure 3.6. The thicket-stage SS exerted the greatest shading effect, with the 14 m SS, 13 m SP, 7 m SP and the 4 m PC exerting less shading effect, in that order.

The percent peretration of light to the nest surfaces is given in table 3.13. Most of the live nests occur at above 80 percent light penetration. It can also be noted that there was only one abandoned site with above 90 percent penetration. Comparison of these results with figure 3.6 suggests a considerable nest-site selection dictated by the

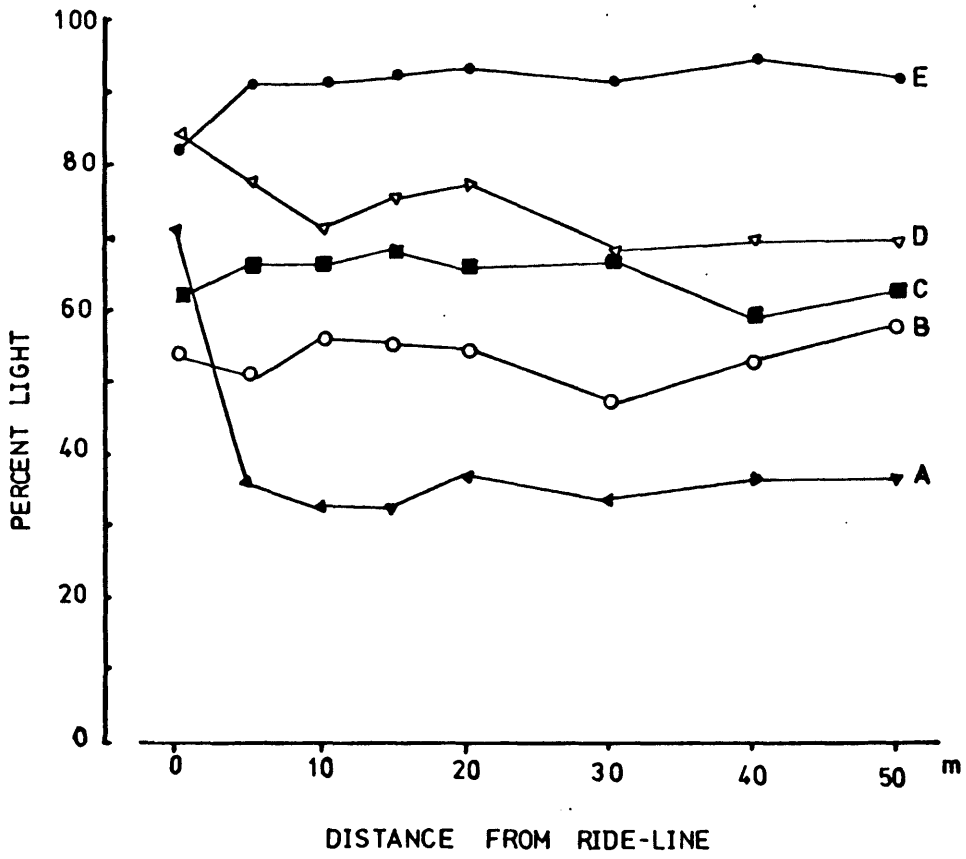


Figure 3.6 The percent light reaching the ground in five 50 m transects through different plantation stands, A to E. See text for explanation.

Table 3.13 The percent light falling on nest sites in Moore's Wood on 27.V.1975.

PERCENT LIGHT	LIVE	DEAD	ABANDONED
50 - 60	1	0	0
60 - 70	4	1	1
70 - 80	7	2	6
80 - 90	12	2	6
90 -100	14	3	1

range of canopies available. The data also suggest a reason for the observed paucity of nests under old SS, in comparison to the number found under old SP, eventhough many young nests are located in young SS and SS–PC mixed stands. Spruce passes through a dense thicket-stage with a very closed canopy, whereas pines do not. It is suggested that the thicket-stage canopy of SS causes the young nests to abandon the nest-sites once shade becomes excessive, and that they do not return when the canopy re-opens as the stand grows older. This stresses the importance of SP as an overhead tree for lugubris in Ireland, as being the only species now under plantation which provides suitable long-term canopy, and also acts as host to aphids.

3.5 SPATIAL DISTRIBUTION OF THE NESTS.

The spatial distribution of ant colonies has attracted interest in recent years principally because this type of analysis allows a number of aspects of community structure to be interpreted. The most frequently used technique is nearest-neighbour analysis, developed originally for use on forest trees. The methods available are reviewed by Southwood (1966, p. 39).

3.5.1 NEAREST NEIGHBOUR TECHNIQUE.

If, in the population to be studied, N is the number of individuals at a density ρ, and the distance r_a of each individual to its nearest neighbour is known, then the mean observed distance is given by

$$\bar{r}_a = \frac{\Sigma r_a}{N}$$

Clark and Evans (1954) derived a method of calculating the expected mean

distance, $\bar{r}_e$ if the individuals in this population were distributed at random,

$$\bar{r}_e = \frac{1}{2\sqrt{\rho}}$$

The ratio, $R = \bar{r}_a / \bar{r}_e$ can be used as a measure of closeness to, or departure from, random expectation. R equals zero when the individuals are perfectly aggregated, and values of 1.0 and 2.149 are obtained if the distribution is random, or hexagonal (maximum spacing), respectively.

Clark and Evans (1954) also provided a means of calculating the significance of R, by deriving c, the standard variate of the normal curve. Values of probability can be read off in tables of the normal distribution.

Previous applications of this method in ant studies include those on Lasius flavus (Waloff and Blackith 1962; Blackith et al. 1963), Solenopsis saevissima (Smith) (Eisenberg 1972), and using an extension of the technique to consider two species simultaneously, Lasius flavus and Myrmica rubra (Elmes 1974). Values of R obtained were: Lasius flavus R = 1.25; Solenopsis saevissima R = 1.32; Myrmica rubra R = 0.78. Baroni Urbani and Kannowski (1974) demonstrated aggregation in Solenopsis invicta Buren colonies using a different analytical approach.

3.5.2 APPLICATION TO LUGUBRIS NESTS.

An opportunity arose in 1974 to study the spatial distribution of the lugubris nests in compartment 450 of Kilcoran Wood. Most of this compartment was planted in 1946 with PC, which proved an unsuccessful forestry crop. Many old SP were dispersed through the compartment and canopy was generally very open. It was known that a large number of nests were located here. When the Forestry Service decided to bulldoze the entire compartment, an arrangement was made to spare and mark all the nests.

A total of 33 nests were located in the compartment. Each nest was mapped accurately by Mr G. Breen using a self-reducing tachymeter (Kern and Co., Aarau, Switzerland), and the calculations were made from a 1:1000 scale map. Figure 3.7 is based on a reduction of this map.

The results, in table 3.14, give a value of R = 1.33, which is significantly different ($P < 0.01$) from random in the direction of uniform dispersal. This result is interesting since no allowance was made for a quarry, road, and a plot of successful PC (0.3 ha) which did not contain any nests. Furthermore, the result was obtained without considering colony size and age, both of which are probable influences on territory size. While a larger sample of nests would have been desirable, it is possible to conclude that the nests in KC-450 were uniformly and not randomly distributed. This spacing can be interpreted to suggest that the observed density (1 nest per 4609 m^2) approached the maximum possible under pine plantation in Ireland. The result may also indicate that a certain degree of competition existed between the nests and, if so, this is further evidence that polycaly is not common in Irish lugubris colonies (see 4.7).

3.5.3 APPLICATION TO URALENSIS NESTS

Table 3.14 also contains results of a similar analysis carried out on all the living mounds in the map provided by Rosengren (1969, figure 2) for a polycalic nest system of uralensis in Finland. As expected, the value of R = 0.72 indicates a significant ($P < 0.01$) departure from random expectation in the direction of aggregation. It can be concluded that the nearest-neighbour technique is sensitive enough to indicate the existence of aggregation caused by a polycalic nest system, and this supports the view expressed above that Irish lugubris nests are not aggregated.

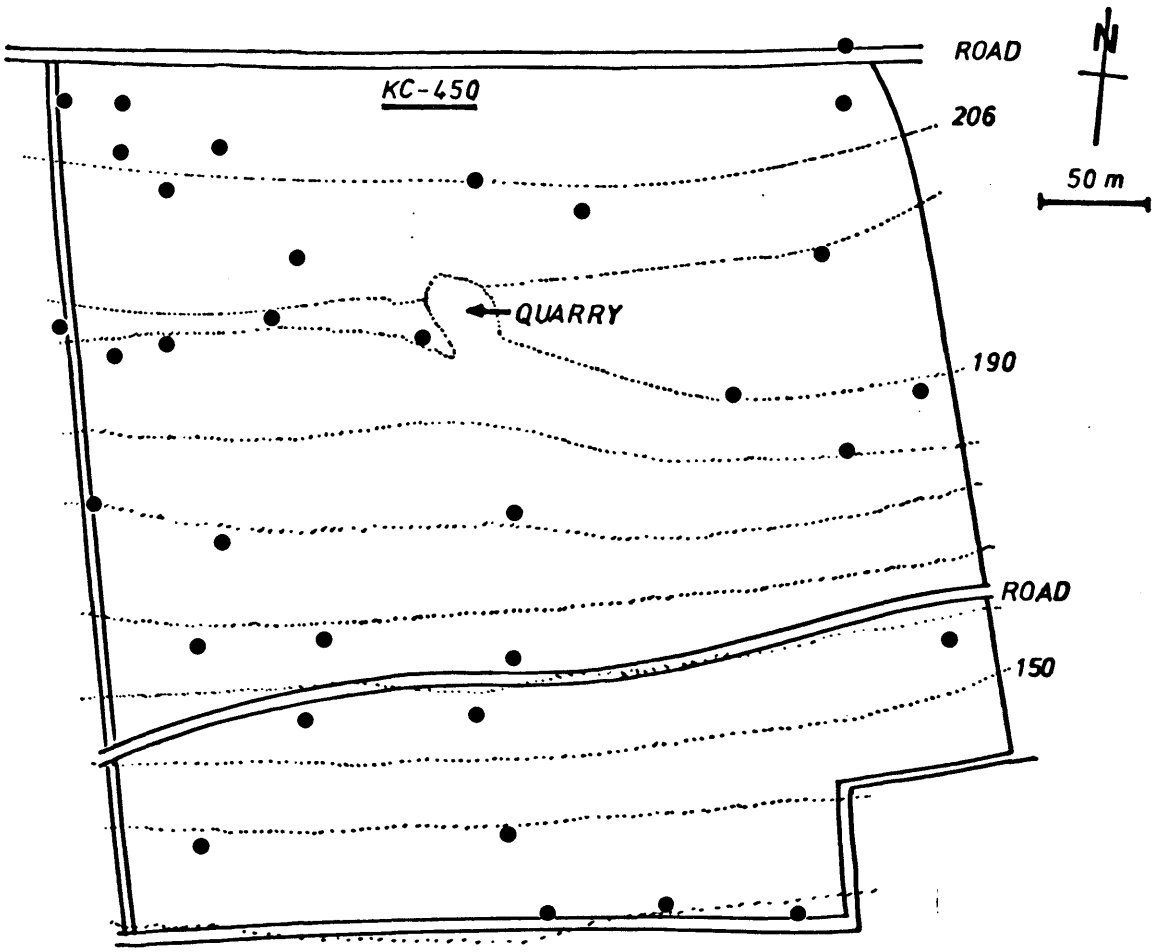


Figure 3.7 The nest distribution in compartment 450 of Kilcoran Wood during summer 1974. Two roads are indicated and the other boundaries are ride-lines. The dotted lines are 8 m contours.

Table 3.14 Nearest neighbour analysis of lugubris and uralensis* nests. The terms are as used in the text.

	lugubris	uralensis
Area (m^2)	152 090.5	18 210
N	33	25
ρ	0.00022	0.00137
R	1.33	0.72
P	< 0.01	< 0.01

* data from Rosengren (1969, figure 2).

4.0 ROUTE TRAFFIC DYNAMICS AND COLONY PARAMETERS

Ant foraging strategies are legion. Among them, the raiding bands of driver ants, the pheromone trails of species such as Lasius fuliginosus, and Solenopsis spp., and the foraging routes of wood ants are well-known. Sudd (1967, p.48) suggested that the term "route" be applied to the tracks of wood ants, and the term "trail" be applied to the pheromone-based foraging method. This convention is followed here.

A number of aspects of foraging ecology, considered here, were reviewed by Carroll and Janzen (1973). These authors suggested that foraging behaviour of ants can be considered under these broad aspects: spatial distribution of foragers in the foraging arena, the timing of forager activity in the 24-hour cycle and seasonally, the type and quantity of food, and the numbers of foragers. In addition to observations on each of these aspects, this chapter also contains colony size estimates of five nests using the mark-release-recapture method.

4.1 ABBREVIATIONS, TERMS AND METHODS.

Where possible, abbreviations and terms used here are consistent with those proposed by Rosengren (1971), and are as follows:

(1) An ant column is defined as a "spatial concentration of ants moving in the same direction" along an ant route, which is "a way fixed in relation to topography along which ant columns are observed to be moving during several successive inspections" (Rosengren 1971).

(2) C (="conservants") are ants resighted on the route on which they were marked, and D (="deviants") are ants resighted on any other route (Rosengren 1971).

(3) RF = "route fidelity" is equal to $100.C/(C+D)$. In some experiments, where different colours are used in a route system, $RF = 100.\Sigma C/(\Sigma C + \Sigma D)$ (Rosengren 1971).

(4) Foragers will be denoted by a two-letter abbreviation of the material being carried: H = honeydew; P = prey; V = vegetation; in any combination (e.g. HP = honeydew + prey) or combined with "A" (for "alone") if only one material is being carried (e.g. HA = honeydew alone). NA (= "not assigned") are those foragers travelling towards the nest, apparently unloaded.
(5) Adult-carrying behaviour refers to the carrying of live, unharmed ants by nestmates. The abbreviation AC will refer to the "adult carrier" and CA will refer to the "carried adult" during adult-carrying behaviour.

Methods:

Most of the observations were made in Kilcoran Wood (with one in Moore's Wood and one in Glengarra Wood) during the summer/early autumn of 1974 and 1975. Various nests were chosen for study (each is described with a map); choice of nest was made on the basis of accessibility, routes with good traffic and absence of recent disturbance by forestry management. The study nests will be referred to by a single letter (A to J) and can be identified by reference to table 4.1. The use of a number of study nests facilitated the running of a number of experiments simultaneously; a much longer term study would be required to obtain exactly the same amount of data from a single study nest because of the limitations of marking.

Ants were marked, on the gaster, with a spot of HUMBROL (Hull, England) enamel paint using a pine-needle as an applicator (the "individual" method). Such marks have been observed seven months later, but most had faded or chipped-off after a month. The following different colours could safely be distinguished in the field: white, orange, yellow, green, blue and red. Ants were removed from the route (distance from nest given in relevant section, usually about two to three metres), counted and placed in a FLUON-coated basin. After marking they were retained about 30 minutes for drying and then released on top of the nest. Gloves were always used for handling as a protection against the formic acid. Mortality prior to

Table 4.1 A list of the study nests used for the experiments described in chapter 4.

NEST	IDENTIFICATION
MW-267a	A
KC-451h	B
KC-440g	C
GG-902c	D
KC-438b	E
KC-457a	F
KC-441a	G
KC-452b	H
GG-936d	I
GG-936b	J

release was in the order of two percent.

During 1975, an additional method of marking was employed: ants were counted into FLUON-coated basins, and sprayed with HUMBROL aerosol paint held c. 250 mm away (the "spray" method). This method allowed quick marking of large numbers. Only one colour was used, though the spray method was used in conjunction with the individual method. The spray mark appears to be rather more permanent, though there is a risk of applying too much paint and immobilizing the ants.

Ants marked by both methods did not appear to be affected by the mark and have been observed to carry out all forager duties with apparent normality. Similar conclusions have been made by Rosengren (1971) and Kiil (1934) both of whom have used a marking method identical to the individual method. Rosengren's alternative method of spraying aerosol paint onto an ant column on the route does not allow population estimation, and was not used. The methods used differ from those of Økland (1931) and Dobrzanska (1958), who did not remove the ants from the route for marking, as this precludes marking large numbers.

Sightings of marked individuals are termed "recaptures", and were counted in two ways, viz. (a) a five-minute count was made at a census point on each route, using a stop-watch and a tally-counter. If the flow of traffic was too great for accurate counts - as when a number of different colours were used, the count was performed by first counting separately the ants travelling to, and then those from, the nest. When low counts were expected, longer counts (up to 15 minutes) were made. (b) By scanning portion of, or all of, one of the routes and noting all marked ants. Both of these counting methods differ slightly from those of Rosengren (1971) though they yield similar data. Most of the data presented here are based on 10 five-minute counts on each route of the study nests. Relative activity of each route was estimated from the total

five-minute counts for that route compared to the total five-minute counts for all routes.

On each occasion ground and air temperature, time of observation and estimated cloud cover were noted, though the counts are generally presented as averages of pooled data. Counts were made on various occasions and dates, no more than three per day. An attempt was made to spread the time of making the count as evenly as possible to avoid any bias due to diurnal rhythms.

4.2 ROUTE FIDELITY: AN INTRODUCTION.

It is well known that individual forager wood ants return repeatedly to forage in approximately the same site - "site fidelity" (Økland 1931; Kiil 1934; Otto 1958). Rosengren (1971) studied the fidelity of foragers to individual routes leading to the foraging sites ("route fidelity"). The work of Kiil (1934) and Dobrzanska (1959) also suggested that a certain degree of task preference, or "division of labour" existed amongst wood ant foragers. Considered together, the effect of these foraging characteristics has been interpreted (Økland 1931; Dobrzanska 1958) as a means of partitioning the foraging territory amongst the available workers.

However, in many of the earlier studies just referred to, not only has the earlier nomenclatural controversy obscured the nature of the species studied, but also, the studies were not pursued on a strictly quantitative basis. Furthermore, data obtained by Holt (1955, table 11) for aquilonia suggested that "it is evident that a particular forager does not always use the same track". This was a contradiction of earlier work and has been discussed by Sudd (1967, p.82). Sudd suggested that there may be specific or regional differences in fidelity, or differences between prey-hunters and honeydew carriers. This situation could only be clarified by quantitative studies on different wood ants.

Rosengren (1971) provided a detailed quantitative study of route fidelity and aspects of task fidelity of both rufa and polyctena, and added notes on lugubris, uralensis, Formica sanguinea Latreille, and F. exsecta Nylander. He demonstrated route fidelity in rufa, polyctena, lugubris and uralensis . Route fidelity in rufa was lower in May than later in the season, and the fidelity did not lessen with time.

This section contains the results of observations made on lugubris route fidelity during the present study. Experiments were designed to examine aspects of the forager route fidelity, (a) to obtain a baseline figure for RF, (b) to study fidelity at a Y-junction, and to individual trees, (c) the effects of various treatments on RF, and (d) the effect of long-term absence from the route on fidelity.

4.2.1 ROUTE FIDELITY.

Observations were made at nest A during April 1974. A map of the route system is given in figure 4.1a. The nest is located near a 39 year-old PC stand and a young SS/PC stand (see figure 5.2), and has been in its present site for five summers. It previously occupied a nearby roadside site. The route system has been similar since 1972, though the tendency of Cinara piceae, the main honeydew source, to change from tree to tree during the year imposes local changes in the final destination of each route.

On 17-18.IV, a total of 375 foragers on route 1 and 325 on route 5 were marked 2 m from the nest by the individual method, using different colours. From 19-27.IV a total of two five-minute counts and seven scans of the entire route system were made. The results were pooled and are given in figure 4.1b. Since there was no significant difference between the the number of deviants (D) from either route ($\chi^2 = 0.46$, 1 d.f., $P>0.3$), the data from both routes were pooled to give a RF of 86.

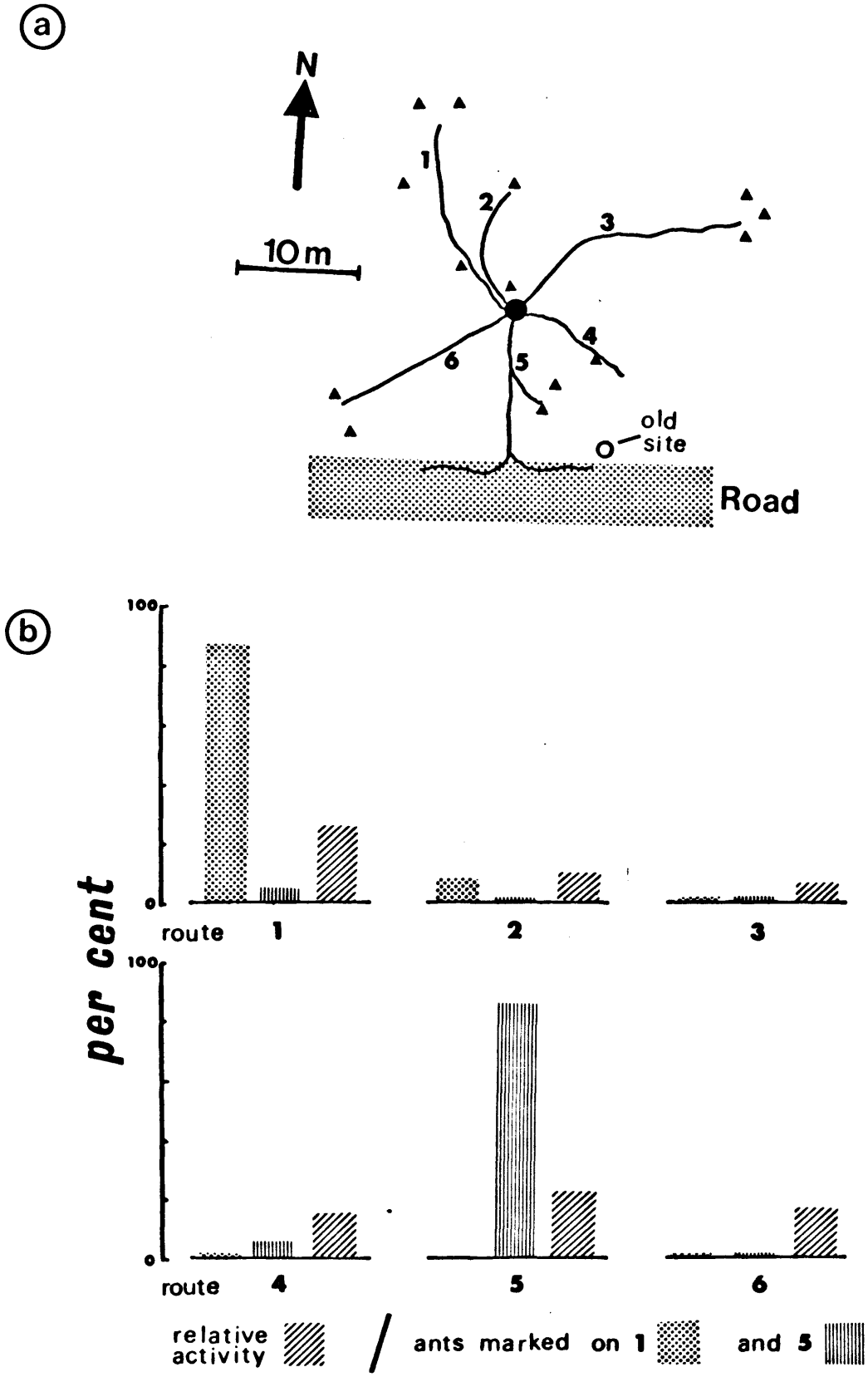


Figure 4.1 Route fidelity studied at nest A during April 1974. (a) map of the route system, (b) the numbers of ants marked on routes 1 and 5 resighted on all routes. The relative activity of each route is also given.(▲ are SS aphid trees.)

Additional examples of route fidelity are given in figure 4.2. These data are based on the count method (usually 10 counts on each route) at a census point two metres from each nest. In all cases the ants were marked by the spray method, and were taken from route 1, as given in the nest diagrams. The values obtained for RF were 63 at nest G, and a range from 88 to 100 at the other nests.

The data in figure 4.1 demonstrate a convincing route fidelity in lugubris. It can also be seen from both figures 4.1b and 4.2 that D are most likely to occur on the routes adjacent to the "marked" route. The results are similar to Rosengren's (1971) for rufa and polyctena, and suggest that Holt's (1955, table 11) observations on aquilonia are exceptional and need confirmation (calculated as here, RF = 55). The single low value for RF (=63) recorded here is also difficult to explain. However, it can be noted that the marking date coincided with the mass-appearance of Adelges sp. (laricis Vallot ?) on European larch, and that foragers from this nest formed a route of over 225 m to these trees. It is interesting to suggest that the low RF was caused by some form of recruitment away from the marked route. Recruitment behaviour was demonstrated in Campanotus socius Roger by Hölldobler (1971) and in Formica exsecta, rufa, and polyctena by Rosengren (1971). The latter author thought the recruited ants were young "naive" foragers, but if the above interpretation is correct, then recruitment may be more general.

The experiments described in the following sections are further sources of RF values, and their controls are included here. All the available RF values obtained in the present study are plotted on a time of year scale in figure 4.3, regardless of the year the results were obtained. Rosengren (1971) suggested, on the basis of evidence from a single nest of rufa that there was seasonal variation in RF, beginning low early in the foraging season (his first observations in May gave an RF

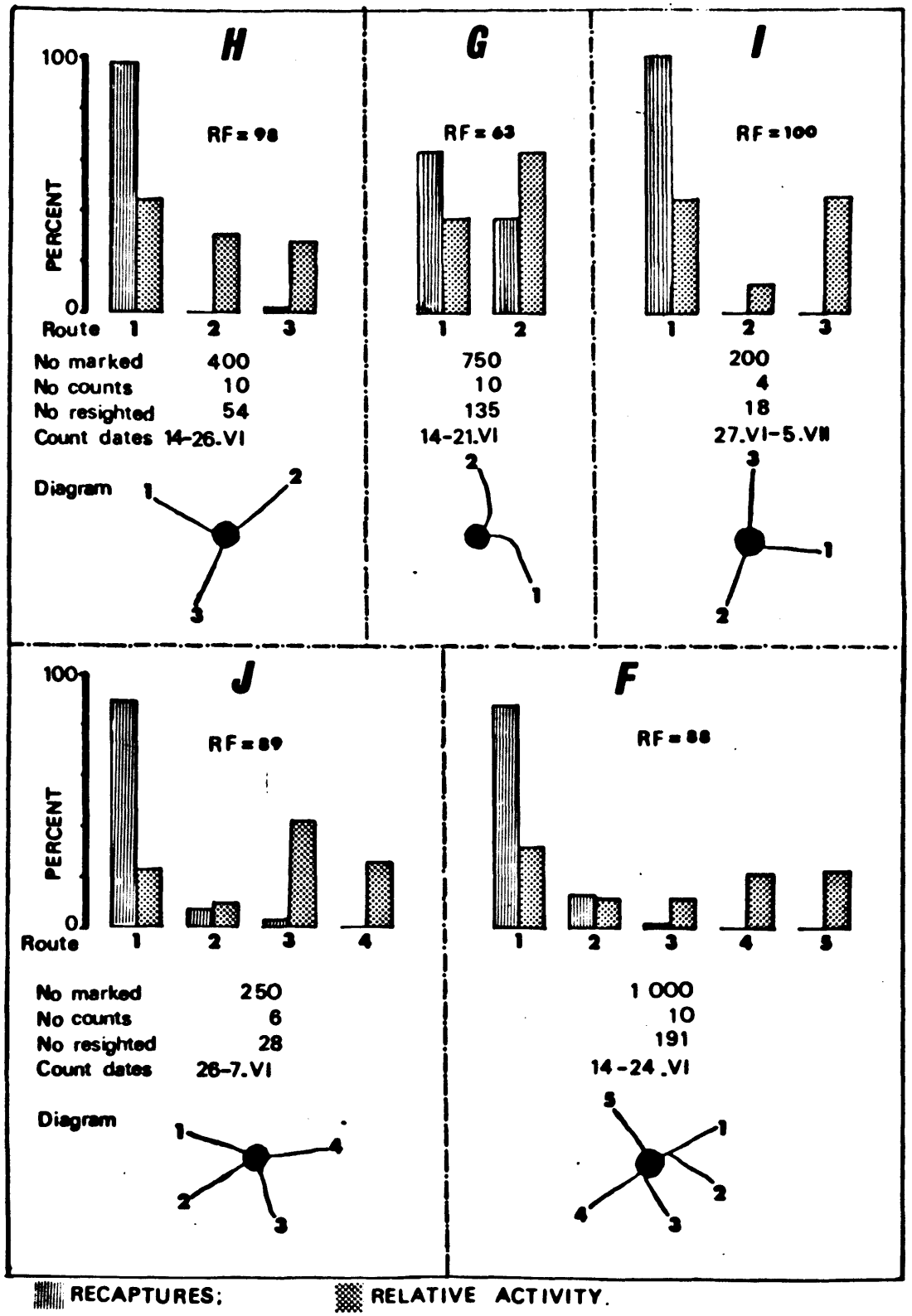


FIGURE 4.2 THE ROUTE FIDELITY OF FORAGERS WHICH WERE SPRAY-MARKED ON ROUTE 1 OF NESTS H, G, I, J, AND F DURING SUMMER 1975.

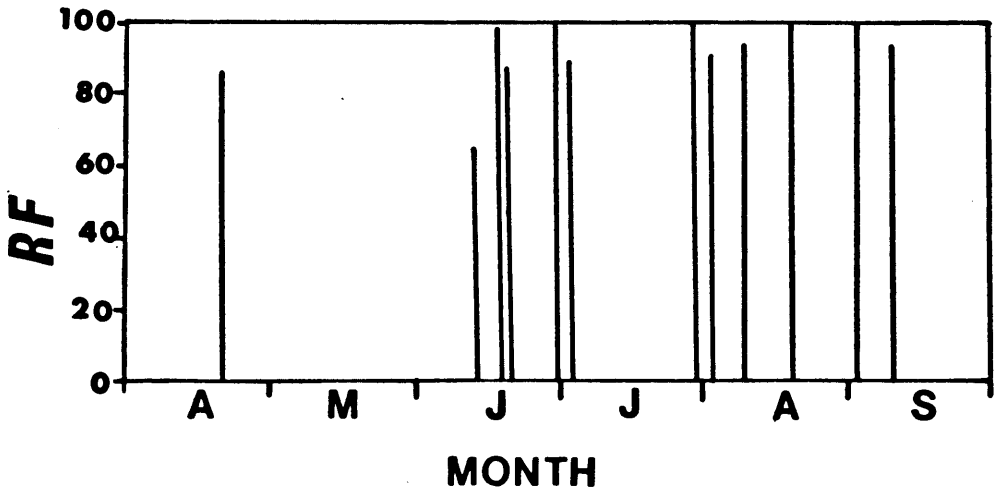


Figure 4.3 Route fidelity at various nests at different times of the year.

value of 70), and becoming higher with the advance of the summer (RF 85 in July and 96 in August). The data in figure 4.3 suggest a considerable inter-colony variation of RF in lugubris, without any apparent increase in RF during the year.

4.2.2 THE Y-JUNCTION EXPERIMENT

From July to September 1974, observations were made on route 1 of nest B, a large active nest located in a 29 year old pine stand. A map of the route system is given in figure 4.4. Route 5, shown in figure 4.4, was not present during 1974, although a certain amount of scattered, unmonitored foraging did take place on the ride line. The aphid attended was Cinara pini, which occurred on the few scattered SP amongst the otherwise pure PC stand.

Route 1 had an obvious Y-junction about 11 m from the nest, giving rise to two branches, A and B. Branch A led to a single SP tree w, while B led to three SP trees x, y and z. The short portions of the route leading to each of these trees will be referred to as sections x', y' and z', and these arise from a common stem called "MAIN". The following numbers of foragers were marked by the individual method (using a different colour for each) on these dates:

500 from A and 500 from B on 24.VII
250 from z on 26-7.VII
150 from y on 27-8.VII
100 from x on 28.VII

The samples from A and B were taken 2 m from the Y-junction, and those from x, y, and z were taken as they descended their respective tree.

Two series of counts were made at a census point on all routes. The first was made from the 26-29.VII and the second from the 27.VIII to 17.IX. Both series consisted of 11 five-minute counts on all routes and 11 scans of the entire route 1. During the scans, the data from the different sections of route 1-B were recorded separately.

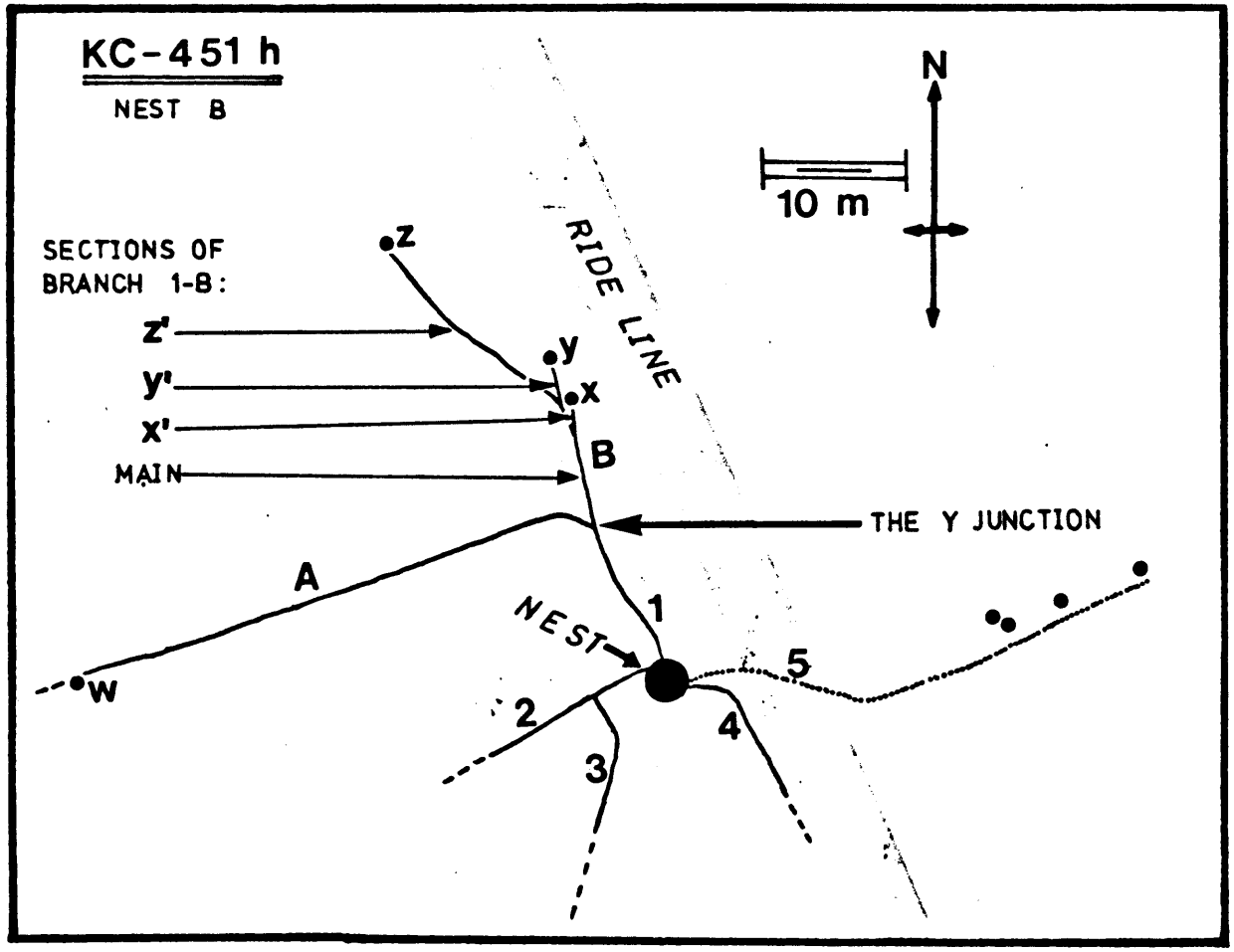


Figure 4.4 The route system of nest B during 1974 and 1975. ● = SP aphid trees.

The data were analysed to provide the following information: (a) a RF value for route 1, for branch A and B, and also for sections x', y', and z'; (b) the effect of time on RF, by comparing the data from series 1 and series 2; and (c) the total forager population on route 1 and its deployment.

Table 4.2 gives the data of the Y-experiment from which the RF values of route 1 and at the Y-junction were calculated for both series of data. The RF value of 100 for route 1 fell to 90 a month later, and this was statistically significant ($P < 0.001$). However the RF at the Y-junction remained much the same during both series of observations. This may indicate that, over a prolonged period of time, foragers are more likely to change to different routes than to branches of the same route, though all the RF values are still very high after 30 days.

Table 4.3 gives the data obtained by marking foragers from three aphid trees. The data were obtained as follows: eleven scans of route 1-B were made 30 days after marking, and the counts obtained for different sections of the route recorded separately. In this way, an ant marked on tree x was scored as C if sighted on section x', but as D if sighted on either section y' or z'. The calculated RF of 93 shows a remarkably high long-term fidelity to individual trees within a route system. The expected and the observed numbers seen were similar ($\chi^2 = 0.31$; 2 d.f., $P > 0.2$) and indicate a consistency in the marking and counting procedures.

The count data of series 1 was applied to the capture-mark-recapture formula (see 4.6) to give the details of the forager deployment on the route system of nest B, and the results are given in table 4.4.

4.2.3 EFFECT OF ABSENCE FROM THE ROUTE ON FIDELITY.

One of the intrigueing characteristics of wood ant routes is their longevity. Stäger (1936) reported routes lasting 14 years in wood ants,

Table 4.2 Data from the Y-junction experiment at nest B during 1974.

	C	D	C + D	RF
series 1 route 1	205	0	205	100
series 1 Y-junction	848	22	870	97
series 2 route 1	134	10	144	93
series 2 Y-junction	763	32	795	96

X^2-tests on the data:

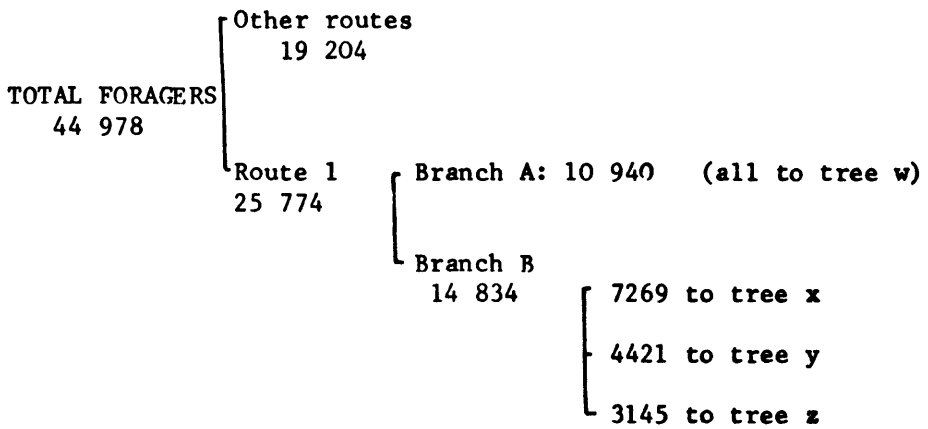
route 1 (series 1) and route 1 (series 2): $X^2 = 14.66$, $P<0.001$.
Y-junction (series 1) and Y-junction (series 2): $X^2 = 2.96$, N.S.
route 1 (series 1) and Y-junction (series 1): $X^2_2 = 5.29$, $P<0.05$.
route 1 (series 2) and Y-junction (series 2): $X^2 = 2.43$, N.S.

Table 4.3 Results of the marking of foragers from the three SP trees x, y, and z on route 1-B of nest B. Numbers in parentheses are considered as D, and RF is calculated from the data for sections x', y', and z' (see text).

	MARKED ON		
SIGHTED ON	x	y	z
MAIN	15	21	16
x'	13	0	0
y'	(2)	23	(3)
z'	(1)	0	50
Totals:	31	44	69
Expected:	28.8	43.2	72.0

Overall RF: 93.

Table 4.4 The deployment of foragers on the route system of nest B during July 1974, estimated by the capture-mark-recapture method applied to the series 1 (26-29.VII.1974) data.



Chauvin (1962) described a route system of polyctena over a six year observation period, and Rosengren (1971) observed that the route system of a rufa colony remained relatively unchanged for nine years. It has been noted during this study that the route system of lugubris remains unchanged, or almost so, from year to year. This is especially obvious in pine stands, where the SP with Cinara pini remain constant aphid trees from year to year. The tendency of C. piceae on SS to change from tree to tree during the year, acounts for minor changes in the route systems of attendant ants. Small changes in the route do occur: thus in the Y-junction experiment reported above, branch 1-A was marked, for the observer's benefit, with eight pairs of small stakes (butchers' skewers); after the resumption of foraging in 1975, the route now adopted still passed through six pairs of stakes, but had deviated slightly around two pairs. Nevertheless, the branch route 1-A was essentially unchanged.

The effect of absence from the routes during winter (about three months) on RF merits consideration. However, experimental foragers from KC-451f failed to overwinter successfully in a polythene bag kept in a cold room at 2 - 4°C, and no observations were made.

The following experiment however, tests the effect on RF of long-term absence from the route system during summer 1975. The same nest and route system (nest B, route 1 before the Y-junction) as studied in 4.2.2 was used again here.

At regular intervals during summer 1975, 700 to 1000 foragers were removed from route 1 and maintained separately in FLUON-coated pans near an opened window in an unheated building near the laboratory. Some regularly-dampened nest material and peat was provided, and honeywater on cotton wool was given as food. Even so, mortality after one month's confinement was considerable, and can be gauged from the number released

on each occasion (table 4.5). Following release on the 10.VIII, 10 five-minute counts were made on each route from 17-28.VIII. Table 4.5 gives the number released, their period of absence from the route, and also the results of the counts. There is a significant difference between the results obtained for the 14 and 32 days samples when compared to the 0-day control (χ^2 = 5.26, 1 d.f., $P<0.05$; and χ^2 = 10.11, 1 d.f., $P<0.01$, respectively), but not between the results for 14 and 32 days (χ^2 = 0.90, 1 d.f., $P>0.7$). This indicates that absence from the routes has a measurable effect on RF. Kiil (1934) showed that absence of five days caused no reduction of fidelity of wood ant foragers. However, these results are similar to those obtained by Rosengren (1971) for rufa isolated from the nest for 30 days.

4.2.4 THE EFFECT OF "REMOVING" AN APHID TREE.

During the end of August and early September 1974, an experiment was carried out on route 3 of nest C to study the effect of temporarily removing access to an aphid tree on the RF of honeydew carriers (HA). A map of the route system is given in figure 4.5. Route 3 was very suitable for this experinent as it led only to a single SP (the aphid was Cinara pini) and foragers did not travel beyond it. Hence it was safe to assume that the aphid tree was the major food source of the route.

On 27.VIII, a total of 400 HA and 155 preycarriers (PA) from route 3 were marked by the individual method, using different colours. Three series of counts (10, 10, and three counts, respectively; up to four in any one day) were made on each route. The first series (from 28.VIII to 5.IX) act as a reference point with series 2 (from 7-10.IX) During series 2, the foragers were effectively excluded from their aphid tree by a grease-band (Corry and Co. Ltd., Bone Lane Industrial Estate,

Table 4.5 The effect of absence from route on RF, studied on route 1 of nest B during summer 1975. Marking was either by the spray (a) or individual (b) method.

days absent	0	14	32	46	61
number released	569	371	569	21	91
marking method	a	b	b	b	b
C	77	42	42	2	3
D	0	3	6	1	3
C + D	77	45	48	3	6
RF	100	93	88	67	50

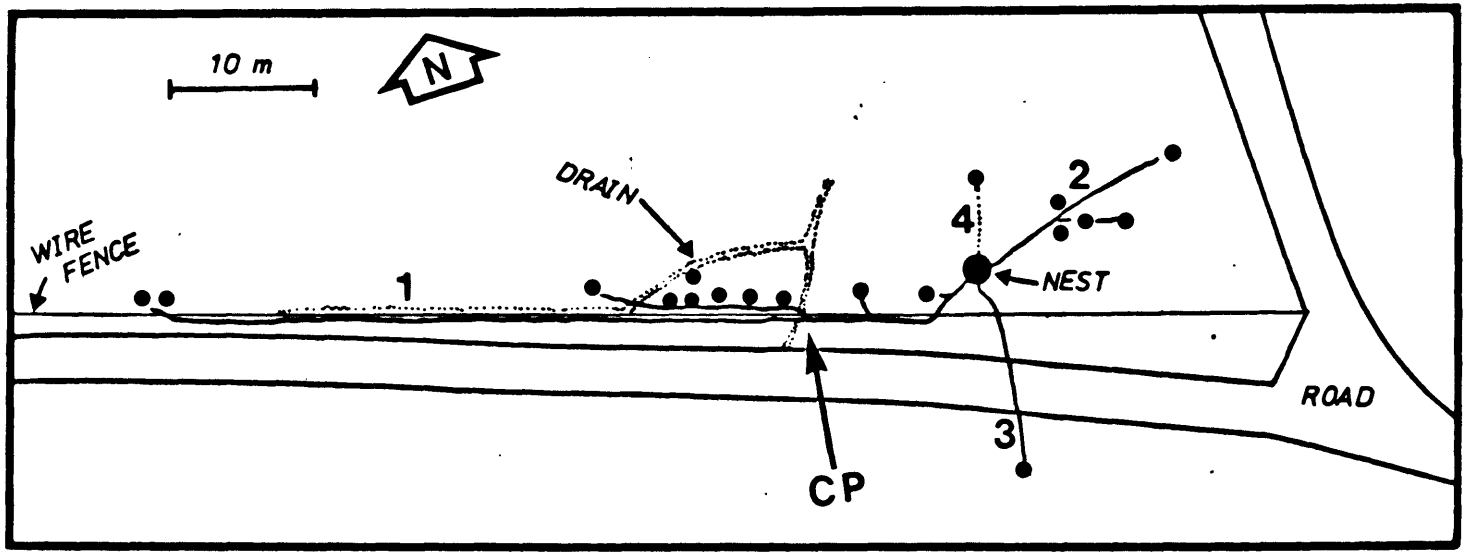


Figure 4.5 Map of the route system of nest C during 1974 and 1975. The observations described in 4.4.1 were made at point CP. ● are SP aphid trees.

Newbury, Berks., England). The series 3 counts, all made on the 15.IX, were to monitor possible after effects.

The results are given in figure 4.6 where it should be noted that different scales are used for the route 3 and routes (1 + 2) data. Though other factors are likely to be involved, there seems to be a clear relationship between numbers of foragers passing in five minutes and ground temperature (correlation between total foragers and temperatures: series 1, $r = 0.63$; series 2, $r = 0.82$). Note that the traffic on route 3 was lower, proportionately, during counts 7, 8 and 9 (correlation between number of foragers and temperature for route 3, series 2: $r = 0.16$, N.S.). However the number of ants marked as HA and resighted remained quite constant throughout the observations, with only slight drop-off with time. Very few marked ants appeared on either route 1 or route 2: RF for series 1 data, based on 100 recaptures was 100; RF for series 2 data, based on 62 recaptures was 94; RF for series 3 data, based on 11 recaptures was 100. There was a statistical difference between the number of D in series 1 and series 2 and 3 pooled together ($\chi^2 = 6.61$, 1 d.f., $P<0.05$), but this is probably due to the effect of time on RF (see 4.2.2).

The best interpretation of the data, which is supported by the field observations, appears to be that the RF of foragers on route 3 was not changed during the experiment. However the traffic on route 3 was lower during the latter counts of series 2. This can be explained by the fact that the the foragers were observed to loiter around the grease-band, and on the route, eventually to return empty to the nest. Consequently, lower traffic counts were obtained, even though the ants did not change their allegiance to route 3. Normal foraging resumed when the tree was "restored" and subsequent checks of routes 1 and 2 did not show-up any influx of marked ants onto these routes.

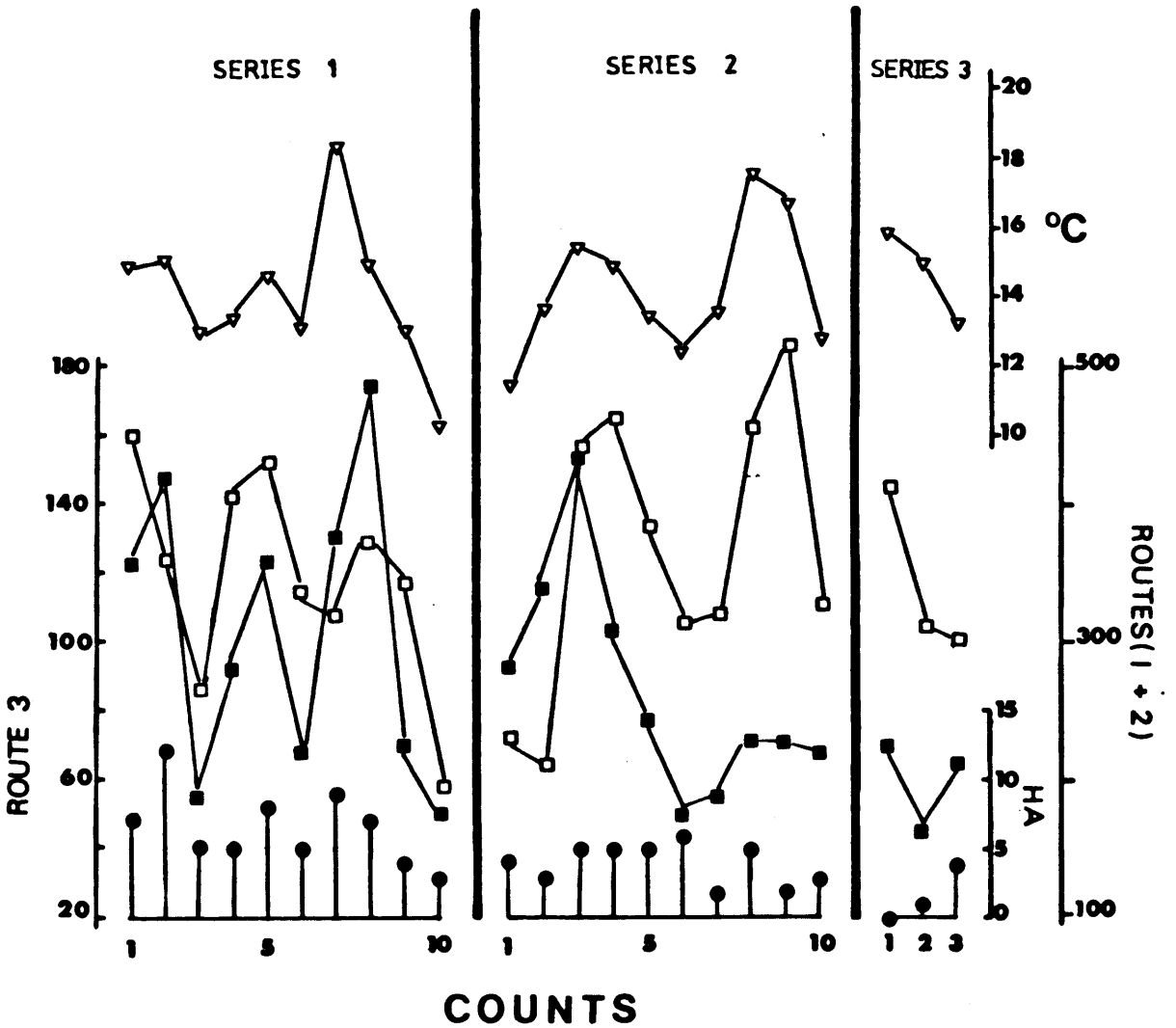


Figure 4.6 The effect on forager RF of "removing" an aphid tree. See text for explanation. The heavy vertical lines enclose those counts made with the greaseband in position. KEY: ■ = route 3 counts; □ = counts of routes 1 and 2 pooled; ● = number of HA sighted; ▽ = ground temperature.

4.2.5 EFFECTS OF VARIOUS TREATMENTS ON RF

Weir (1957) showed that the effects of anaesthesia with ether, carbon dioxide and nitrous oxide on laboratory colonies of Myrmica rubra were significant and different. All treatments reduced longevity, and the first two also reduced oviposition. However, Rosengren (1971, figure 6) mentions in passing that carbon dioxide anaesthesia did not effect the RF of rufa foragers, though he does not give the data. Otherwise there seems to be little information on the subsequent behaviour of anaesthetized ants.

Many studies have been made on the effect of different anaesthetics on the behaviour of Apis mellifera L. The results obtained by Ribbands (1950) and Simpson (1954) suggest that chloroform anaesthesia does not impair the memory, change the forager behaviour, or reduce the longevity of treated bees. Carbon dioxide and nitrogen anaesthesia did not impair the memory; however, treatment with both of these anaesthetics and also nitrous oxide anaesthesia caused a permanent change in forager behaviour - pollen-collecting activity was entirely eliminated.

An experiment was performed at nest D to assess the effect, if any, of carbon dioxide-, nitrous oxide-, and chloroform-anaesthesia on RF of treated workers. In addition, the effect of the phosphorus-32 mass-marking technique, described in 4.6, was tested side-by-side.

Nest D is a large active nest with six short foraging routes leading to both SS and SP aphid trees. A map of the route system is given in figure 4.7. Foragers from route 1 (taken 2 m from the nest) were confined in FLUON-coated basins and treated with nitrous oxide, carbon dioxide, and chloroform. Treatment was continued for three minutes after movement ceased. This method worked well with carbon dioxide and nitrous oxide and recovery was fast from these. However recovery from this amount of chloroform anaesthesia was slow - many ants had not recovered

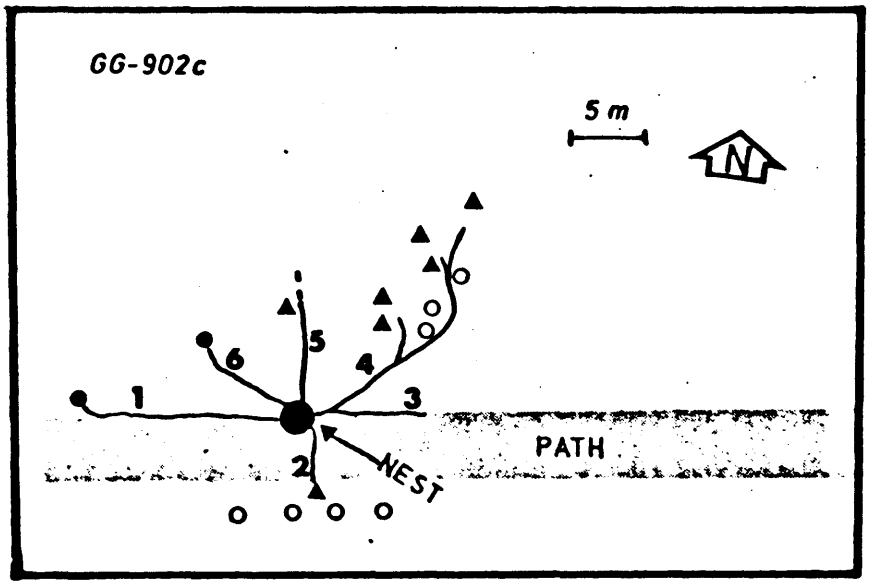


Figure 4.7 The route system of nest D during 1975. o = SP and Δ = SS, and the symbols are blacked in when the trees are aphid trees.

after four hours, and about 30 percent of the chloroform-anaesthesia sample was obtained by subjecting a further sample of foragers from route 1 to chloroform vapour and exposing them to air immediately movement ceased. These recovered quickly from this shorter anaesthesia. The phosphorus-32 (P-32) treatment was as described in 4.6. A total of 375 ants were marked for each treatment, those given P-32 treatment were spray marked, and the others were marked by the individual method using different colours. A no-treatment control was also marked.

The results in table 4.6 are based on nine five-minute counts on each route. These show that the effect of three of the treatments was not significantly different from the control when compared by the χ^2 test. The result for the treatment with nitrous oxide anaesthesia is just significant at the five percent probability level though the low counts preclude conclusive comments. It thus seems that treatment with these anaesthetics has little effect on RF of foragers.

4.3 OBSERVATIONS ON TASK FIDELITY.

Task fidelity refers to the phenomenon of the same ants performing the same tasks over a period of time. In recent social insect literature it is referred-to synonymously with the term polyethism - and analogously with polymorphism (see Sudd 1967, p. 154; Wilson 1971, p.476).

Worker wood ants show weak polymorphism, characterized by monomorphic allometry and a tendency towards bimodalism in size-frequency diagrams (see Kiil, 1934 and van Boven, 1961 on wood ants, and Kloft et al., 1973 on the American species integra. Otto, 1959 showed that polygynous and monogynous rufa and polyctena colonies had different polymorphic characteristics.) This corresponds to group 2 in Wilson's (1971, p.141) scheme for the evolution of worker sub-castes.

Table 4.6 The effect of various treatments on the RF of lugubris foragers. χ^2 was calculated by comparing each column with the control.

	P-32	NITROUS OXIDE	CARBON DIOXIDE	CHLOROFORM	CONTROL
C	22	41	74	70	50
D	3	0	7	7	5
RF	88	100	91	91	91
χ^2	1.62	3.93*	0.01	0.0	-

* = $P < 0.05$.

There have been many attempts to discover if any size-duty relationships exist in worker ants. These studies have followed two broad lines, firstly biometric studies of ants captured at various tasks, and secondly observations on marked ants. The classic study of Buckingham (1911) on Pheidole and Campanotus showed that, in C. americanus Mayr, while workers of all sizes participated in both nest duties and foraging, there was a preponderance of different size classes of workers performing different duties. Adlerz (1886, quoted by Kiil 1934) provided similar observations for wood ants, and Kiil (loc. cit.)provided data on wood ants and two species of Campanotus.

Otto's (1958) study of a laboratory colony of polyctena with individually-marked workers demonstrated important divisions of labour which Sudd (1967, figure 8.1) has summarized. He showed that workers younger than 40 days were confined to nest duties, and that older workers foraged. This change in behaviour was associated with change in the maxillary gland cell-size, and degeneration of the ovaries (Otto 1958; Kirchner 1964). Similar data were obtained for Apis mellifera by Lindauer (1952).

The present observations relate to outside duties ("Aussendienst" of continental authors), firstly fidelity to the load carried, and secondly, observations on the sizes of workers participating in ant-carrying behaviour.

4.3.1 FIDELITY TO LOAD CARRIED

Observations on duties performed by different sizes of workers were reported by Adlerz (1886, quoted by Kiil 1934), Økland (1931) and Kiil (loc. cit.) for wood ants, Otto (1958) for polyctena, Dobrzanska (1959) for wood ants, and King and Walters (1950) provided data for the American species rufa melanotica.

Unfortunately, these studies have not been carried out uniformly and it is difficult to deduce an integrated picture. Figure 4.8 contains an attempt at collating data from four of these sources. Both Adlerz (1886, quoted by Kiil 1934) and Dobrzanska (1959) classified foragers into small, medium, and large and gave data for the numbers of each category performing different duties. Dobrzanska's data were based on laboratory colonies and her class "immobile in nest" includes ants not observed to carry out any function. Comparison of figure 4.8a and b suggests similar trends: ants attending aphids tend to be smaller than those in the nest. Similar conclusions can be made by comparing figure 4.8c and d. Note that Kiil's (1934) data in figure 4.8d were based on workers from two different nests.

It appears that, considering the duties mentioned above, the relationship between polyethism and polymorphism is weak, though some trends do occur.

This conclusion does not exclude the possibility that a task fidelity exists which is unrelated to worker size differences. Thus Dobrzanska (1959) observed a rufa worker attend aphids on one 50 mm stalk of Melampyrum for 21 days - a considerable fidelity to task and site. Kiil (1934) presented data which suggested a certain degree of task fidelity existed, especially between foragers of prey and nest material on the one hand, and honeydew carriers on the other.

Two sets of observations were made on task fidelity of honeydew carriers (HA) and prey carriers (PA). HA refers to foragers with obvious honeydew-swollen abdomens found on the route system. Note that Adlerz' results (cf. figure 4.8a) suggest that these may be different individuals to the actual aphid attenders. Doubtful loads were counted as NA ("not assigned") and all the observations were made at a time of year when ants with swollen abdomens due to enlarged fat bodies were not on the route system.

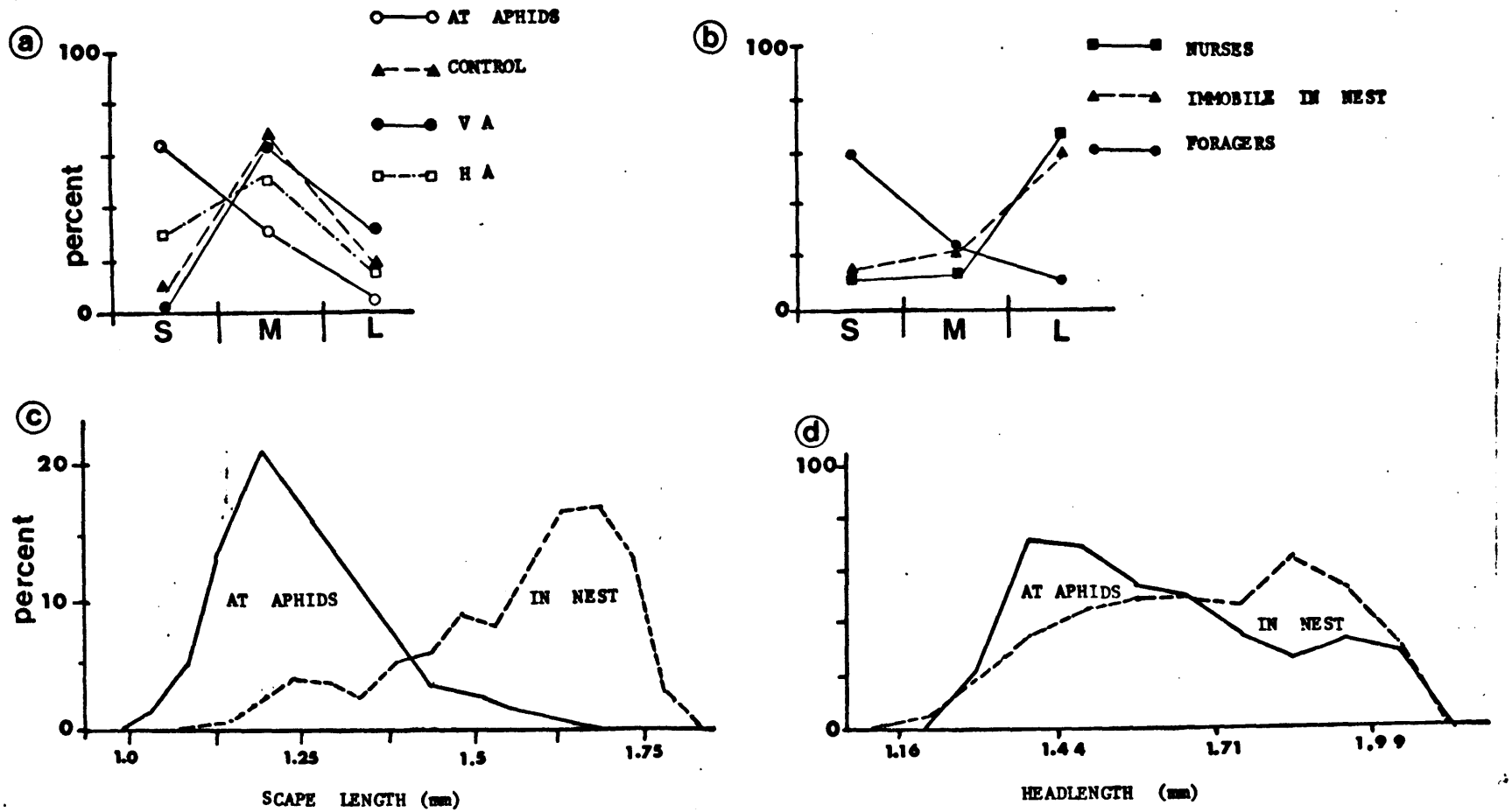


Figure 4.8 Some size:duty relationships reported in the literature for Formica spp. All give the percent foragers of different sizes (S = small, M = medium, L = large) performing various duties. (a) wood ants, after Adlerz (1886); (b) rufa after Dobrzanska (1959); (c) the American species rufa melanotica after King and Walters (1950); and (d) wood ants after Kiil (1934).

The first observations were made in conjunction with the exclusion of foragers from their aphid tree during early autumn 1974, and a description of that experiment and a map of the route system was given in 4.2.4. (The observations reported here were completed before the greaseband was placed in position.) A total of 400 HA and 155 PA were marked on route 3 by the individual method, using different colours for each. The results of 10 five-minute counts, during which all returning marked foragers were classified according to the load they carried, are given in table 4.7.

There was no significant difference between the subsequent tasks of ants marked as HA or PA ($\chi^2 = 7.69$, with 3 d.f., $P > 0.05$), although if resightings as HA or PA only are considered, the difference is significant ($\chi^2 = 8.03$, with 1 d.f., $P < 0.01$). There were also more NA amongst ants marked as PA. It is interesting to speculate that NA are foragers which have searched for a specific food item in vain, and return empty to the nest.

A similar experiment was conducted at nest E, a large active nest with a 72 m route to a SP aphid tree. A total of 300 HA and 300 PA were marked by the individual method on this route, on 22.VIII.1975. From 5-29.IX a total of 10 15-minute observations were made at a census point 3 m from the nest, during which all returning foragers, including the marked ants, were classified according to the load they carried. In addition, scans were made of the entire route and record was kept of the loads being carried by ants previously marked as HA and PA.

The results are shown as histograms in figure 4.9, where the "route" histogram is based on count data only (a total of 1444 ants), while the histograms "PA" (81 ants) and "HA" (131 ants) are based on pooled data of 10 scans and 10 counts. The results suggest a greater tendency for PA to be resighted carrying prey, and for HA's to be resighted carrying honeydew, as compared to the usual distribution of these activities on

Table 4.7 The experiment at nest C to study task fidelity, autumn 1974.

MARKED AS:	HA		PA	
RESIGHTED AS	number	percent	number	percent
HA	68	88.3	20	46.5
PA	3	3.9	6	14.0
NA	6	7.8	16	37.2
VH	0	0.0	1	2.3
Totals:	77	100.0	43	100.0

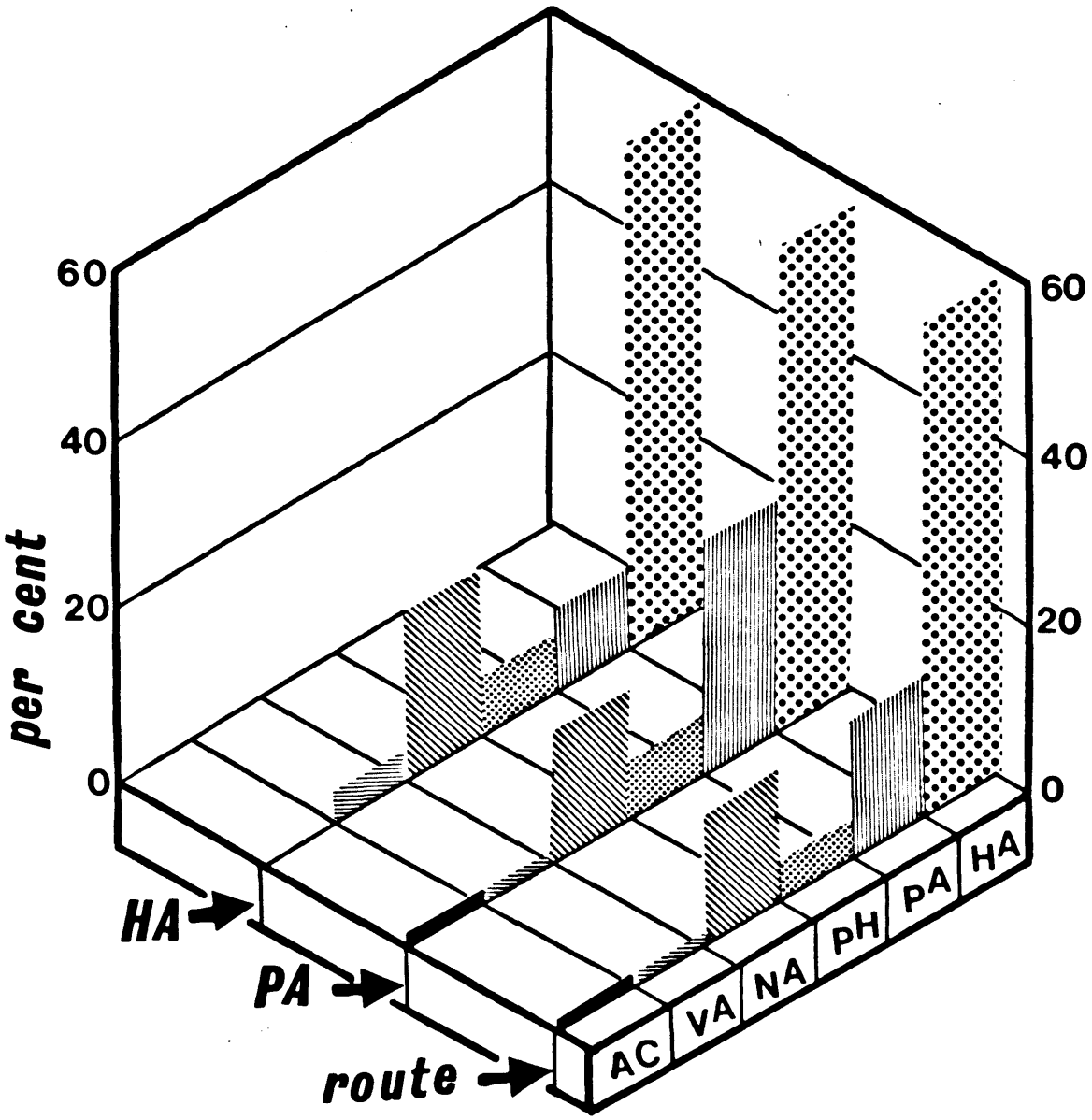


Figure 4.9 The duties performed by foragers marked as HA and PA compared to the usual distribution of forager duties on the "route". Observations at nest E, August-September 1974.

the route. None of the histograms is statistically different however (χ^2 tests on the absolute numbers), even when resightings as HA or PA alone are considered.

It can be concluded that this evidence suggests an absence of strong fidelity to honeydew and prey carrying amongst lugubris foragers.

4.3.2 ADULT-CARRYING BEHAVIOUR.

Adult-carrying of live unharmed ants by fellow nestmates is one of the more interesting aspects of ant behaviour. A review by Möglich and Hölldobler (1974) summarizes the relevant literature. The phenomenon has been reported from various species among the Myrmeciinae, Dorylinae, Ponerinae, Myrmicinae, and Formicinae, and Gamboa (1975a) has also observed the behaviour in an attine. Many observations of social-carrying behaviour have been made on the formicines, where the behaviour is most uniform and stereotyped.

The function of adult-carrying is not always clear. In Acromyrmex v. versicolor (Pergande) the behaviour involves ejection of ants from the nest and occurred most frequently above ground temperatures at which foraging ceases (Gamboa 1975a). In Campanotus herculeanus L., workers carry alatae back into the nest if they leave either too late or early in the flight periods (Möglich and Hölldobler 1974).

In Formica the adult carrier (AC) holds the carried adult (CA) by the mandibles, and suspended underneath the carrier, with legs folded in a "pupal" posture (PLATE 1). It is generally agreed in wood ant literature, that adult transport represents a form of recruitment to nest site: either from constituent mounds to other mounds of a polycalic system, or from an old nest site to a new site. Kneitz (1964) has described the carrying of polyctena workers with enlarged fat bodies from the summer to the winter nest. Rosengren (1971) observed adult

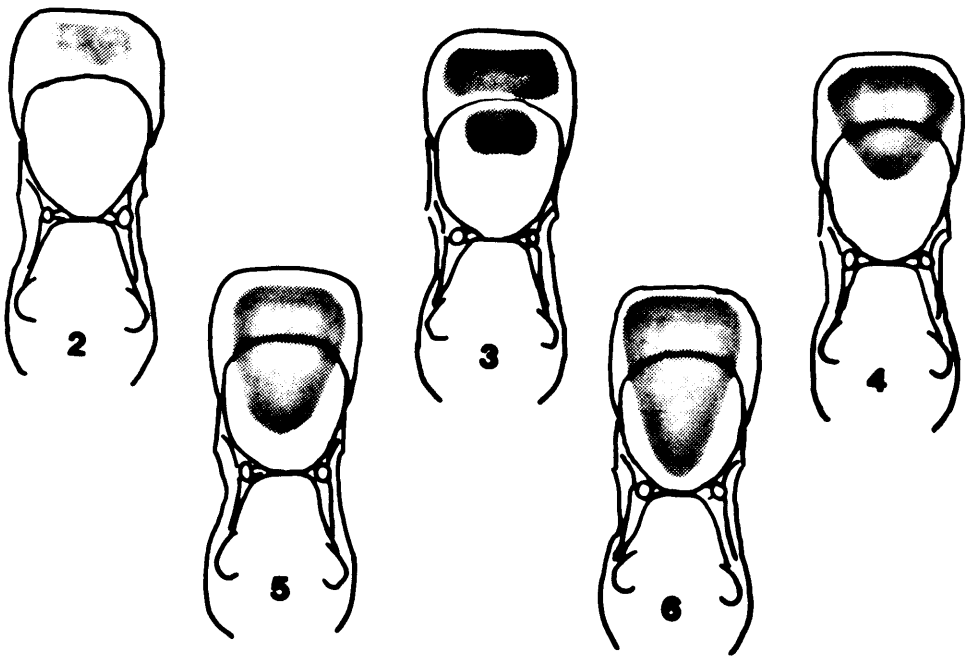


Figure 4.10 Thorax rufosity groups (after Yarrow 1955).

Size-frequency histograms are given in figure 4.11a. There is a resemblance between the results for AC and the "route" samples on the one hand, and between the CA and the "nest" samples on the other hand. Statistical comparisons (χ^2 tests on the raw data; adjacent cells with less than five ants were pooled) were equivocal: AC and "route" samples gave $\chi^2 = 23.22$, with 7 d.f., $P < 0.01$; CA and "nest" samples gave $\chi^2 = 14.54$, with 8 d.f., N.S. However it was obvious that some size selection process was involved: the headwidth ratios of CA/AC are given in figure 4.12. In 90 of the 100 pairs of CA/AC, the carried ant was smaller than the ant carrying it. Most CA were 0.7 to 0.9 times the size of their respective AC, and the ratio was smaller in 39 pairs.

The frequency histograms for the different rufosity classes were given in figure 4.11b. There was an evident trend for a preponderance of groups 2 and 3 amongst larger ants, and for smaller ants to belong to darker-thorax classes (groups 4 to 6). Similar observations were made by Kloft et al.(1973) in their study of the American species integra.

Adult carrying was also observed in the "conventional" mode: nest moving occurred at Galtee-776a on 18.V.1975, when the nest moved to a new site 3 m distant. A five-minute count of ants travelling in each direction yielded these results:

to new nest: 143 AC (+ 143 CA) and 88 other ants;

to old nest: 4 AC (+ 4 CA) and 286 other ants.

Adult-carrying accounted for 76.4 percent of traffic on the "recruiting" route, but only 2.8 percent on the other route. (ground temperature: 24.6°C; 17.00 hours)

Further observations were made on nest moving in Kilcoran Wood. The old site was destroyed by fire on 26.V.1975 and the ants were moving to a new site 53 m away. Two five-minute counts of ants travelling in

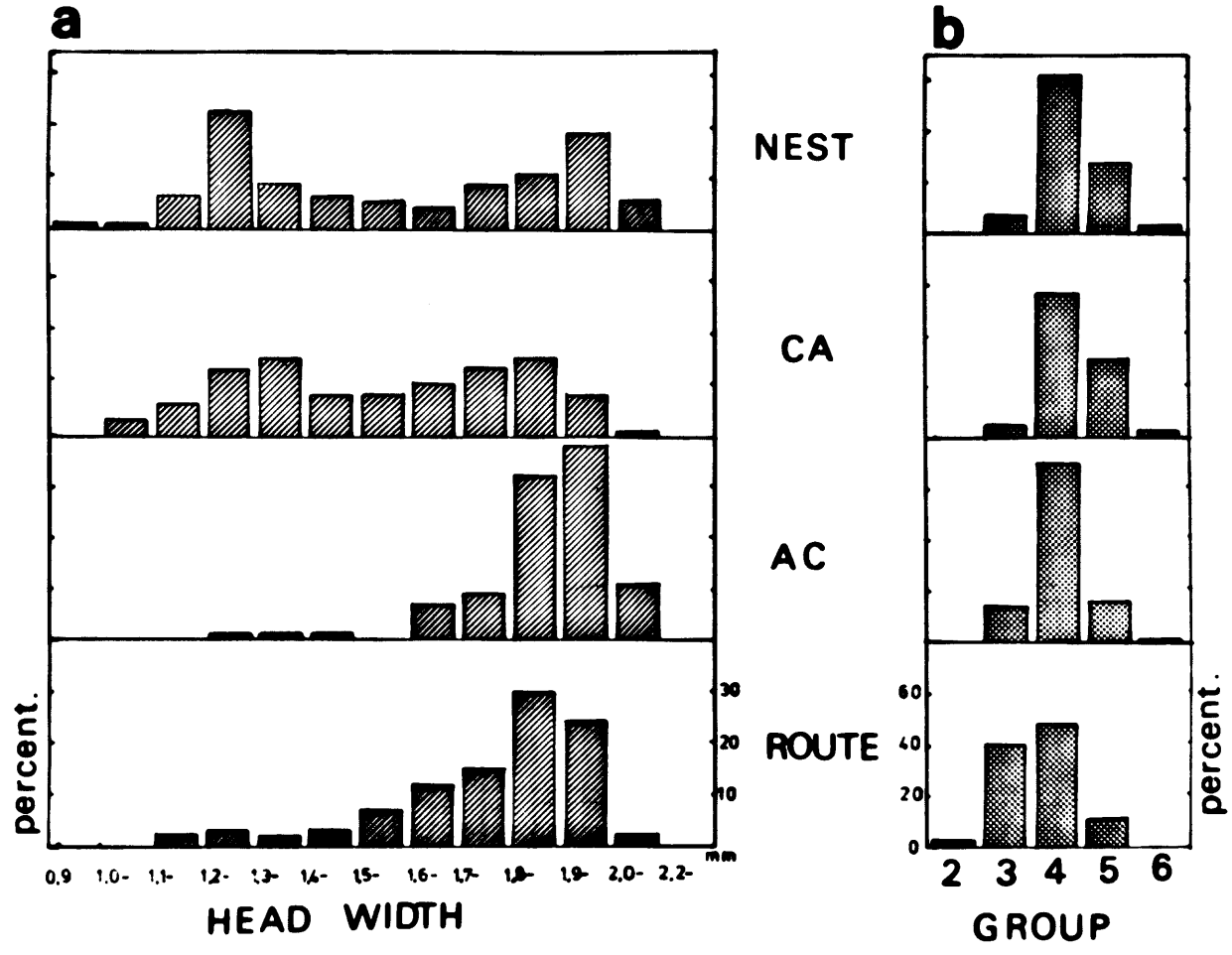


Figure 4.11 (a) Headwidths and (b) rufosity groups of four samples of worker lugubris.

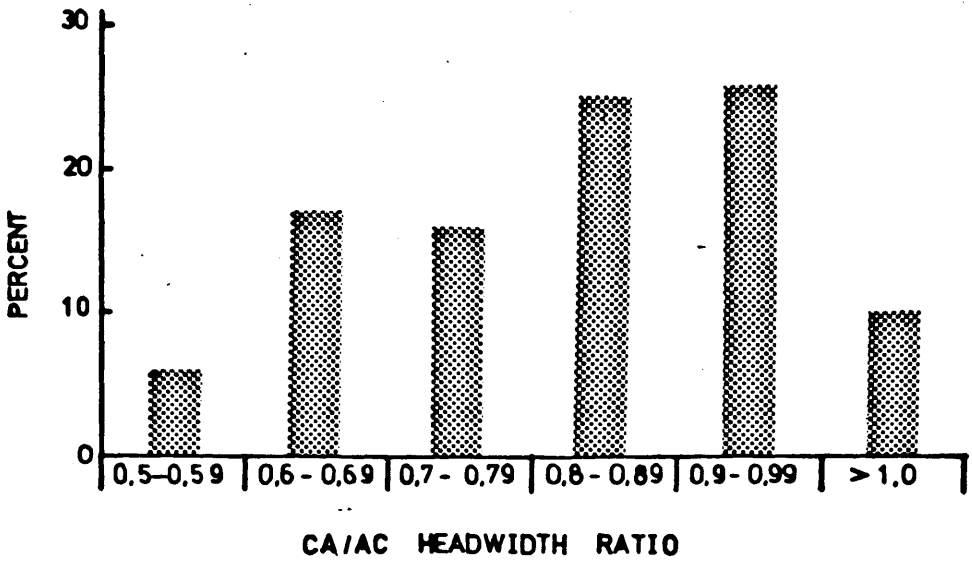


Figure 4.12 The carried adult:adult carrier headwidth ratios of 100 pairs of ants participating in adult carrying behaviour taken from nest C during May 1975.

each direction were made at 19.45 on 29.V.1975; ground temperature 16.6°C (CL = carrying larva; CP = carrying pupa).

to new site: 1 CL, 1 CP, 69 AC + 69 CA, 45 other workers.

to old site: 117 other ants.

to new site: 1 CP, 38 AC + 38 CA, 58 other ants.

to old site: 1 AC + 1 CA, 101 other ants.

Thus 68 percent of the ants travelling to the new site were involved in carrying behaviour.

4.4 RHYTHMS OF FORAGING.

Wood ants have attracted much attention because of their predatory potential and its possible applications in forestry management (see references in Cotti 1963). Yet, one of the most fundamental considerations in assessing their importance as predators, namely a study of the cycles of foraging activity, has not been given proportionate attention. In this section, results of observations on the foraging activity are presented together with a discussion of some meteorological and seasonal factors affecting the foraging cycle.

This type of data has been provided by Ayre (1958, 1959) for the American species subnitens, and Horstmann (1970, 1972) made a detailed study of polyctena. In addition, various aspects of the foraging dynamics of wood ants have been treated separately: prey-hunting was reviewed by Adlung (1966) and Otto (1967), and studies on honeydew gathering include those by Zoebelein (1956) and Müller (1956, 1958). Chauvin (1965) and deBruyn and Kruk-deBruin (1972) studied diurnal rhythms of forager traffic in polyctena, and Holt (1955) described the distribution of aquilonia foragers in the foraging arena. Comparison of foraging rhythms is facilitated by studies of other ant species, including Atta cephalotes (L.) (Lewis et al. 1974 a, b), Acromyrmex

versicolor versicolor (Gamboa 1975b) and Veromessor pergandei (Mayr) (Clark and Comanor 1973). Bernstein (1974) considered a number of aspects of seasonal foraging in three species of desert ants.

In summary, Ayre's data for subnitens showed that foraging began at temperature 10.3°C, rose to a maximum at 22.7°C and ceased at 38.3°C. The data for polyctena (after Horstmann) suggested that foraging began at ground temperature 6°C, rose almost linearly with temperature to a maximum at 20-25°C and fell off rapidly above 25°C. The data for other species of ants are similar: Gamboa's data for Acromyrmex showed a drop-off of foraging above 32°C, ceasing at 38-42°C ground temperatures; Clark and Comanor gave 9°C as the starting point for Veromessor foraging, with drop-off at 33°C and an upper limit at 40.5°C. Although other factors are involved, the diurnal variation in ground temperature, considered alone, imposes a bimodal pattern on foraging activity when mid-day ground temperatures exceed the upper limit for that species. Considered together, the data for the different species mentioned seem remarkably similar.

In the absence of detailed studies of lugubris traffic dynamics, observations were made to describe foraging rhythms on some representative days and to consider these data alongside recorded temperature and cloud cover data.

4.4.1 DAY COUNTS OF FORAGER TRAFFIC

Long-term wood ant traffic studies are hindered by the periods of observation they require and by the lack of a suitable ant-counter or recorder. Dibley and Lewis (1972) developed a photocell ant-counter for their studies on Atta cephalotes, and obtained interesting long-term results (in Lewis et al. 1974 a, b) using it. However an ant-counter developed in conjunction with Mr V. Neff (see appendix III), based on a

similar principle, was not entirely satisfactory in the field: contrary to Dibley and Lewis' (loc. cit.) claim for Atta, lugubris workers tended to congregate around the light beam at night and gave spurious results. Similarly, Chauvin's (1965) device, based on a microbalance suspended across a route and connected to a clockwork recorder, appears difficult to calibrate - apart from the difficulties he experienced in "coaxing" the ants to traverse it.

In the absence of a suitable recorder, counts of traffic were made as follows: a census point was established on route 3, 13 m from the mound of nest C (point "CP" in the route system map in figure 4.5). On each of four days (one in 1974, and three in 1975) two five-minute counts (one of foragers travelling towards - "TO", and the other of foragers travelling from - "FROM", the nest) were made every half hour, starting before dawn and ending after dusk. The first and last counts each day were made with the aid of a slight beam from a flashlight. When counting the TO foragers, a record was kept of the different loads being carried. During the 1975 counts, a further five-minute period every hour from 10.00 to 19.00 was spent removing all prey items from passing prey carriers. Ground and air temperatures were recorded simultaneously on a Grant recorder, and a visual estimate of cloud cover was also made.

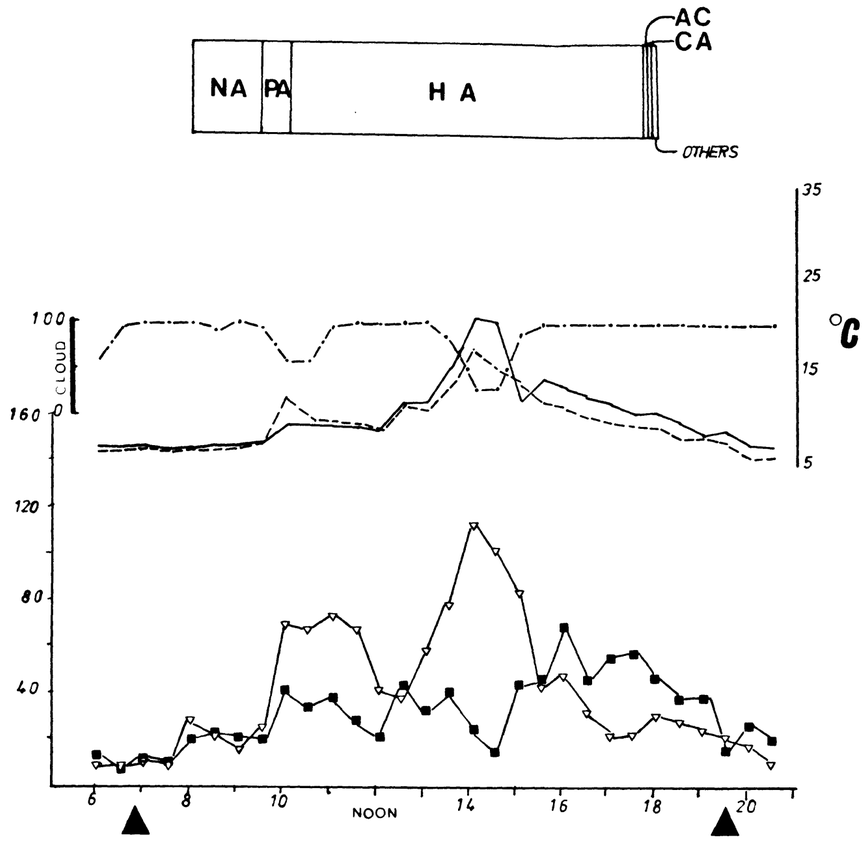
The results of the observations are given in figure 4.13. The days chosen were representative of the foraging cycle for the time of year, though all the observations were made during spells of fine weather. There was a bad local thunderstorm at 21.00 hours on 6.VI.1975, but the observations made immediately after it did not yield any unusual results.

Reference to the graphs in figure 4.13 shows that the cloud cover did not affect foraging, except in so far as it modified temperatures. Foraging traffic began and ceased at ground temperatures of 6 - 8°C. Above this temperature, a linear correlation existed between the total number of foragers passing in five-minutes (y) (i.e. the five-minute TO

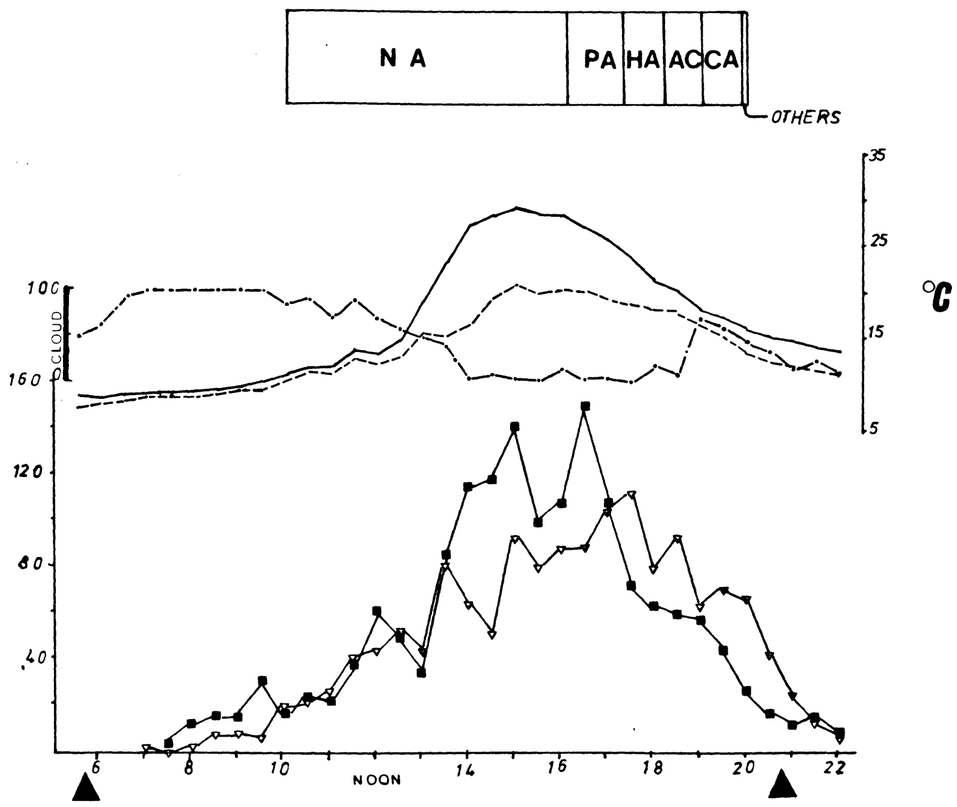
Figure 4.13

Half-hourly forager counts at a census point 13 m from nest C on four days. Half-hourly readings for ground and air temperatures and a cloud-cover estimate are also provided. The bar-charts summarise the loads of all returning foragers during the day-light counts.

5.X.1974



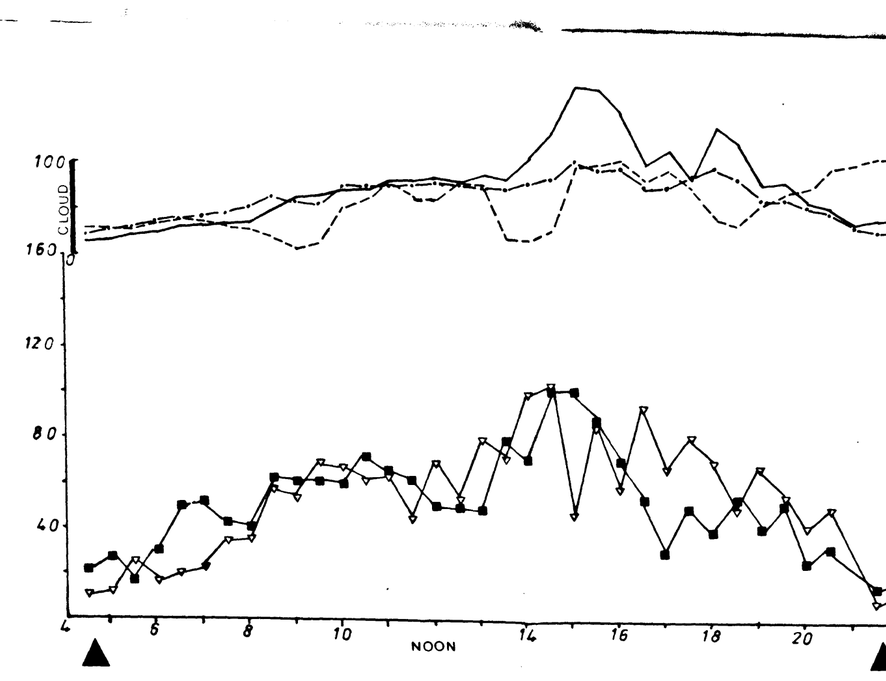
23.IV.1975



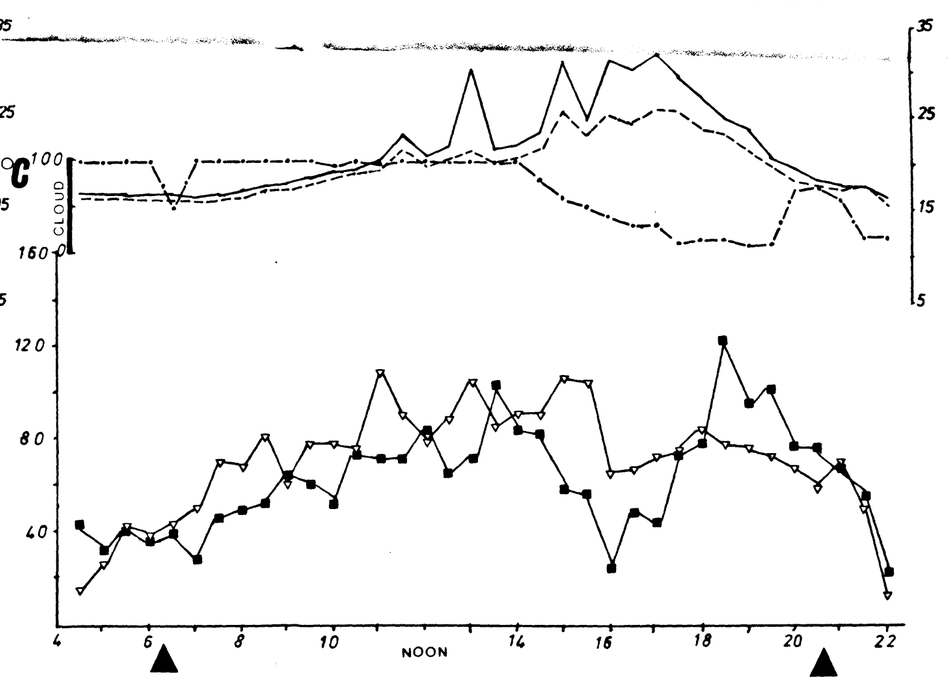
KEY

- ------ AIR TEMP.
- ——— GROUND ''
- —·—·— CLOUD
- ▲ DAWN/DUSK
- —▽—▽— TO ANTS
- —■—■— FROM ''

6.VI.1975



27.VIII.1975



NO. OF ANTS

TIME OF DAY

and FROM counts summed), and temperature (x) in the range 7 to 20°C. Surprisingly, air temperature seems to be a better predictor of forager numbers than ground temperature. This is presumably due to the fluctuations in ground temperature even during the five minutes the count was being made, whereas air temperature does not fluctuate to the same extent. The regression equations are as follows:

(a) for 5.X.1974,

with ground temperature, $y = 7.49x - 2.92$, $r = 0.80$ (1)

with air temperature, $y = 10.84x - 27.28$, $r = 0.90$ (2)

(b) for 23.VI.1975,

with ground temperature, $y = 14.09x - 115.10$, $r = 0.92$ (3)

with air temperature, $y = 16.69x - 135.46$, $r = 0.95$ (4)

(c) for 6.VI.1975,

with ground temperature, $y = 10.36x - 73.52$, $r = 0.78$ (5)

with air temperature, $y = 17.98x - 184.92$, $r = 0.86$ (6)

(d) for 27.VIII.1975,

with ground temperature, $y = 13.04x - 121.19$, $r = 0.80$ (7)

with air temperature, $y = 16.39x - 167.99$, $r = 0.82$ (8)

Equations 2, 4, 6, and 8 are plotted in figure 4.14. The differences noted may represent seasonal variation of traffic response to temperature. Notice that on 5.X.1974, the traffic was moving at 08.00 hours at a ground temperature of 6.7°C. Similar numbers of foragers only occurred about 2°C higher on the other days.

Each half-hourly total five-minute count from the 27.VIII.1975 data, is plotted against ground temperature in figure 4.15. It can be clearly seen that total forager activity rose to a maximum at 24°C and declined rapidly above 27°C. Although no actual cut-off point was observed on this day, it was frequently noted that route traffic ceased above 33°C ground temperature. At this point all the foragers remained in the shade. However, traffic was rarely interrupted for more than a few minutes because a moment's cloud immediately restored traffic. Ground

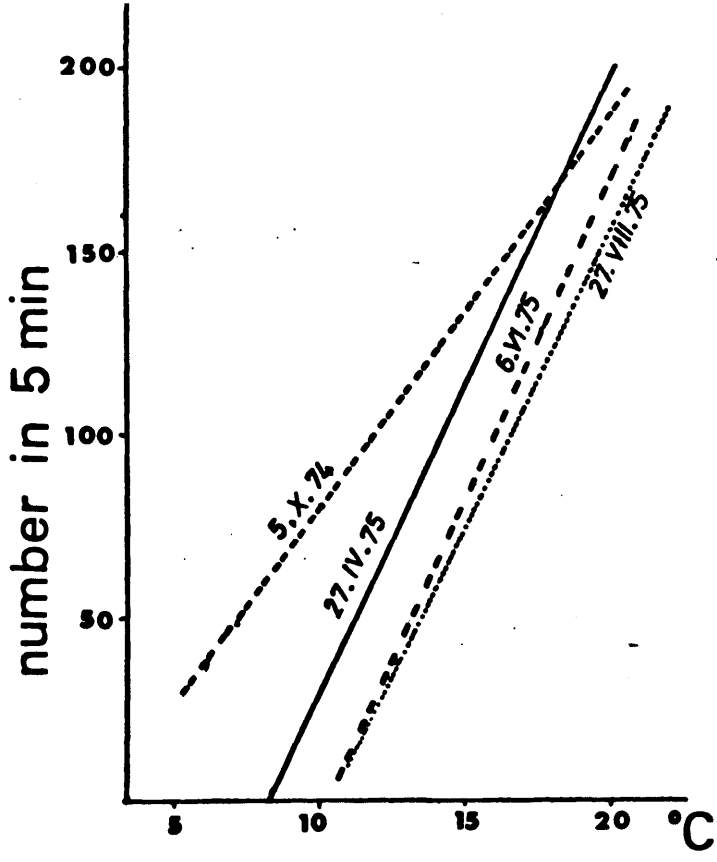


Figure 4.14 The relationship between total five-minute forager counts and air temperature at route 1, nest C on four days. The regression equations are given in the text.

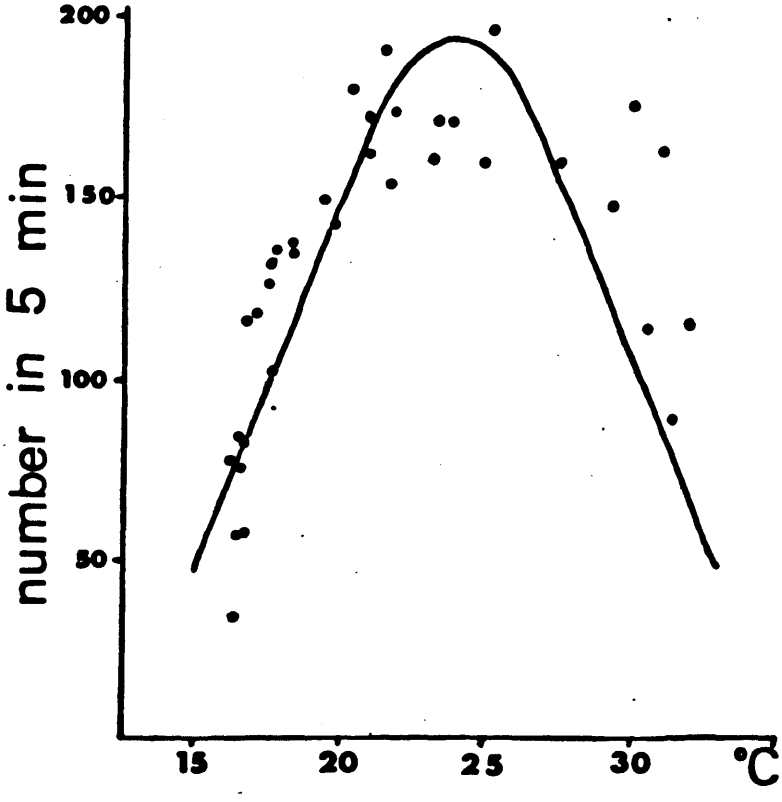


Figure 4.15 Total five-minute counts of foragers at different ground temperatures on route 1, nest C, 27.VIII.1975. The line is a fitted normal curve.

temperature fluctuations up to 40°C were noted during the present study. At these temperatures, the exposed nests' surfaces were entirely deserted, often for quite long periods.

It is interesting to note that the data in figure 4.15 is very similar to that obtained by deBruyn and Kruk-deBruin (1972) for polyctena and the present data is also well fitted by a normal curve of the following form:

$$N = \frac{c.e^{-\frac{1}{2}\left(\frac{T-\mu}{\sigma}\right)^2}}{\sigma\sqrt{2\pi}}$$

where N = number of foragers passing per five minutes,

T = temperature in °C,

μ = the optimum temperature (24°C),

σ = the standard deviation of T (= 5.4°C),

and c = a constant which varies with time and place (= 2615).

Further similarities between polyctena and lugubris will be described in 4.4.2.

Comparison of the bar-charts in figure 4.13 summarizing the data on the loads of returning foragers, provides some idea of the colony's seasonal food requirements. Prey-hunting was most important in April, and decreased steadily to October. Empty foragers (NA) were most frequent in April, at the beginning of the season when honeydew is scarce. Adult-carrying behaviour was highly seasonal, being most evident in April, still appreciable in June, but negligible from then on. The honeydew carriers (HA) quickly rose from nine percent in April, to 73 percent in June, and up to 77 percent in October.

Horstmann (1970) reported, for polyctena, that both the number of prey items carried per 100 ants, and also the actual number of prey items being carried, increased with temperature. Analysis of the data from

lugubris, obtained from 08.00 to 20.30 hours on the 23.IV.1975, when prey-carrying was relatively most important, shows that there was no relationship between ground temperature and the proportion of PA amongst returning foragers (figure 4.16a, $r = -0.26$, N.S.), although a clear relationship existed between the actual number of prey items being transported to the nest and ground temperatures (figure 4.16b, $r = 0.67$). There was also a tendency towards a higher proportion of PA in the earlier part of the day (figure 4.16d; comparing the two halves of the observation period using the raw data, $\chi^2 = 14.32$, with 1 d.f. $P<0.001$).

Gamboa (1975a) reported that adult-carrying behaviour in Acromyrmex v. versicolor was most prevalent at 38–40°C, just after the colony had shut down all forager traffic. In contrast, the ant carriers (AC) in lugubris occur at a wide range of ground temperatures, and a graph of the percentage of AC among returning foragers on 23.IV.1975 is reasonably-well ($r = 0.52$, $P<0.02$) fitted by a line (figure 4.16c). However, there was no diurnal pattern.

4.4.2 OTHER OBSERVATIONS ON ROUTE TRAFFIC

(a) Time intervals between ants.

Holt (1955) showed that traffic flow away from an aquilonia nest was random; he did not state the time of year of his observations. Since then, evidence has been provided that rufa, polyctena, and Formica exsecta (Rosengren 1971) and Campanotus socius (Hölldobler 1971) possess a form of recruitment behaviour. Part of Rosengren's evidence was a demonstration that outgoing polyctena foragers are aggregated under low traffic conditions (his observations were made in October), whereas returning foragers pass randomly. He interpreted these groups as foragers being actively recruited to food. Chauvin (1965) has also noted these groups of foragers in polyctena which he describes (1970,p.65)

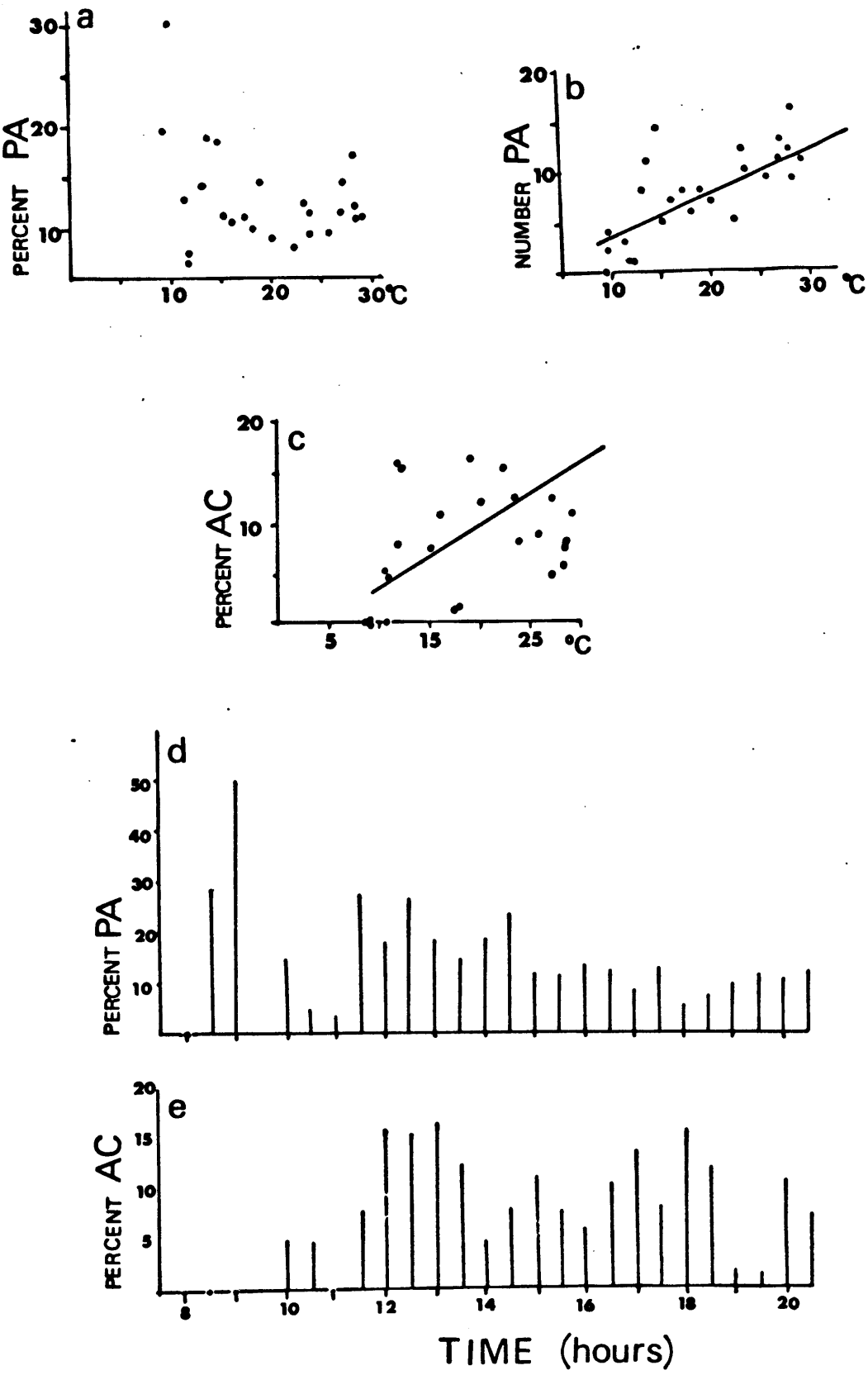


Figure 4.16 The percent PA (a), the number of PA (b), and the percent AC (c) at different ground temperatures, and the percent PA (d) and percent AC (e) at different times of the day. All the data are from the 23.IV.1975, at route 1 of nest C.

as " 'gusts' . . . of seven to ten insects separated by dead periods". Similar groupings of foragers were frequently seen on lugubris routes at many times of the year.

The present data consist of a single set of observations designed to compare results obtained with lugubris (route 4, nest B see figure 4.4) with those obtained for Lasius fuliginosus, a species well-known to follow scent trails (Carthy 1951). Both observations were made on 24.VIII.1975. A record was made by speaking into a Phillips' cassette tape-recorder each time an ant passed. This was transferred manually to a laboratory chart recorder. Overall timing error was always less than +1.5 percent and ignored.

If the foragers are passing randomly on the route/trail, then the number expected in a time interval t_1 to t_2 is given by

$$N(e^{-mt_1} e^{-mt_2}) \quad \text{(Holt 1955)},$$

where N is the number of intervals observed, m the reciprocal of the mean interval, and e the base of natural logarithms. Comparison of the observed and expected values (table 4.8) shows that only in the case of the lugubris TO sample, was there a departure from random expectation. While this is in agreement with Holt's observations, it clashes with Rosengren's (1971) hypothesis.

Rosengren's data were collected differently: he counted the numbers passing in 35 15-second intervals for both TO and FROM traffic, and made six replicates. He tested his data by the index of dispersion (Southwood 1966, p.36) and demonstrated significant aggregation in five out of six of the FROM observations, but in none of the TO observations.

A re-examination of the chart record made during the present study, using Rosengren's criterion of the number of ants per 15 s, provided three replicates for lugubris FROM data, and one set each for lugubris TO and Lasius fuliginosus TO and FROM. These were analysed by the same method

Table 4.8 The intervals between successive foragers of Formica lugubris and Lasius fuliginosus. (O = observed; E = expected)

INTERVALS (s):		0 - 2	2 - 4	4 - 6	6 - 8	8 - 10	10 - 12	12 - 14	14 - 16	16 - 18	18 - 20	>20	TOTAL	mean interval	X^2	P
F. lugubris TO	O	42	21	10	9	9	4	9	3	5	1	10	123	7.39	17.49	<0.05
	E	27.7	21.1	16.1	12.3	9.4	7.1	5.5	4.2	3.2	2.4	14.0	123.0			
FROM	O	64	31	29	22	13	14	7	10	10	4	18	222	7.61	13.63	>0.1
	E	48.8	37.5	28.9	22.2	17.1	13.1	10.1	7.8	6.0	4.6	25.9	222.0			
L. fuliginosus TO	O	38	22	11	11	6	8	6	1	2	1	4	110	5.35	8.27	>0.5
	E	32.6	22.4	15.4	10.6	7.3	5.0	3.5	2.4	1.6	1.1	7.1	110.0			
FROM	O	24	25	18	7	10	8	3	6	1	5	8	115	7.42	12.98	>0.1
	E	25.6	19.7	15.0	11.5	8.8	6.7	5.1	3.9	3.0	2.3	13.4	115.0			

as used by Rosengren (1971) and the results were: in one of the three FROM observations for lugubris there was significant aggregation, but all other sets of data were well-fitted by random expectation.

It seem safe to conclude that at the time of year the observations were made, lugubris and Lasius fuliginosus traffic is essentially random. The observations made in the present study suggest that the "gusts" described by Chauvin are not confined to FROM traffic, and hence may be caused by factors other than recruitment.

(b) Journey times.

Holt (1955) studied the journey times of aquilonia foragers by observing paint-marked individuals and reported that an average foraging journey lasted 129 minutes. This was followed by an average of 31 minutes spent in the nest before returning to forage again.

From 12.20 to 18.50 hours on 27.VIII.1975, a continuous observation was made at a census point on route 1, 13 m from nest C (see map of route system in figure 4.5). At various times a total of 120 foragers were marked individually, without removing them from the route. Some groups were travelling TO the nest and others FROM the nest. In addition to providing information on journey times of foragers, it was hoped that by noting the different groups of ants as they passed to the aphid trees and back to the nest, without removing them from the route, that it would be possible to see if there were regular groups of ants which tended to stay together - i.e. if temporal separation of foragers existed. This fact has an important bearing on the forager fidelity studies, where counts made at various times of the day have been compared directly.

The results of the observations are presented in figure 4.17 where the different marking series are shown separately. Time 0 was at 12.20 hours. The time each group was marked is indicated by a solid bar and

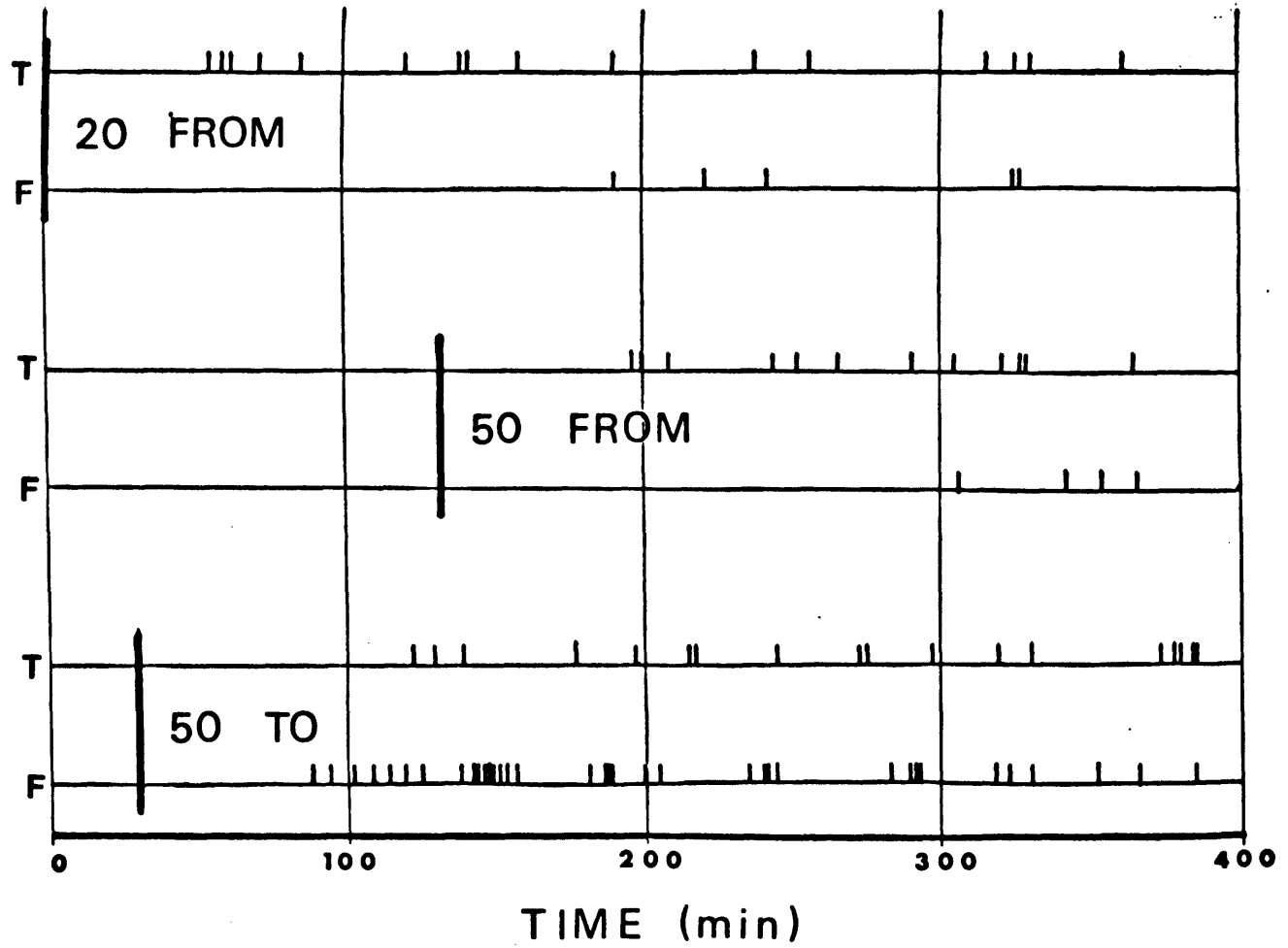


Figure 4.17 The journey times of foragers on route 1 of nest C on 27.VIII.1975. See text for explanation.

details are given of the number marked and the direction they were travelling when marked. Each subsequent sighting of an ant is indicated by a stroke on the TO ("T") or FROM ("F") line, whichever the case. Of the two groups marked as they travelled FROM the nest, the first resighted ant, now travelling TO the nest, passed 56 and 64 minutes later. In the group marked as they travelled TO the nest, the first was resighted, now travelling FROM the nest, 58 minutes later. However, it is obvious that even after 390 minutes observation, considerable variation existed in the time spent by individuals in performing their tasks, and a number of attempts at manipulating the data failed to uncover any underlying cycle. On the following day, casual observation suggested that the marked and unmarked individuals were well-mixed on the route.

A second observation was made on the following day at the SP aphid tree (species of aphid: Cinara pini) on route 3 of the same nest. On this occasion, starting at 11.30 hours, 75 ants were marked as they ascended the tree, without removing them from the tree, and the time was noted as each marked ant descended the tree. However, once they left the tree, foragers were not allowed to return and become confused with other marked ants. During 215 minutes of observation, a total of 49 marked ants were sighted, and the average time spent on the tree was 106 minutes.

At ground temperature 20°C, foragers take approximately 40 s to proceed along 1 m of route (see p123). At this rate of progress, the return journey to a 20 m distant aphid tree takes c. 27 minutes. This can be added to the 106 minutes spent on the tree to give an average journey time of 133 minutes. This is very similar to Holt's (1955) figure of 129 minutes for aquilonia.

Reference back to figure 4.17 shows that the first of the 50 foragers marked as they travelled TO the nest did not re-appear until 59 minutes

later, and that 120 minutes seems a fair average for the time spent travelling to the nest, time in the nest and time to travel back to the census point. At the rate of progress used above, the time spent on the route would be 17 minutes, leaving 103 minutes as the time actually spent in the nest. This is considerably longer than the estimate of 31 minutes given by Holt (1955) for aquilonia.

Both these estimates can be added to give a total journey time estimate of 236 minutes (3.93 hours).

(c) Other variables affecting foraging speed.

Holt (1955) and deBruyn and Kruk-deBruin (1972) studied the effect of temperature on the running speed of aquilonia and polyctena, respectively. Running speeds of lugubris foragers were recorded by measuring the time taken by individual ants to pass under two lengths of thread suspended 150 mm apart (similar to Holt's six inches) across route 1 of nest C. Observations were made alternately on ants travelling to and from the nest (except at 6-7°C when only FROM ants were available). Bias was avoided by choosing the next available ant travelling in the right direction, and an observation was only disregarded if the ant veered from the route. Ground temperatures were recorded at least every 10 observations using a white-painted copper-gauze shield (Long 1953) over the thermistor probe.

An analysis of three groups of observations (t-tests) showed no differences between the TO and FROM data and both were pooled, as were observations made on the same occasion at 0.5°C of each other. A total of 527 ants were timed, although above 30°C the points plotted are based on less than five ants each.

The results are shown in figure 4.18 where a linear relationship is evident. In figure 4.18b the data for aquilonia (data from table 7 in

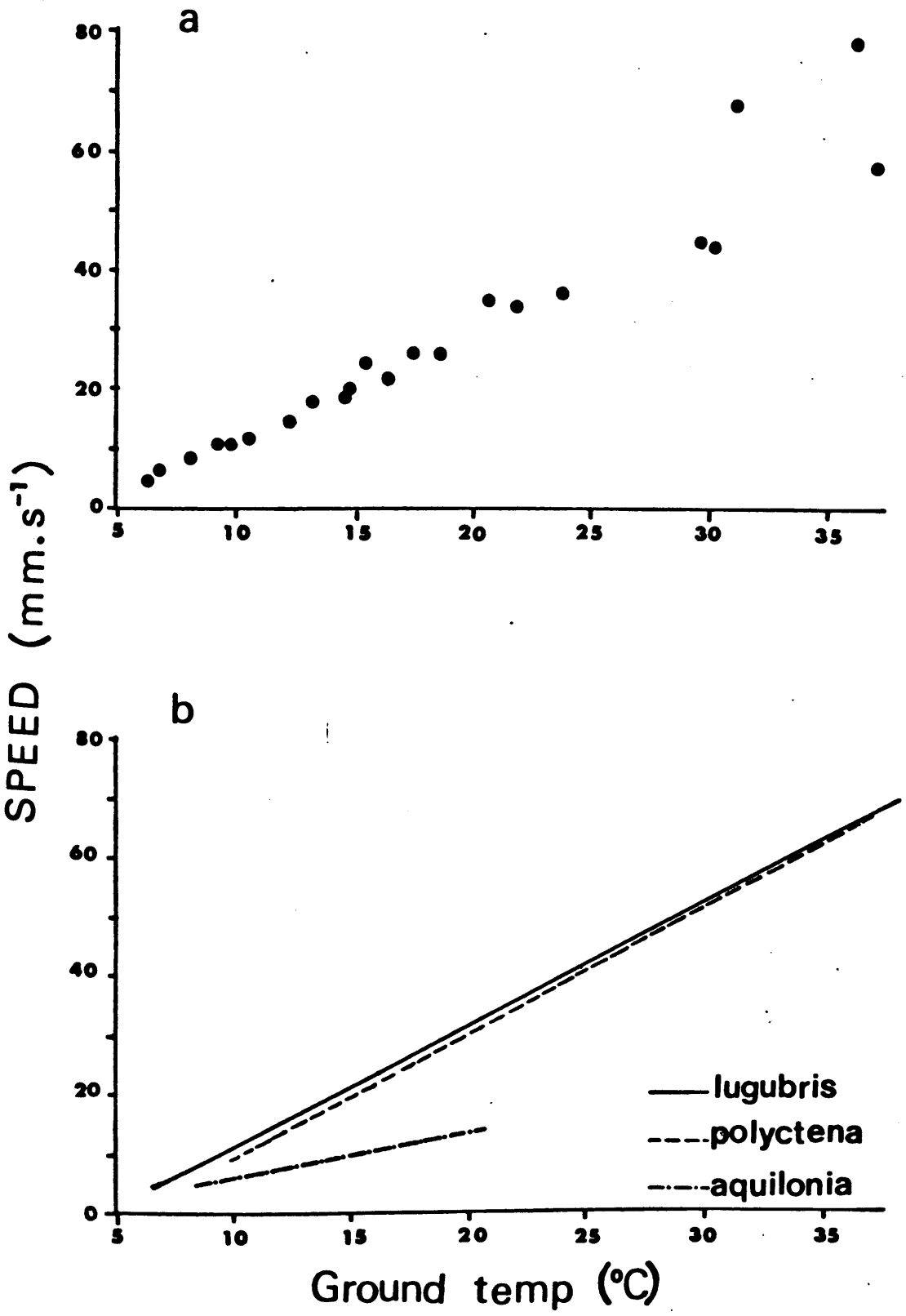


Figure 4.18 The relationship between running speed and ground temperature. (a) The observed points for lugubris foragers, and (b) the regression lines for lugubris (present study), polyctena (from deBruyn and Kruk-deBruin 1972), and aquilonia (after Holt 1955).

Holt, 1955, transformed from feet per minute to $mm.s^{-1}$ and a regression line fitted) and polyctena (from deBruyn and Kruk-deBruin 1972) are shown together with the line for lugubris. The regression equations are:

lugubris	$y = 2.03x - 8.34$,	$r = 0.96$;
polyctena	$y = 2.1\,x - 11.1$,	r not given;
aquilonia	$y = 0.75x - 0.90$,	$r = 0.93$.

The results for polyctena and lugubris show a very similar response to temperature, and both are very different to the graph for aquilonia. This may represent interspecific variation.

These graphs probably represent the ideal situation as regards speed variation at different temperatures, and it is better to differentiate between running speed, timed over short cleared stretches of route, and actual progress, timed over longer distances (e.g. 1 m) without considering any obstacles. For example, on 28.VIII.1975, ground temperature 22.8°C, 11 foragers on route 3 of nest C averaged 38.2 s to cover 1 m on a stretch of the route with few obstacles. This is equivalent to 26.2 $mm.s^{-1}$ or 70.1 percent of the speed predicted from the temperature:speed graph for lugubris.

Holt (1955) also noticed no significant difference between the speed of uphill and downhill movement in aquilonia, without giving data, and O'Rourke's (1947) observations on wood ants in Switzerland gave similar results. However observations on 28.VIII.1975 at the SP aphid-tree of route 3, nest C yielded the following data: the times taken by 50 ascending foragers were significantly different ($P<0.05$) from those of descending foragers (timing method was as described above). The following is a summary of the results:

UP: average time (s) 7.05 S.D. 1.80

DOWN: average time (s) 6.11 S.D. 2.28 ($t = 2.26$; 98d.f.)

The conflict in results may be due to the difference between speed and progress, as O'Rourke (loc. cit.) timed the ants over 1 m.

4.5 QUANTITIES OF FOOD ITEMS.

In this section information already presented is considered, along with additional data, to give estimates of the quantities of food collected by a lugubris nest during the year.

4.5.1 THE ACTIVE SEASON

The field observations suggest that active foraging occurs from mid-April to the end of October at ground temperatures above c. 8°C. The average number of hours above 8.5°C air temperature in Kilkenny, the nearest available station (50 km from the study area) is given in figure 4.19. This is based on 1960 to 1974 data from the Meteorological Service. An estimate of 3333 work hours per year (≃ 139 days) can be given for lugubris foragers, based on this data.

4.5.2 FOOD ITEMS

The percentage of returning foragers carrying honeydew and prey items on the following dates were (data from figure 4.13):

	23.IV	6.VI	27.VIII	5.X
honeydew	8.9	73.3	73.4	76.9
prey	12.2	11.3	9.1	6.2

Since honeydew was not available in large quantities until mid-May, the low figure for honeydew in April was disregarded, and this leaves an average figure for honeydew of 74.5 percent of loads. The average percent of loads for prey items is 9.7.

(a) Prey items.

The identity of the prey items removed from returning foragers on 23.IV, 6.VI, and 27.VIII (all 1975; see 4.4.1) during five minutes every hour from 10.00 to 19.00 is given in table 4.9. It can be seen that

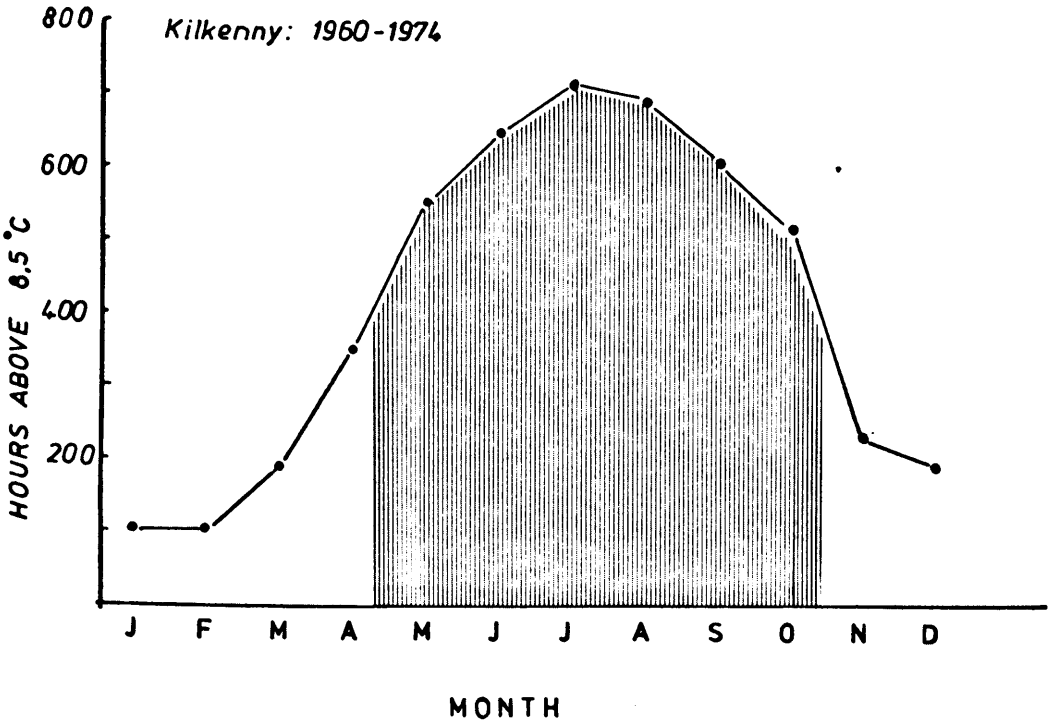


Figure 4.19 The average number of hours above 8.5°C dry-bulb temperature at Kilkenny, 1960-1974 (Meteorological Service data). The foraging season of lugubris is shaded.

Table 4.9 The prey items taken from *lugubris* foragers on three days.

	23.IV.1975	6.VI.1975	27.VIII.1975
Lumbricidae	9	13	6
Chilopoda	2	2	1
Araneae	11	4	2
Collembola	6	1	2
Neuroptera	0	1	1
Aphididae	0	1	3
Lepidoptera larvae	0	6	0
Coleoptera	3	6	0
Formicidae	1	12	7
other Hymenoptera	1	5	7
Diptera	21	17	24
others	6	6	5

Diptera were the most frequent prey items, and that lumbricids, spiders and other ants were also important. These prey items seem representative of those taken by lugubris in Ireland, though, perhaps Collembola, lumbricids, and slugs are taken more frequently in damp weather.

An estimate can be made of the total prey items taken by nest C during the year, as follows:

Active season:	3333 hours;
Average foraging journey:	3.93 hours;
number of foragers:	24 895 (taken from table 4.11; 9.7 percent prey carriers);
Annual total prey items:	2.05×10^6.

(b) Honeydew:

Honeydew is the most important food item of wood ants, and studies on the quantities of honeydew carried into the nest include those of Zoebelein (1956) and Horstmann (1970, 1972). Zoebelein weighed 100 polyctena foragers taken as they ascended the tree and subtracted this figure from the weight of 100 foragers taken descending the tree. This gave an average load of honeydew as 5.84 mg per ant. Similar observations on aquilonia foragers (Holt 1955) gave an average honeydew load as 1.9 mg. Horstmann (1970, 1972) reported that crop volumes of honeydew in polyctena varied from 0.5-4.5 mm^3.

During mid-September 1975, samples of foragers were taken as they ascended and descended two aphid trees: SS (with Cinara piceae) and SP (with Cinara pini). These were maintained separately in vials with FLUON-coated sides and weighed about 1 hour after sampling to the nearest 0.1 mg. Subsequently, the headwidth of each ant was measured to the nearest 0.03 mm using a binocular microscope fitted with an ocular micrometer.

The results are shown in figure 4.20 and show that at the time of year these observations were made, Cinara piceae-attending ants carry relatively more honeydew: at headwidth 1.8-1.9 mm (the most frequent size-class on the route - see figure 4.11) the honeydew load was 6.0 mg in C. piceae-attenders, but only 4.8 mg in C. pini-attenders. This represents, respectively, 52 and 34 percent of the forager's weight.

A calculation, similar to that used above for prey items, gives 76 kg per year as the total input of honeydew at nest C, and 198 kg per year for nest B (the nest with the largest estimated number of foragers; see table 4.11). These figures seem reasonable when compared to those given by Zoebelein (1956) for polyctena, viz. 290-320 kg of honeydew collected per year.

4.6 FORAGER, WORKER-BROOD AND COLONY POPULATION ESTIMATES

The literature provides few estimates of total colony population of wood ants or of related Formica spp. (cf. Wilson 1971, p.438; and also Bodenheimer 1937; Brian 1965, p. 5). Those estimates that exist are based on total counts (Yung 1900; Cory and Haviland 1938; King and Walters 1950; Ayre 1957) or on observations made on colonies during migration (Forel 1874, quoted by Yung 1900). An attempt has been made here to provide total forager- and total colony-population estimates, using the capture-mark-recapture (CMR) formulae.

4.6.1 INTRODUCTION TO CMR

CMR methods are frequently used in ecology for population estimation. Le Cren (1965) reviewed the history of the method, and attributed it to the Danish worker, C.J. Petersen, though the method was also developed independently by Lincoln (1930) - hence frequent reference to the "Lincoln Index". However Cormack (1968) mentions that Laplace

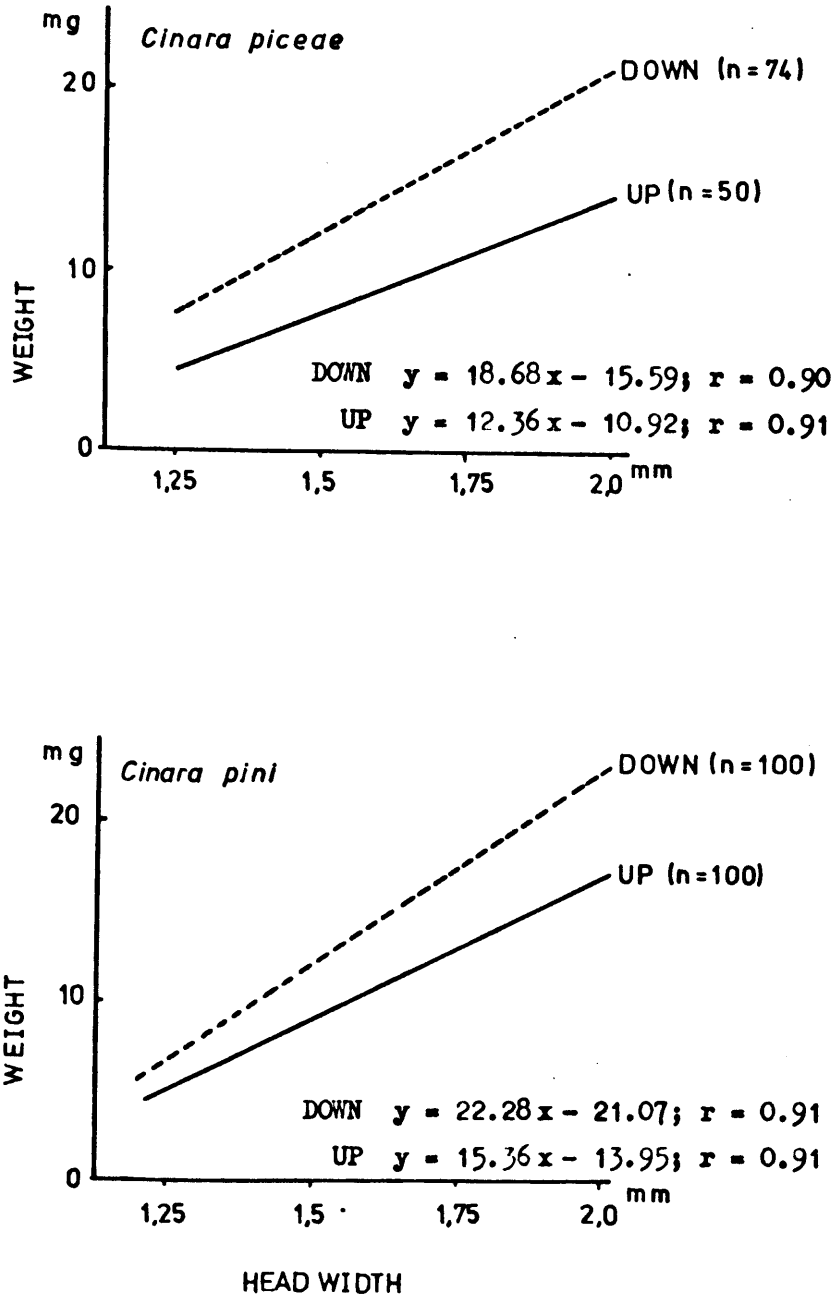


Figure 4.20 The relationship between liveweight and headwidth of lugubris foragers, empty (UP) and carrying honeydew (DOWN) after attending two species of aphids, Cinara piceae and C. pini.

estimated the population of France in 1786 using a modification of the method.

Southwood (1966, p.75) provides a detailed review of CMR methods. The basic formula is

$$\hat{N} = \frac{M\ n}{m}$$

where $\hat{N}$ is the estimated population, M the total number of marked animals, n the number of animals in the second sample, and m the number of marked animals in the second sample. Bailey (1952) has shown that a more accurate population estimate is given by

$$\hat{N} = \frac{M\ (n + 1)}{(m + 1).}$$

This, the "unbiassed formula", is used here. An estimate of the variance of N is given by

$$\text{Var } \hat{N} = \frac{M\ (n + 1)(n - m)}{(m + 1)^2 (m + 2).}$$

The following assumptions are made in applying the formulae:

(a) the mark is permanent for the duration of the experiment,
(b) the probability of capture of a marked individual is equal to the proportion of marked animals in the population,
(c) the population is closed, i.e. there is no emigration or immigration,

and (d) mortality and natality are negligible.

Assumption (a) has caused the greatest hindrance to ant studies. Assumption (b) includes the effects of the mark on behaviour or mortality of the marked individual.

4.6.2 MATERIALS AND METHODS

Five nests were chosen for the field observations. They reflected the mound size variation usually encountered, and were all "solitary" nests - i.e. no neighbouring nests occurred close enough to suspect that they were constituent mounds of a polycalic colony. (PLATES 2 and 3)

The laboratory experiments used worker ants taken either from KC-458a or nest D on a number of sampling occasions.

Marking methods which have been used in previous CMR studies on ants include:

(a) mutilation: Brian (1972);
(b) paint: Chew (1959); Waloff and Blackith (1962); Ayre (1962);
(c) external radioactive mark: Odum and Pontin (1961); Golley and Gentry (1964); Nielsen (1972 a,b; 1974); Erickson (1972);
(d) internal radioactive mark: Brian et al. (1965); Stradling (1968; 1970); Brian and Elmes (1974).

A useful review of marking methods is given by Smith (1972). Marking methods that have been used in other insect studies (Southwood 1966, p.57) such as fluorescent dyes and powders usually require that the second sample be killed to allow detection of the marked individuals, and were not considered here.

In the present study, estimates were required of both forager and total colony population. Consequently, it was decided to adopt spray paint marking for the forager estimate, and a radioactive mass-marking technique (precise method to be decided by experiment) for the colony size estimate.

The forager estimate was obtained from similar-type data as obtained in the route-fidelity study (sections 4.2 and 4.3). Samples of ants were marked by the spray method, and "recaptured" by counts on each route.

Two methods of mass-marking ants using radioactive labels have been employed, (a) external and (b) an internal mark.

(a) External radioactive marks

External radioactive marks are applied by immersing the insects in a radioactive solution to which a wetting agent has been added. The method follows Roth and Hoffman (1952) and was first used on ants by Odum and Pontin (1961). Objections have been raised to the use of this

for ant studies (e.g. by Stradling 1970 working on Lasius flavus and by Erickson 1972 working on Pogonomyrmex californicus (Buckley)), because the mark is transferred to unmarked ants by mutual grooming behaviour. Nielsen (1972 a,b; 1974) has shown, however, that in Lasius alienus (Först), if sufficient drying time is allowed before mixing the radioactive and non-radioactive ants, the mark is not then transferred. A small scale experiment showed that this is also true in lugubris: groups of foragers were immersed in a 200 ml solution containing 5 μCi phosphorus-32 with a few drops of TEEPOL added as a wetting agent. Immersion lasted one minute. After immersion, some ants were mixed immediately ("WET") with non-labelled ants, and the others ("DRY") were allowed dry for five hours before mixing. Two replicates were set up for each, in one the non-labelled ants had a funiculus removed, while in the other, labelled and non-labelled ants could not be separated by sight. The radioactivity levels were read 24 hours later and are given in table 4.10.

The results show that it is always possible to separate primarily and secondarily marked individuals in the "DRY" samples. However, while the method has inherent attractiveness due to the facility of marking large numbers quickly, each ant has to be individually counted on a Geiger-Müller type instrument after resampling. Since an automatic sample changer was not available, this method could not be used for large numbers.

(b) Internal radioactive marks

The use of internal radioactive marking for CMR purposes is fraught with difficulties due to trophallaxis (Gösswald and Kloft 1963). However, Stradling (1968, 1970) showed that by feeding a radioactive solution, and subsequently starving for a number of days, to be determined for each species, that transfer of food to unlabelled ants

Table 4.10 An experiment to test the dipping method of radiolabeling. Some ants ("WET") were mixed immediately with non-labeled ants, and the others ("DRY") were allowed to dry for five hours before mixing. Two replicates were set up for each; in one, the non-labeled ants had a funiculus removed (results in parentheses). The radioactivity levels were read one day later and the levels of individual ants are given in counts per minute.

	WET		DRY	
replicate:	1	2	1	2
	704	229	373	320
	229	228	234	284
	206	234	219	188
	172	194	182	183
	113	169	177	175
	(98)	162	(65)	75
	(86)	157	(44)	62
	(68)	122	(44)	53
	(57)	108	(40)	49
	(45)	93	(37)	47
	BACKGROUND 51		BACKGROUND 40	

was nil. By using radiophosphorus (P-32), high counts were obtained which allowed quick detection by autoradiography.

The following experiments were designed to test the efficacy of the P-32 internal marking method for application to lugubris:

(a) to decide the appropriate number of days feeding for optimal marking,

(b) to decide the length of starvation period required to prevent transfer of radiolabel to non-labelled ants by trophallaxis,

(c) to study retention of the mark,

and (d) study the requirements for adequate detection by autoradiography.

In all these experiments, the radioactive solution (Stradling 1968, 1970) consisted of 1 mCi P-32 (as orthophosphate, supplied by the Radiochemical Centre, Amersham) in 5 ml of 25 percent honey-water. The same ratio of phosphate to honey-water was maintained throughout the experiments, and the quantity of solution administered was doubled at the end of a fortnight (half-life of P-32 is 14.7 days). Ants were kept either in disposable plastic dishes (diameter 90 mm) or in plastic basins with FLUON-coated sides, and with filter paper or a piece of sponge moistened to maintain humidity. Experiments were carried out at both 20°C and at ambient temperatures.

Radioactivity levels were checked on a Nuclear Chicago gas flow meter. Live ants were read in this meter, by first cooling them on ice, and then placing them on a planchette under an upturned "sieve" (a cap from a plastic tube, with its end removed and replaced by nylon netting). When possible, the ants were killed with chloroform and read in the meter dead. Readings obtained by both of these methods have not been compared directly as live and dead ants gave slightly different readings.

The experiments:

(a) Fifty ants were maintained in plastic dishes at 20°C and fed on 0.2 ml of full strength radioactive solution. Their individual

radioactivity levels were checked alive daily for six days. The results are shown in figure 4.21 and indicate that while high counts were obtained on all days, that the ants were uniformly and highly marked by day 3.

(b) A number of dishes, each with 50 ants, maintained and fed as in (a) were used as a store of radiolabelled ants. All food was removed at the end of three days. Thereafter, starting with 0-day starvation, 15 labelled ants were mixed with 15 unlabelled ants. Two replicates were set up for each day: one, a control, in which the unlabelled ants were marked either by mutilation (removing the funiculus) or by a spot of paint on the gaster, and the other, in which the labelled and unlabelled ants could not be distinguished by sight. After 24 hours all were killed with chloroform and their radioactivity levels checked. The results in figure 4.22 are representative of three repeats of this experiment. Slight transfer of label was present in days 0 to 2, eventhough it always seems possible to identify the primarily and secondarily labelled individuals. Nevertheless, transfer at day 3 was negligible.

(c) Ten ants, set up as described in (a) had their radioactivity levels read alive on the first four days, and thereafter at irregular intervals for a total of 83 days. The results (figure 4.23) indicate a convincing retention of the mark.

(d) Larger scale experiments were carried out at ambient temperatures using ants maintained in plastic basins during August 1975 and using ants from GG-902c. Four hundred ants were fed on 0.1 ml P-32 solution per 100 ants on each of two days. Food was removed on the third day.

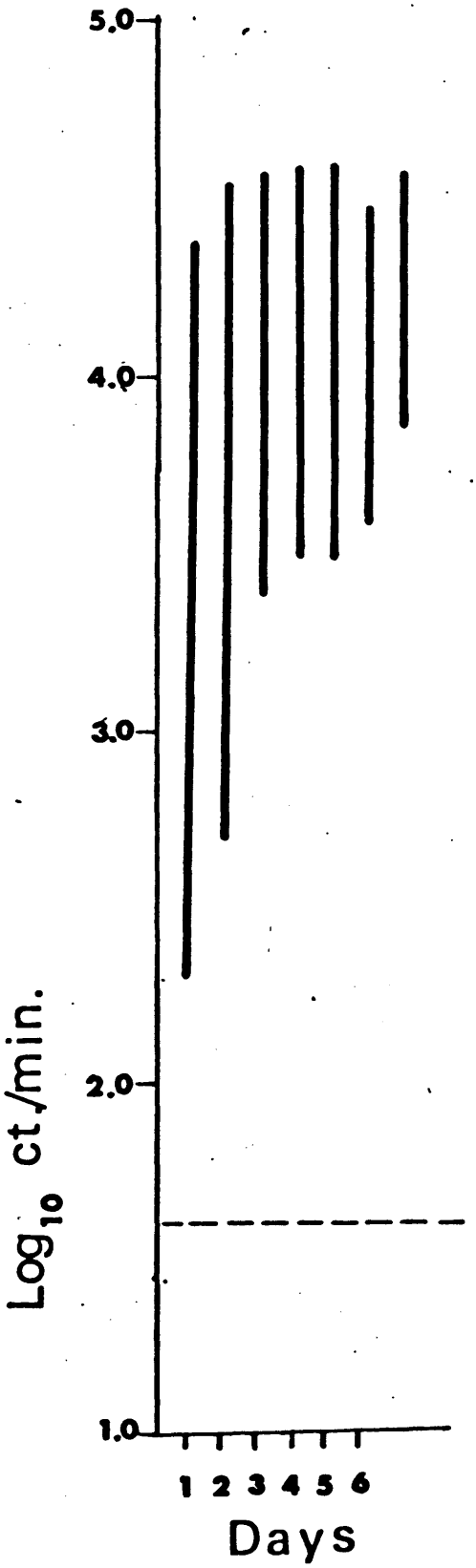


Figure 4.21 Uptake of radiolabel by 50 lugubris workers. The lines indicate the observed range of radioactivities on different days. (-----, background)

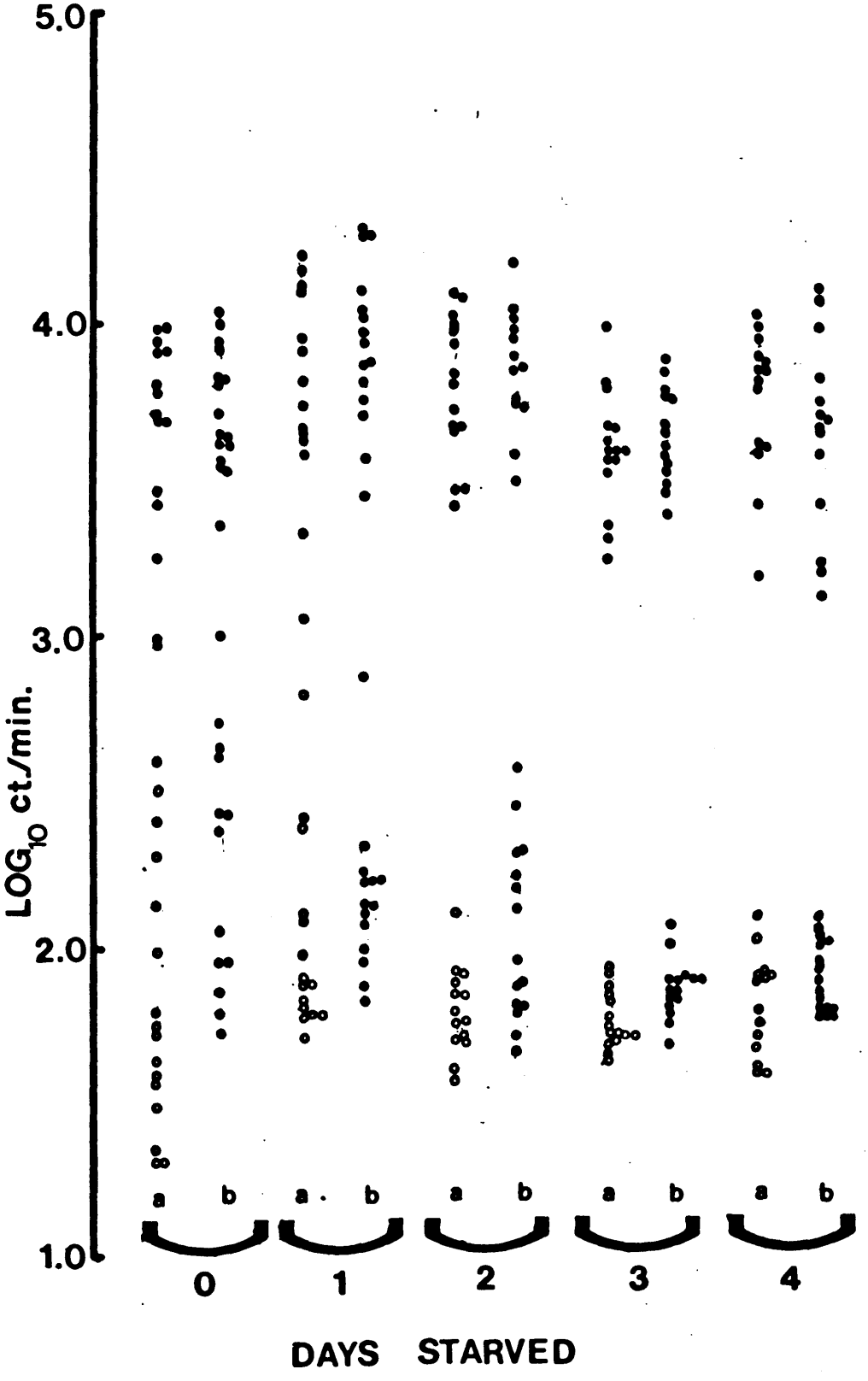


Figure 4.22 Experiment to decide the number of days starvation to prevent transmission of radiolabel to non-labelled ants.
o = non-labelled ants marked with paint on the gaster; • = all other ants. (a) and (b) are two replicates for each day.

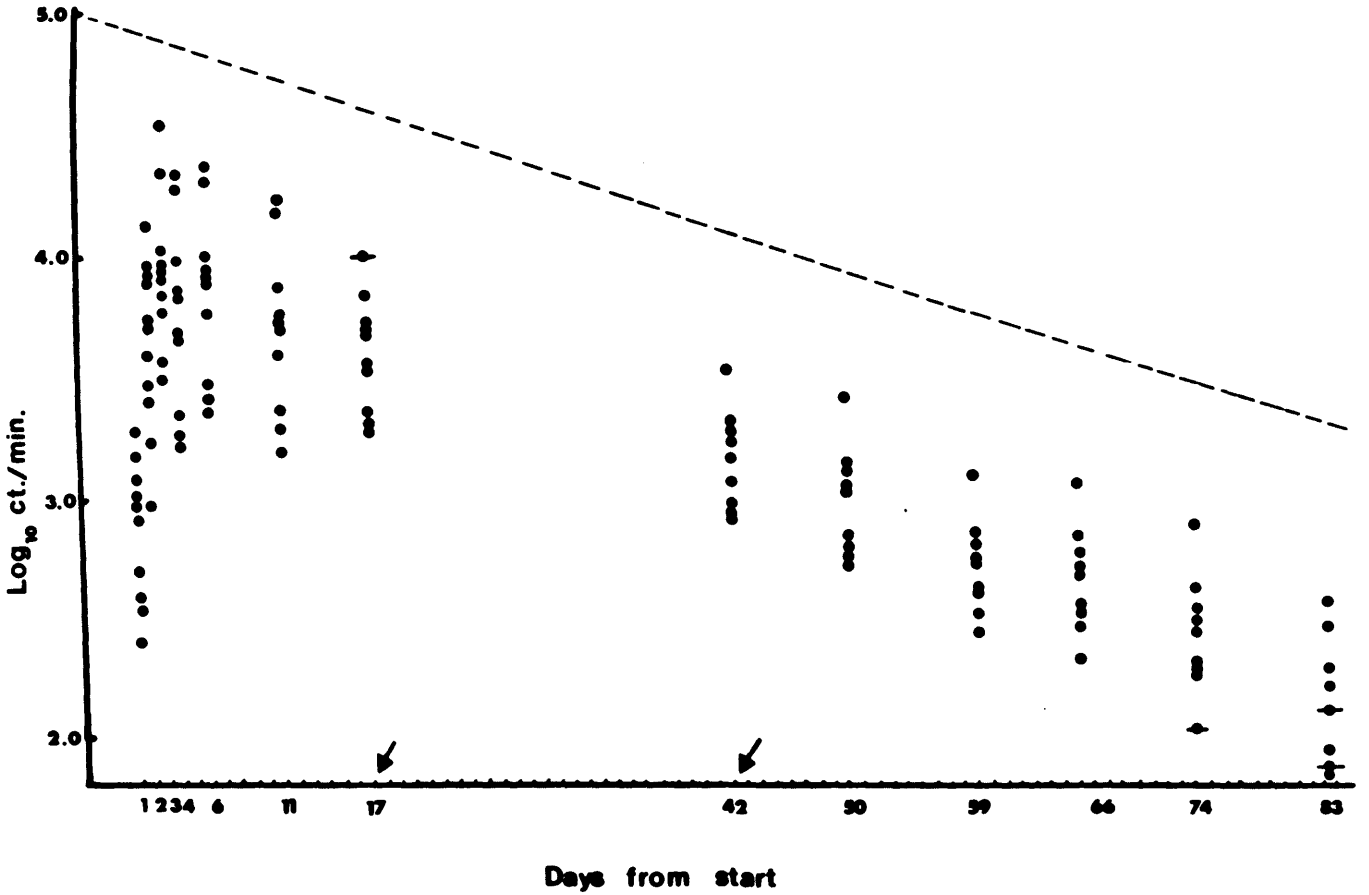


Figure 4.23 Retention of radiolabel by a group of 10 lugubris workers. Non-radioactive honeywater was provided on days 17 and 42 (arrowed). - - - - decay curve of P-32; ⊷ dead ant.

Thereafter, 25 labelled ants were mixed with 175 unlabelled ants; this was repeated for 0 to 3 days starvation. The mixed ants were killed after 24 hours, and placed on X-ray film, envelope unopened, on the side marked "tube side" (KODIREX film, manufactured by Kodak, London). After 10 minutes the film was developed for three minutes in Kodak D19 developer and fixed. In all cases (0 to 3 days starvation) 25 spots could be clearly counted.

A repeat of this experiment, 0 days starvation, 25 labelled ants mixed with 75 unlabelled ants, did show some transfer to unlabelled individuals (i.e. more than 25 spots could be counted on the developed X-ray film). It was thus decided that three days starvation, combined with a 10 minute exposure on X-ray film was the best procedure to adopt.

Summary of the marking method:

(a) Samples of ants were removed from nests. Sampling bias was avoided by sampling from various parts of the nest, including up to 0.5m into it.
(b) The samples were hand-sorted and counted simultaneously.
(c) The ants were maintained in plastic basins and fed on radioactive solution: 0.5 mCi P-32 in 5 ml of 25 percent honey-water solution at the rate of 0.1 ml to each 100 ants on each of 2 days (i.e. 1000 ants received 1 ml of radioactive solution on each of 2 days), applied to cotton wool as described above. On the third day, 1 ml of non-radioactive honey-water was applied to the wool to increase availability of the radioactive marking solution.
(d) On day 4 all food was removed.
(e) After three days starvation, ants were replaced on top of the nest.
(f) 24 hours later, the nest was resampled as in (a),
(g) handsorted as in (b),
(h) anaesthetized with carbon dioxide and autoradiographed for 10 minutes.

Although there was some mortality at stage (h) most of the ants survived and were released at the end of the experiment. Except for the handsorting and counting (b and g) the method was quick and straightforward. With practice it was possible to process 600 ants per hour through the slow stages, and about 500 on each sheet of X-ray film.

The effect of marking on the subsequent behaviour of marked individuals is not always considered as it is often difficult to test. However it was concluded in 4.2.5 that the P-32 internal marking treatment used here did not affect the route fidelity of P-32 labelled ants. Skaife (1968) has also reported that two species of ants were apparently not affected by high doses of X-rays and radioiodide treatment.

4.6.3 RESULTS

(a) Forager estimates

Table 4.11 gives details of the numbers marked at each nest, the numbers of "recaptures", the forager estimate of the route on which the ants were marked ("$\hat{N}$-route"), and its standard deviation. Forager estimates based on other available data are also given in this table. The total route-forager population was extrapolated from the estimate for the marked route on the basis that the average traffic flow on each route is proportional to the forager population of that route. This assumption seems justified by the linear correlation between average route traffic per five minutes and route forager-population estimate on all routes studied (figure 4.24).

(b) Colony-size estimates

Table 4.12 gives the numbers marked, the number of recaptures, the colony population estimate and its standard deviation for each of the five nests studied.

(c) Worker-brood estimates

An estimate of the number of worker pupae present in the nests on 19.VII.1975 was obtained for four of the five nests, as follows: all the brood in the accessible part of the nest was quickly removed into a basin. The total volume of the brood was obtained using a canister

Table 4.11 Estimation of forager numbers by the capture-mark-recapture method. The reference numbers are as used in figure 4.21, and other terms are explained in the text.

NEST	M	m	n	$\hat{N}$-route	S.D.(%)	TOTAL FORAGERS	5-MIN COUNT	ROUTE/ YEAR	REFERENCE NUMBER
*J	250	42	413	2407	345 (14.3)	10 465	41.3	1; 1975	1
A	325	16	75	1453	302 (20.8)	12 988	59.0	5; 1974	2
A	375	10	148	5080	1411 (27.7)		74.0	1; 1974	3
*I	200	18	287	3032	655 (21.6)	6 906	71.7	1; 1975	4
C	555	100	1032	5676	534 (9.4)	24 895	103.2	1; 1974	5
D	900	136	1079	7094	564 (7.9)	38 345	107.9	1; 1974	6
E	375	50	1234	9081	1233 (13.6)	34 011	137.1	1; 1975	7
*H	400	53	1517	11 244	1489 (13.2)	27 159	151.7	1; 1975	8
B	500	91	2012	10 940	1108 (9.9)	45 357	182.8	1-A; 1974	9
B	500	141	4212	14 834	1220 (8.2)		382.9	1-B; 1974	10
B	569	77	2402	17 530	1940 (11.1)	64 686	240.2	1; 1975	11
*F	1000	168	3252	19 249	1437 (7.5)	59 594	325.2	1; 1975	12
*G	750	135	4601	25 379	2136 (8.4)	**	460.1	**; 1975	13

* Further data on these nests are given in tables 4.12 and 4.13.

** Data from two routes considered simultaneously.

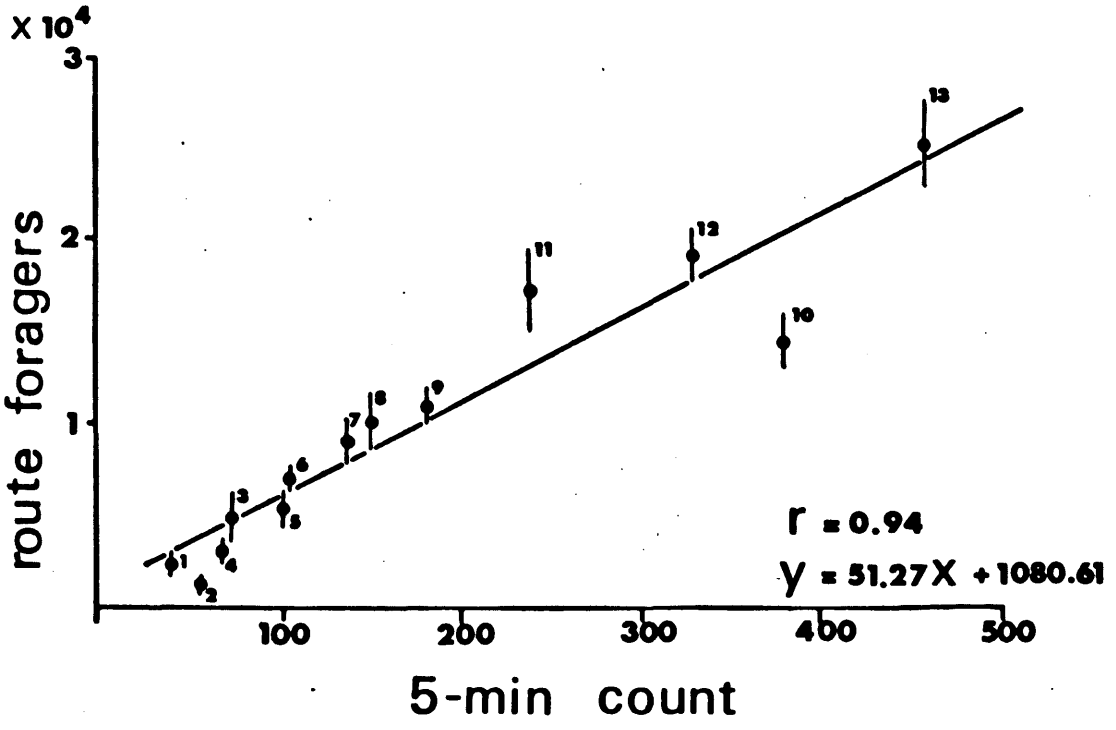


Figure 4.24 The relationship between route forager estimate and average total five-minute count. The points are shown ± S.D., and the reference numbers are as given in table 4.10.

Table 4.12 Estimates of five *lugubris* colony populations using the capture-mark-recapture method. The terms are explained in the text.

NEST	M	n	m	$\hat{N}$	S.D. (%)
F	1646	1294	29	71 052	12 613 (17.8)
G	1486	2265	84	39 615	4 191 (10.6)
H	893	2124	54	34 502	4 551 (13.2)
J	946	1067	55	18 042	2 326 (12.9)
I	785	648	51	9 797	1 291 (13.2)

(0.57 litre in volume) and this was multiplied by the total count of brood in a representative canister-full of brood at each site. At nest F the brood was not concentrated into a single large "brood centre" - as at the other four nests, nor was it on two other occasions during the next fortnight, and no brood estimate was obtained for this nest. The results obtained are part of table 4.13.

(d) General

The results of the forager, colony-size and worker-brood estimates are brought together in table 4.13. Even though the data are based on only five nests, some trends appear. The percent foragers seems fairly consistent at each nest, though comparative data on similarly-sized colonies of other species does not seem to be available. Lewis (1975) recently suggested that foragers comprised only six percent of the total colony population of Atta octospinosus (Reich), but it may be reasonable to expect more "within" nest activity associated with the fungus gardens of leaf-cutting ants.

The percent brood at four nests suggests a high brood ratio in the smaller nests I and J, while the proportion of brood at the other two sites was about half of this. Both nests I and J were immature nests during 1975 and did not produce alatae, whereas H and G both produced alatae. There may be a high brood ratio in immature nests which eventually levels off as the nests reach maturity.

4.6.4 COMPARISON WITH PUBLISHED RESULTS

It is appropriate to consider these results in the light of previously published studies. Published values for colony size in Formica are given in table 4.14, where it can be seen that the species' colony-sizes can be considered in two broad categories, those with less populous colonies - up to a few thousand in population size, and those

Table 4.13 Some population parameters of five *lugubris* colonies.

NEST:	I	J	H	G	F
colony estimate	9797	18 042	34 502	39 615	71 052
forager estimate	6906	10 465	27 159	25 379	59 594
worker brood	4536	6 648	5 170	7 590	*
percent foragers	70.5	58.0	78.7	64.1	83.9
percent brood	46.3	36.8	15.0	19.2	*

* = no data.

Table 4.14 Some colony size estimates of *Formica* spp.

SPECIES	COLONY SIZE	REFERENCE
wood ants	114 000	Forel (1874, quoted by Yung 1900)
wood ants	19 933 - 93 694	Yung (1900)
exsectoides	8229 (+ 11 queens)	Andrews (1929)
exsectoides	41 326 (+40 queens) 237 103 (+1407 queens)	Cory and Haviland (1938)
pallidefulva nitidiventris	541 - 7050	Talbot (1948)
"incerta"	107 - 1668	Talbot (1948)
rufa melanotica	c. 50 000	King and Walters (1950)
perpilosa	2000 - 3500	Schumacher and Whitford (1974)
lugubris	9797 - 71 052	present study.

with larger colonies, the wood ants and related species.

A complication arises when considering the colony size of wood ant colonies, that of polycaly. This problem was avoided in this study by choosing isolated nests for study. Many figures are mentioned for colony-size in wood ant literature, and it is often difficult to know to what species they refer, whether to a polycalic colony or to a single nest, or, how they were estimated. Holt (1955) accepted an estimate of 100 000 to 150 000 workers in a large wood ant nest on the basis of a calculated 59 200 foragers in his large, isolated aquilonia study-nest. (This figure was obtained using a different procedure to the CMR methods used here.) Brian (1965, p.6) concluded from a literature survey that wood ant colonies ranged up to 300 000 workers.

Forel (1874, quoted by Yung 1900) estimated the colony-size of a wood ant nest which he observed moving site at 114 000, and suggested that the colony-sizes of wood ant nests range from 5000 to 500 000 workers. Yung (loc. cit.) dismissed the upper range as overestimates, though it is quite possible that Yung and Forel studied different species. Reference to the first two graphs in Horstmann (1970) gives maximum values of 16.4 and 8.2 foragers leaving and entering two different nests of polyctena each second. Transformed to "five-minute counts" as used here, this corresponds to 4920 and 2460 respectively. If the linear relationship in figure 4.24 is assumed, this is approximately equal to 127 000 and 260 000 foragers. In comparison, the highest forager estimate in table 4.11, that of nest B during 1975, corresponded to an average total five-minute count of 889. Wellenstein (1973) mentioned transplanting 150 to 200 litres of polyctena nest material, and estimated 480 000 ants to each 200 litres. It thus seems possible to reconcile large estimates for some wood ants, especially flourishing polycalic polyctena colonies, with lower estimates for other species.

Yung's (1900) results are especially interesting. In total colony counts of five wood ant nests, he obtained the following results: 19 933, 47 828, 53 018, 67 470, and 93 694. These results are very similar to the estimates obtained here, and support the view that not all wood ant species have equally populous colonies (Bodenheimer 1937).

4.7 COLONY LIMITS STUDIED BY RADIOISOTOPES

Investigations of food exchange between neighbouring ant nests using radioisotopes include those on polyctena (Gösswald and Kloft 1958, 1963), Lasius minutus Emery (Kannowski 1959b), Pheidole megacephala (F.) (Mortreuil and Brader 1962). This method can be used to elucidate communication between nests in the absence of visable exchange of workers. Internest route connections were rarely observed during this study and were generally associated with nest-moving. Furthermore, it was suggested in 3.5 that the nests were overdispersed and that absence of polycaly was a possible explanation. Observations were made to obtain further information on this aspect of lugubris biology.

The method followed here is that of Gösswald and Kloft (1963) except that P-32 only, and not a mixture of P-32 and radioiodide was used. The radiolabel was provided in four polythene tubes (15 x 70 mm) placed at the nest perimeter and consisted of 10 ml solution of 25 percent honey-water containing 0.4-0.6 mCi P-32. Study sites were chosen where mounds occurred close together.

The first experiment was carried out in compartment 455 of Kilcoran Wood (see map of site in figure 4.25) during July-August 1974. Nest 455h received 0.5 mCi P-32. Samples of 25 workers were taken from all the nests three and 10 days later and read on the Gas Flow meter, and also on a Nuclear Chicago scintillation counter. Only nest 455i was secondarily radioactive. This nest was evidently a daughter nest of

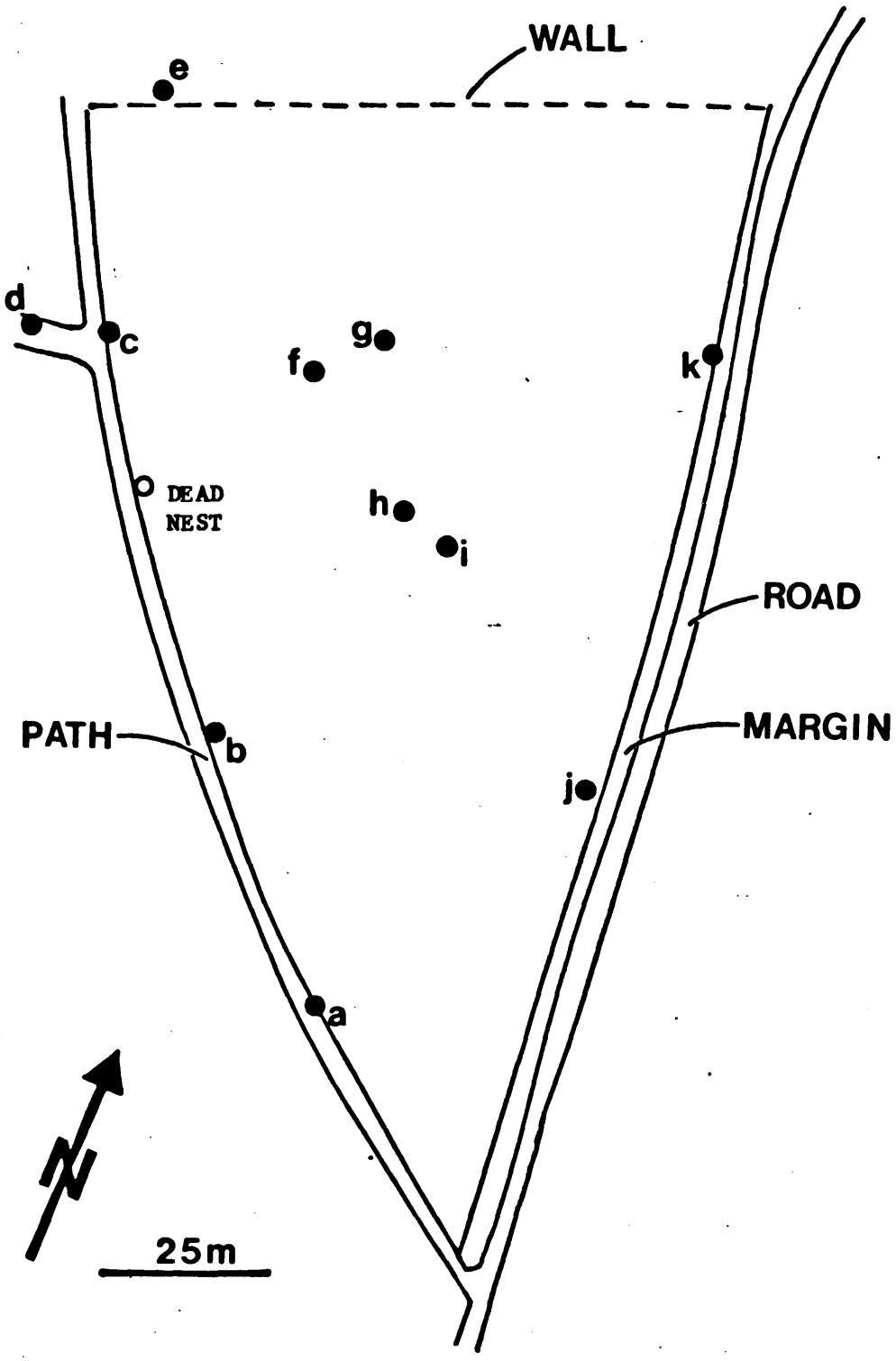


Figure 4.25 Map of the nest sites in compartment KC-455 during 1974.

KC-455h and both attended aphids on the same tree.

Two sets of similar observations were made in Glengarra Wood during August 1975. Figure 4.26 gives a map of the sites and the arrows indicate the direction of nest movements during early 1975. In compartment 902 (figure 4.26a), 0.4 mCi P-32 was given to nest a. Subsequent collections of ants from the neighbouring nests yielded radioactive ants at site b only - the abandoned site of colony a. In compartment 937, 0.4 mCi P-32 was given to nest f. Subsequent collections showed that ants in site a were secondarily marked.

Of these three sets of observations, only in the last was there any sign of true polycaly. In this case, there was no evidence to suggest that either nest was a daughter nest of the other, and neither were they a single colony in the act of moving site. However, bearing in mind that sites with adjacent nests were chosen, and the limited extent of the observed transmission of the radiolabel between nests, it seems that large-scale food-exchange between nests is not common in Irish lugubris. This supports the suggestion that polycaly is not common in lugubris colonies here. These results contrast with other work, e.g. Gösswald and Kloft (1963) demonstrated transmission of food for over 200 m within the constituent mounds of a polycalic polyctena colony.

4.8 CONCLUSIONS

The observations on route fidelity demonstrated a convincing route fidelity in lugubris, and yielded results very similar to those obtained by Rosengren (1971) for rufa and polyctena. Rosengren suggested that forager RF was enhanced as the season advanced. While this may be so when individual nests are considered, the present results suggest considerable inter-colony variation in RF, which is not associated

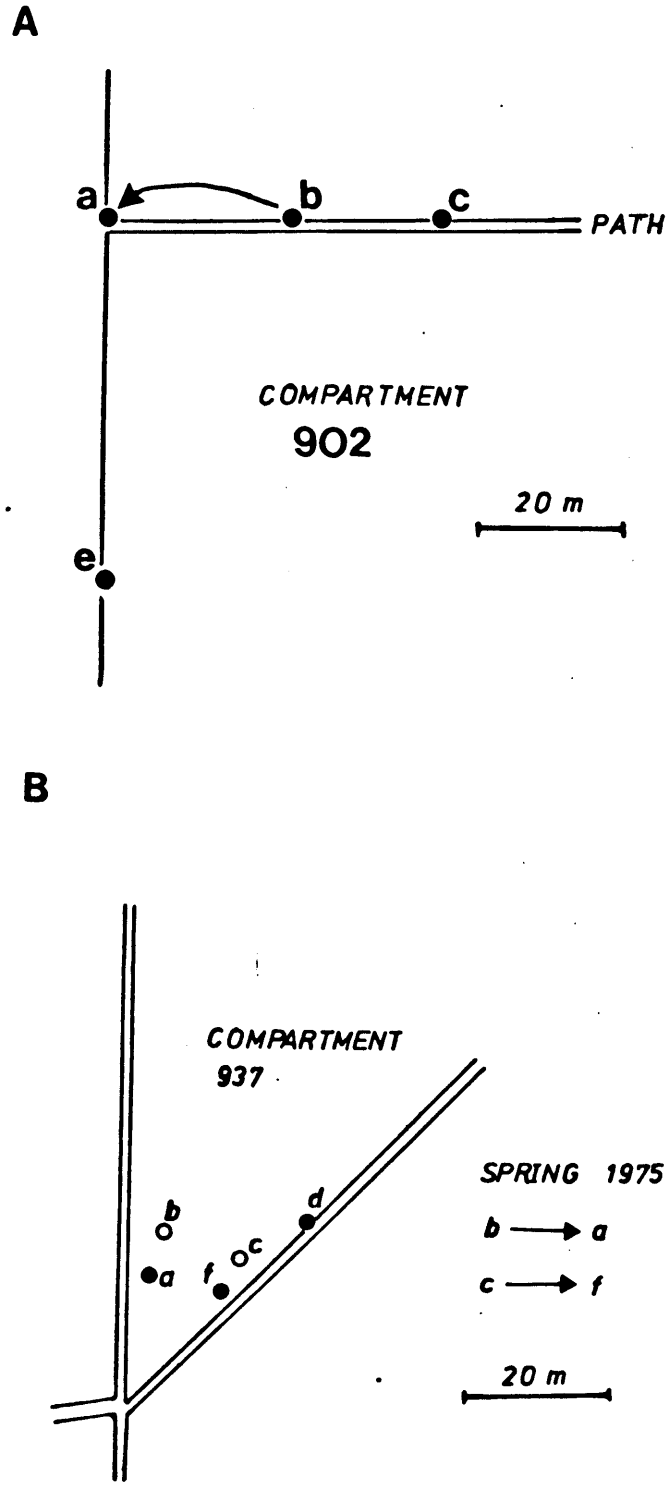


Figure 4.26 Map of the sites in Glengarra Wood where colony limits were studied using P-32. The arrows indicate nest site movements during spring 1975.

with the time of year. The observations at the Y-junction showed that time had a significant, if not a great effect, on forager RF. However, fidelity even to the actual tree visited was remarkable for over a month. Forager RF was apparently unaffected by treatment with various anaesthetics, and this is in agreement with earlier work on the honeybee (Ribbands 1950; Simpson 1954). The unchanging nature of forager site-fidelity in the absence of recruitment was well-demonstrated by the experimental "removal" of an aphid tree: the RF of foragers attending aphids on this tree remained stable for three days.

Route fidelity can be considered as part of fidelity to the actual foraging site. Foragers return to these sites regularly and this leads to "partitioning" of the foraging grounds (Dobrzanska 1958). In contrast, Holt's (1955) study emphasized the apparent random nature of wood ant foraging, which he nevertheless considered to be a stable foraging system. Rosengren (1971), on the other hand, described an almost unchanging fidelity to foraging site. The results described here suggest a somewhat more changing foraging strategy - a low RF (= 63) was once recorded which may have been due to mass recruitment of experienced foragers. Furthermore, the final destination of the forager routes were repeatedly changing in young SS stands, whenever the aphid Cinara piceae changed host trees. However, the route and site fidelity did lead to the establishment of stable foraging systems, whose structures remained relatively unchanged from year to year.

There were no readily identifiable groups of foragers associated exclusively with prey- and honeydew-carrying. These conclusions concur with those of Kiil (1934) for wood ants. However, the adult-carrying behaviour observations did yield trends suggesting that adult carriers were similar to a sample of ants taken from the route, and that the carried adults were akin to a sample from the nest. While these observations are as suggested in the literature (Möglich and Hölldobler

1974) the behaviour as observed in Irish lugubris seems somewhat aberrant: it was most commonly associated with route traffic early in the foraging season, but not, apparently, with inter-mound traffic. This "random" type of adult-carrying behaviour may be a vestige of other more "functional" behaviour, and it does not seem by have been reported previously. It would be interesting to obtain reports of adult-carrying behaviour in other monocalic wood ants. Adult-carrying was also observed in the "conventional" nest-moving mode, and on these occasions assumed much greater proportions (76 percent of traffic on one occasion).

The observations made on foraging rhythms demonstrated that temperature accounted for much of the observed rhythmicity. Air temperature was the best predictor of the number of foragers on the route. The numbers of foragers rose to a maximum at 24°C ground temperature, and ceased above 33°C. These results are very similar to those of deBruyn and Kruk-deBruin (1972) for polyctena, and the running speed/temperature response of lugubris was almost identical to that reported by the same authors in polyctena. The very different graph for aquilonia (Holt's 1955 data) is interesting and difficult to explain; the different method of temperature measurement used by Holt (a blackened mercury thermometer) is unlikely to account for a difference of this magnitude.

The proportion of prey items taken was greatest in the early part of the day and the number of prey items was linearly related to ground temperature. Hence, it appears that prey-hunting is limited by availability of prey items and is enhanced by temperatures which allow greater agility. The calculated average foraging return journey time of 3.93 hours allows 6.1 trips per day per forager. The average daily intake of food at nest C was about 14 000 prey items and 55 g of honeydew. Not all the prey items constitute individual animals as

many fragments are carried in to the nest. Various Diptera were the major food items, though earthworms, spiders, and lithobiid centipedes were also taken in large numbers. Honeydew gathering is undoubtedly the major occupation of lugubris foragers since about 75 percent of all loads were honeydew. The two most important honeydew sources were Cinara pini on SP and C. piceae on SS.

The capture-mark-recapture estimates of lugubris route-foragers were linearly correlated with average traffic flow per five minutes ($r = 0.94$), over the range studied. This suggests a certain consistency in the estimation procedure, and the graph may prove useful in providing quick forager estimates in future studies.

The method of P-32 radiolabeling employed was adequate for the present studies, though a development of the dipping technique would be an advantage: large numbers of ants could be marked and released within a few hours. Rapid detection by autoradiography is a major consideration in favour of the method used.

The results of the forager, worker-brood, and colony-size estimates appear reasonable in the light of published estimates of other related species, though they suggest that the colony-size of the nests studied was much smaller than those estimates available for some species, e.g. polyctena.

The results of the observations on the limits of colonies using P-32 support a general field observation: polycaly (and also polygyny) is rare among Irish lugubris colonies.

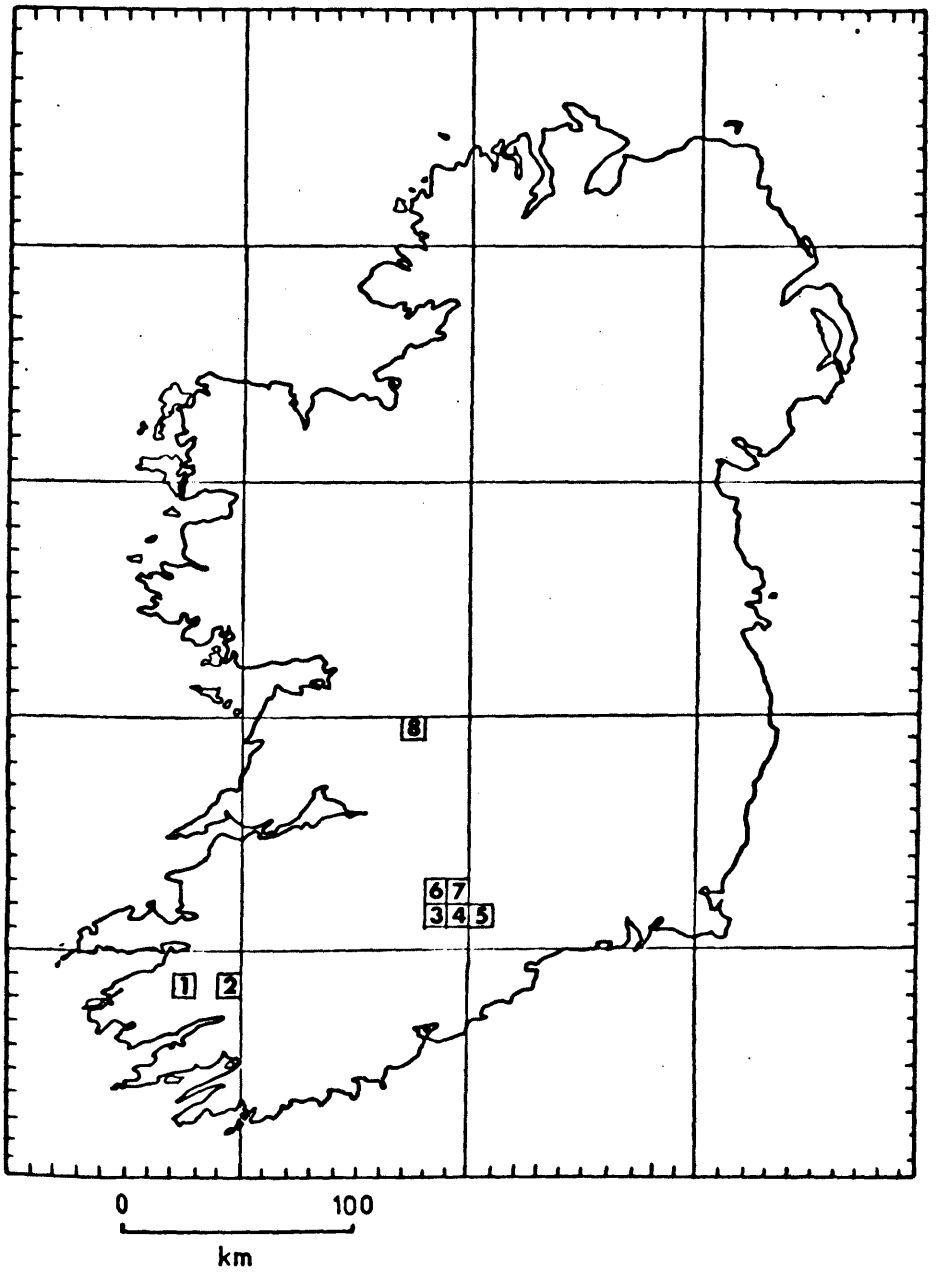


Figure 5.1 Arbitrary identification numbers for the 10-km squares from which aphids and myrmecophiles are recorded. (Based on the Irish grid.)

Table 5.1 The species of aphid attended by *lugubris* in Ireland. Some biological notes are given, and the locality numbers are those given in figure 5.1. * denotes a new Irish record.

SPECIES	HOST PLANT	FEEDING SITE	LOCALITIES	NOTES
Cinara pini (L.)	*Pinus sylvestris*	shoots and branches	3,4,5,6,7,8	common at all sites except Killarney
C. piceae (Pz.)	*Picea sitchensis* + *P. abies*	branches and main stem	2,4,5,7,8	common at all sites.
**C. bogdanowi* (Mordv.)	*Picea sitchensis* + *P. abies*	branches	7,8	seen five times; Moore's Wood and Woodford.
**C. pilicornis* (Htg.)	*Picea sitchensis* + *P. abies*	young shoots	4.7	common until June; not always ant attended.
**C. kochiana* (Börner)	*Larix decidua* + *L. kaemperi*	branches and main stem	4,7	large colonies; only seen in South Tipperary.
**C. abieticola* (Chol.)	*Abies procera*	branches	7	seen twice.
Lachnus roboris (L.)	*Quercus petraea*	branches	2	common in Killarney.
Eulachnus brevipilosus Börner	*Pinus sylvestris*	leaves	7	seen once.
Mindarus abietinus Koch	*Abies procera*	young shoots	7	seen once.
Symdobius oblongus (v.Heyd.)	*Betula pendula* + *B. pubescens*	young branches	2,8	very common in Woodford.
Thelaxes dryophila (Schrk)	*Quercus petaea*	leaves	2	common in Killarney.
Aphis ilicis Kltb.	*Ilex aquifolium*	leaves and young shoots	2,4,8	common in Killarney and Woodford.
A. fabae-group	*Cirsium* sp.	leaves and stem	7	one record of attendance.
A. ruborum (Börner)	*Rubus fructicosus*	leaves and stem	7	one record of attendance.
Chaitophorus beuthani (Börner)	*Salix* sp.	leaves	2	one record of attendance.

in Canada, involving different Cinara spp. which were attended by obscuripes and Dolichoderus taschenbergi (Mayr).

The following is a brief account of the more important species:

(a) Cinara pini This species is the aphid most commonly attended by lugubris; it is visited by foragers from most nests in South Tipperary and was also seen in Galtee Wood, and Woodford. Small colonies are usually formed at the shoot tips of SP, though large colonies were found during August 1975 on branches up to 50 mm diameter. Eggs hatch during late April/first week in May and ant attendance begins immediately. Egg laying begins during the last week of October and the latest observed ant attendance was 3.XI.1974. This species was also visited occasionally by Myrmica ruginodis, Lasius niger and Formica lemani.

(b) Cinara piceae Very large colonies (up to a metre in length on the branch) of this aphid occurred commonly during 1974, though not as commonly in 1975. The species produces large volumes of honeydew which attracts flies and wasps in addition to ants. The only observed large colony of this species which was not attended by lugubris was attended by Lasius fuliginosus. Egg laying began on 30.X.1974, and the latest observed ant attendance was on 15.XI.1974. Newly hatched aphids were first observed on 16.IV.1975, and large numbers of alate aphids appeared from the 19.VI.1975 on. Further observations on this species are described in 5.1.2.

(c) Cinara kochiana Very large colonies (some over a metre in length on the branch) of this species occurred adjacent to nest MW-250a during 1974, but the colonies were not as extensive during 1975. The species is generally present when larch occurs near a lugubris nest and has never been found away from the nests.

Of the other three Cinara spp. recorded in table 5.1, only C. bogdanowi has been observed with a large colony. This was about 0.7 m in length, and occurred on the lower branch of Picea abies in Woodford on 15.IX.1975. C. abieticola has only been observed in small numbers. C. pilicornis occurred frequently away from lugubris nests, though it was always ant-attended near the nests. This species forms small compact colonies near the tips of young spruce growth. Lachnus roboris was always present near the nests in Killarney, but few observations were made on this species.

Two other aphids recorded in table 5.1 merit consideration. Symdobius oblongus was seen in Killarney on Betula pendula, where it was not common, and in Woodford, where it was abundant on 15.IX.1975. Small colonies of this aphid occurred on young shoots of Betula pendula and B. pubescens, and were attended by foragers from all four Woodford lugubris nests. Although both these host trees occur in South Tipperary, this aphid has not been seen there. Aphis ilicis on Ilex aquifolium was attended by lugubris in Killarney and in Woodford. This aphid was found in Coolagarraunroe Wood near Glengarra, but it has never been found attended by lugubris in South Tipperary. However, neither of these aphids are obligatorily ant-attended, though they are relatively important as honeydew sources in Killarney and Woodford.

The adelgids Adelges cooleyi (Gillette) on Pseudotsuga menziesii and Pineus pini (Macquart) on Pinus sylvestris were seen in Glengarra and Moore's Woods but they were not attended by lugubris, as they were not near the nests. Adelges sp.(laricis Vallot ?) on Larix decidua was attended during 1975 by two nests in Kilcoran Wood. The route from one of these nests, KC-441a, was the longest observed during this study (over 220 m long). A low route fidelity was also recorded (figure 4.2) at this site and this may have been caused by recruitment to the adelgids.

Nixon (1951) and Way (1963) have reviewed the extensive literature on ant-aphid relations and Starý (1966) reviewed ant-aphid-parasite relationships. They concluded that one of the benefits which accrues to the aphid, was a disturbance, if not actual removal of a potential predator or parasite. These brief observations can be reported:

(a) Predaceous syrphid larvae were frequently seen among lugubris-attended Cinara piceae, and did not appear to be disturbed by the ants.

(b) Although Hemerobius and Chrysopa (Neuroptera) adults occur frequently, their aphidophagous larvae have not been seen amongst ant-attended aphids.

(c) A large population of Cinara pilicornis appeared on Picea abies in Rehill Wood, which has no lugubris colonies, during June 1975 and these were preyed upon by a large number of the aphidophagous larvae of the coccinellids, Coccinella 7-punctata L. and Adalia 10-punctata L., e.g. 35 coccinellid exuviae were counted on one 1.5 m tree. A similarly large population of C. pilicornis in nearby Glengarra Wood, which were attended by lugubris, was not attacked by coccinellids to the same degree, and may thus have gained some protection by ant attendance.

(d) Of all the Cinara spp. in table 5.1, the only species in which parasitized "mummies" were observed was C. pini, and there was a very low level of parasitism. Lachnus roboris is "completely free of parasites" (Starý 1969).

Many authors, including Pontin (1958) have reported the predation of aphids by ants. Some C. piceae and C. pini apterae and a large number of the June alates of C. piceae were taken as lugubris prey. Many of the remaining alates had their wings damaged by the ants.

5.1.2 OBSERVATIONS ON CINARA PICEAE

Cinara piceae occurred in large numbers on seven year old SS near nest MW-267a during 1974 and 1975. These SS were planted alternately in an SS/PC mixture and occurred over the entire non-shaded area in figure 5.2. This figure also gives details of neighbouring tree stands. The nest has been present at this site at least five years, and probably for longer than the young SS/PC stand. Observations were made to (a) discover the number and distribution of aphid trees and (b) see if the aphid colonies had any detrimental effect on the growth of SS. (A map of the route system of this nest was given in figure 4.1a)

An identification number was attached to each of the 287 young SS trees. During three observations (end.X.1974, 21.IV.1975 and 23.IX.1975) a total of 57 trees were observed with C. piceae. Of these, 45 (= 79 percent) lay within an arbitrarily chosen radius of 13 m on one side of the nest, and to the west of the drain on the other side of the nest (these trees will be referred to as the "inside" trees, and all the others as the "outside" trees). There were a total of 81 inside trees and 206 outside. The remaining aphid trees (11) were scattered throughout the outside trees, and extension of the 13 m radius by a few metres would include many non-aphid trees. At least four of the 11 aphid trees occurring outside the boundary were isolated, non-lugubris attended and with very small aphid colonies.

Comparison of the route system map (figure 4.1a) with figure 5.2 shows another characteristic of C. piceae/lugubris interaction: when C. piceae occurs on young SS - the most frequently observed case, it tends to be present on many trees in a close circle in the nest vicinity. This gives rise to a system of many short routes. Furthermore, C. piceae frequently migrates from tree to tree (apterae were often seen walking on the ground). As a consequence, the lugubris route system

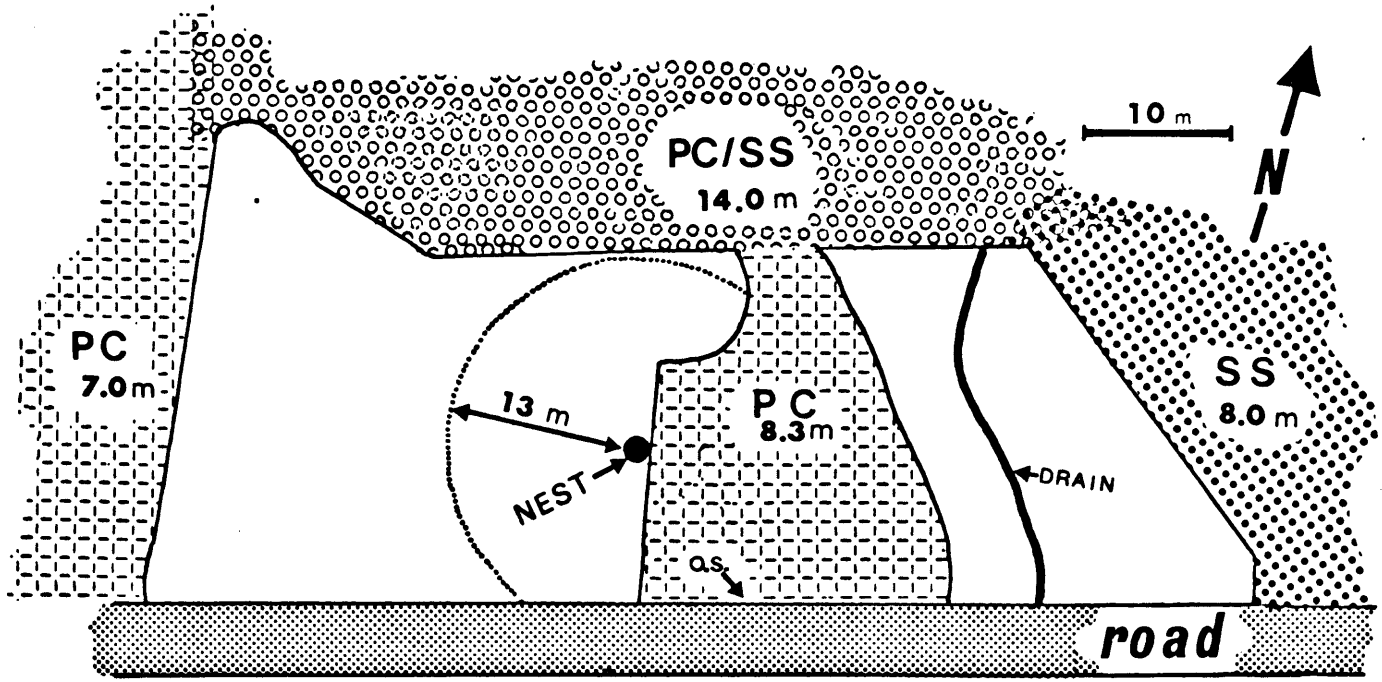


Figure 5.2 Map of the study area adjacent to nest MW-267a. The white area is occupied by seven year old SS/SP, and the 13 m diameter and drain delimit the area where most of the aphid trees occurred. Neighbouring tree stands and their heights are indicated. "O.S." is an old site, last occupied over five years ago.

is constantly changing in this type of habitat. This contrasts with the long, branched system of routes seen in pine stands associated with C. pini. Here, the routes are perennial, and frequently completely cleared of debris for 20 m or more from the nests.

Wellenstein (1973) reported the annual height increment for 10 years of pine trees in the vicinity of an artificially founded polyctena nest. He showed that the trees near the nest had a much smaller increment than those farther away. This difference was caused by the increased population of aphids near the nest.

Such a long-term approach was not feasible in the present study. However, all the SS trees' heights were measured and tested to see if there were differences in actual height between trees nearer the nest and those further away. Three different pairs of samples were taken and compared by t-tests (table 5.2):

Test 1: all inside trees (sample 1) compared to all outside trees (sample 2),

Test 2: all 57 aphid trees (sample 1) compared to all other trees (sample 2),

Test 3: all 57 aphid trees (sample 1) compared to all non-aphid outside trees (sample 2).

While a significant result was obtained in test 1, the other two tests were not significant. Consequently, the results are inconclusive.

5.2 MYRMECOPHILES

Records of the myrmecophiles found in the lugubris nests are given in this section. These species correspond to the "ectosymbionts" of Wilson (1971, p. 390): "those organisms that live on or among their hosts". Donisthorpe's (1927b) classic study remains the major review in this field for Britain and Ireland.

Table 5.2 Comparisons of the heights of young Sitka Spruce with and without colonies of Cinara piceae. See text for explanation.

TEST	SAMPLE 1*	SAMPLE 2*	t	P
1	1.72 ± 0.44	1.94 ± 0.50	3.85	<0.001
2	1.88 ± 0.49	1.86 ± 0.49	0.18	>0.8
3	1.88 ± 0.50	1.91 ± 0.49	0.39	>0.6

* = mean tree height (m) ± S.D.

The term myrmecophile is used here in the broad sense of animals occurring regularly in ants' nests. Wasmann's classification of myrmecophiles (definitions from Wilson 1971, p.390) provides a useful indication of the extent of myrmecophily:

1. Symphiles: "true" guests. . .accepted to some extent by their hosts as though they were members of the colony.
2. Synoeketes: primarily scavengers and predators, are ignored by their hosts.
3. Synectrans: scavengers and predators. . .treated in a hostile manner by the social insects among whom they live.
4. Ecto- and endo-parasites: organisms whose parasitic behaviour is not normally distinguishable from that of similar species that prey on non-social insects. (This category is not considered further here.)

Records of three lugubris myrmecophiles were provided by Bouskell (1905) from Caragh Lake, and Collingwood (1959, 1965) recorded myrmecophilous beetles from the lugubris nests at Woodford and the aquilonia nests at Churchill, county Armagh (referred to as "Armagh" here).

At various times during this study, samples of nest material were sorted on a large white plastic tray. In addition, five nests (the same nests on each occasion) were sampled monthly (April to September) during 1975 to ensure adequate coverage of the active season. Beetles were identified by reference to Joy (1932). Dr P.M. Hammond has checked the identity of a series of the staphylinids and the scydmaenid, and identified Sipalia circellaris. The spiders were identified using Locket and Millidge (1953), the millipedes using Blower (1958) and the pseudoscorpion using Evans and Browning (1954).

Table 5.3 gives a list of the myrmecophiles so far recorded from Irish wood ant nests, and the localities at which some of these species were found during the present study. Three of these species, Nototheca anceps, Sipalia circellaris, and Thyreostenius biovatus are new Irish records.

Table 5.3 Records of myrmecophiles associated with wood ants in Ireland. The "Armagh" records were taken with *aquilonia*, and all the other records are from *lugubris* localities. The locality numbers are those given in figure 5.1.

SPECIES	PREVIOUS RECORDS*	PRESENT STUDY (localities)
STAPHYLINIDAE		
Oxypoda formiceticola Märk.	Woodford, Armagh (b,c)	none
O. haemorrhoa Mann.	Armagh (b), others (d)	none
Thiasophila angulata Er.	Armagh (b), Woodford (c)	2,3,5,7,8
Nototheca flavipes Gr.	Armagh (c)	2,3,5,7,8
N. anceps Er.	-	2,5,7,8
Othius myrmecophilus Kies.	others (d)	3,4,5,7,8
Quedius brevis Er.	Caragh Lake (a), Armagh (b)	none
Sipalia circellaris Gr.	-	2, 3,7, 8
Atheta talpa (Heer)	Armagh (c)	none
SCYDMAENIDAE		
Stenichnus collaris (Müll.)	others (d)	2,7,8
RHIZOPHAGIDAE		
Monotoma conicicollis Aube	Woodford and Armagh (c)	none
M. angusticollis Gyll.	Caragh Lake (a),Armagh(c)	none
CHRYSOMELIDAE		
Clytra quadripunctata L.	Caragh Lake (a)	none
PTILIIDAE		
Acrotrichis montandoni(All.)	Armagh (c)	7,8
Ptenidium sp.(pusillum (Gyll.)*?)*		7
DIPLOPODA		
Proteroiulus fuscus(Am Stein)	others (d)	2,3,7,8
Cylindroiulus punctatus(Leach)	others (d)	2,3,7,8
PSEUDOSCORPIONES		
Neobisium muscorum (Leach)	others (d)	8
ARANEAE		
Thyreostenius biovatus O.P-Camb. /-		5,7,8
Hahnia haveola Simon	others (d)	7

*(a) = Bouskell 1905; (b) = Collingwood 1959; (c) = Collingwood 1965; (d) = other non-myrmecophilous records.

Donisthorpe (1927b) classified all of the beetles, except Quedius brevis and Sipalia circellaris, recorded in table 5.3 as synoeketes; Q. brevis was classified as a synectran. Sipalia circellaris was not included in his list, but it is "an almost ubiquitous woodland litter species" in Britain (P.M. Hammond, personal communication). No "true guests" or symphiles have been recorded with wood ants in Ireland.

The presence of adult myrmecophiles in different months, irrespective of year, is shown in figure 5.3a and an indication of their relative abundance is given in figure 5.3b, which is based on the number of nest samples, out of a total of 62, in which a positive record was obtained for each species. Some species, notably Thiasophila angulata and the millipedes, are present as adults throughout the active season. However, in other species, such as Othius myrmecophilus, there does seem to be an indication of bivoltinism. In support of this suggestion, many staphylinid larvae (unidentified) were noticed in some of the May-June samples. This observation may account for the apparent absence of some species as adults at this time.

Thyreostenius biovatus adults were present in the upper (sampled) part of the nest from mid-May to mid-September. However, they appear to overwinter in the depths of the nest: on 31.I.1974, five adult females and a number of juveniles were discovered in nest KC-458a, at a depth of 0.8m among overwintering lugubris workers (a single adult Nototheca anceps was also taken on this occasion). Spider cocoons, presumably of Thyreostenius have been seen on the walls of old decayed nest galleries during late June. Many juveniles appeared in the samples after mid-July.

Thiasophila angulata and Cylindroiulus punctatus were the most frequently encountered species. Donisthorpe (1927b) noted the frequent occurrence of Proteroiulus fuscus and Blaniulus guttulatus (Bosc) in

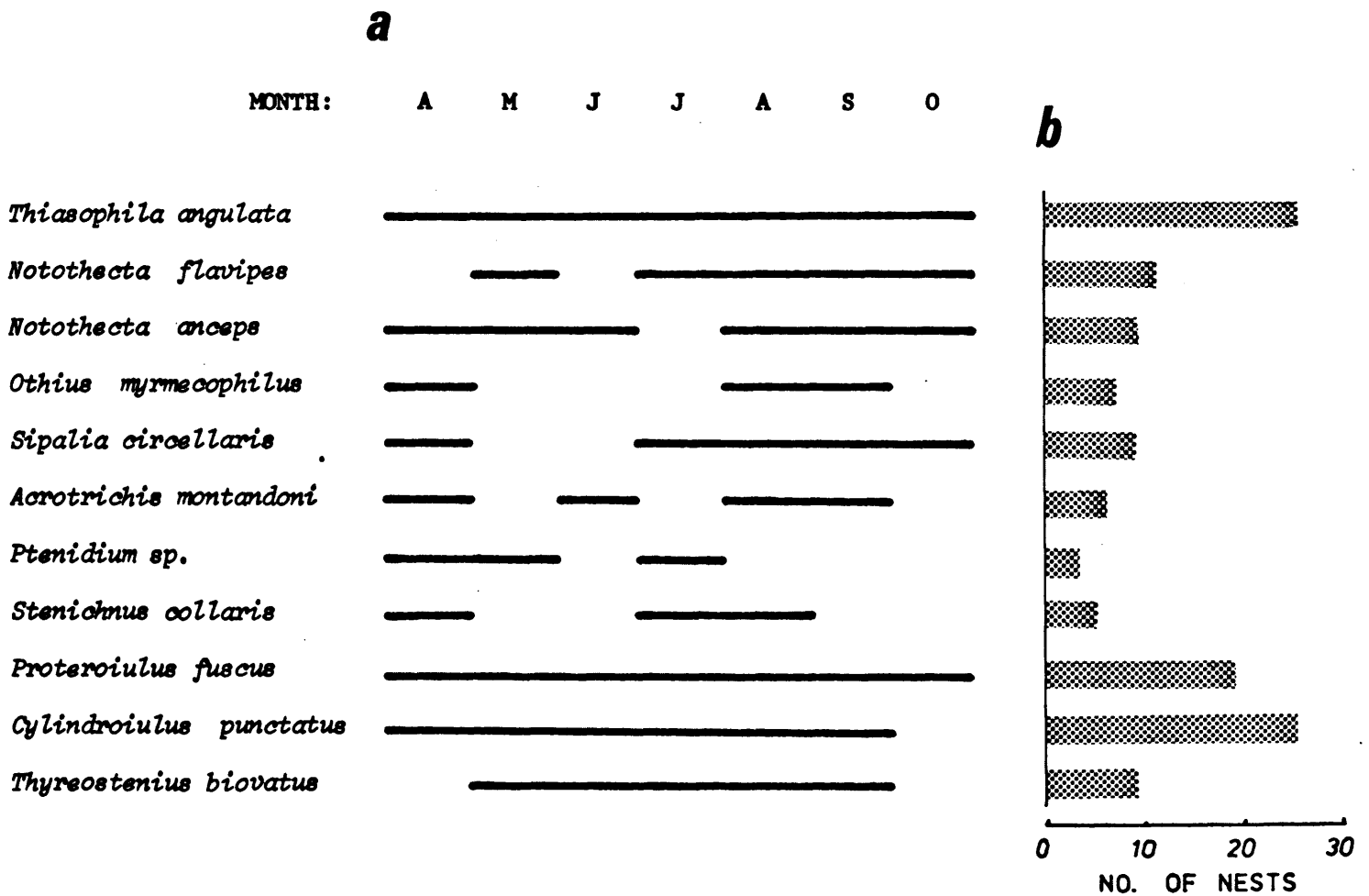


Figure 5.3 (a) The occurrence of adult myrmecophiles in monthly samples from April to October and considering all years. (b) The number of samples, maximum possible 62, in which each species was recorded.

wood ant nests. The latter species, though common in Ireland, has not been seen in lugubris nest material, whereas Cylindroiulus punctatus, which was not mentioned by Donisthorpe (1927b), often occurred in large numbers. Only a single pseudoscorpion was recorded. The isopods Oniscus asellus (L.) and Porcellio scaber (Lat.) occurred on a few occasions. White collembolans, possibly Cyphoderus albinos (Nicolet), occurred in large numbers in a few nests: localities 7 and 8.

In addition to the species for which no specimens were recorded in table 5.3, the following species' absence can be noted: Formicoxenus nitidulus (Nyl.), Coccinella divaricata Olivier, and Platyarthrus hoffmanseggi (Brandt). The first two of these speices have not been recorded from Ireland, but are well-known from wood ant localities in Britain (Donisthorpe 1927a, p.261). Although Platyarthrus is often found with other ants in Ireland, it was not found in South Tipperary; it has been recorded with wood ants in Britain (Donisthorpe, loc. cit.).

Two species of ants occurred in lugubris nest material: a populous colony of Myrmica ruginodis occurred in the side of nest KC-437d, and Leptothorax acervorum colonies were found twice in the nest material. Presumably, these three instances are examples of plesiobiosis - "rudimentary consociation (when) different ant species nest very close to each other, but engage in little or no direct communication" (Wilson 1971, p.351). Donisthorpe (1927b, p.80) reported that L. acervorum colonies "often occur" in nests of wood ants. Observations were also made of encounters between lugubris and L. acervorum workers. at the census point shown in plate 5 . At this point, a lugubris route passed over a timber "bridge" which contained a colony of L. acervorum. Whenever a lugubris forager approached within c. 10 mm of a L. acervorum worker, the latter pressed itself to the substrate and ceased moving in a "death feigning" posture. This behaviour was

repeatedly observed, and L. acervorum workers were never seen attacked by lugubris. These observations are interesting since other Leptothorax species are known (Wilson 1971, p. 371) to form xenobiotic relationships - where "one species lives in the walls or chambers of the nests of the other and moves freely among its hosts" (Wilson 1971, p.357), with other ants.

SUMMARY

1. Formica lugubris Zetterstedt is now known in four Irish vice-counties, viz., North Kerry, South Galway, South Tipperary and Limerick, but it was not found in four other vice-counties where it was previously recorded. It is only common in South Tipperary and most of the observations described in this thesis were made in this area. The distribution pattern is difficult to explain and it seems better to leave open the question of whether the species is indigenous to Ireland.

2. Above-ground activity occurs from late-February to mid-November and foraging begins in April. Inter-nest battles were observed in May of 1973 and 1974 between the same two neighbouring nests, and one of the nests was destroyed on the second occasion.

3. Most active nests produced alatae of both sexes though a few were noted with males only. Flights of alatae were observed on successive June mornings at air temperatures above 17.5°C. A maximum of 25-30 alatae took flight per minute. Internal thoracic temperatures at take-off were 2-4°C warmer than ambient and this may have been due to preflight wing-flapping behaviour. Although de-alate lugubris queens were frequently seen around Formica lemani nests, and twice actually in lemani nests, no further evidence was obtained to suggest colony founding was by way of temporary social parasitism. It is concluded that colony fragmentation is the more frequent mode of colony founding. It is also suggested that polygyny is rare since no colony queen was ever seen.

4. Foragers visit flowers in the early part of the year. Distinct routes were formed to Rhododendron ponticum nectaries during 1974.

5. A census of the nests in three plantation woods (total 1398 ha) yielded the following nest densities (nests/100 ha): 7.2, 9.9, and 32.1. The maximum observed density in one forestry compartment (15.2 ha) was 2.2 nests per ha (0.0002 nests per m^2).

6. A total of 112 nests were observed since 1973. Of these, 91 were still alive in 1975 and 79 had remained at the same site. Nests were abandoned at a rate of eight percent per annum, annual mortality was nine percent and new nests appeared at c. five percent per annum. Nest abandoning was most frequent among small nests.

7. Nest, tree, location, soil, and vegetation variables were recorded at 184 nest sites. The results suggest that the nests are approximately the same age as their overhead trees. Scots pine is the most important overhead tree, and Sitka spruce is also important until it reaches thicket-stage canopy. Nests are excluded by pure stands of Pinus contorta, and few sites were associated with larch. Nests occurred on slopes up to 34° (most frequently at $5-10^{\circ}$), at soil pH up to 7.7 (most frequently 3.6-4.0 pH units), and up to the artificial tree line (most frequently at 150-200 m altitude). Sites apparently occurred independently of aspect.

8. Temperature profiles of Vaccinium myrtillus, Calluna vulgaris, and to a lesser extent, Pteridium aquilinum showed that these plants considerably affect ground insolation. Light penetration to most (68 percent) live nests ranged from 80-100 percent, while 86 percent of abandoned sites occurred at light penetration of 70-90 percent.

9. Nearest neighbour analysis suggested that the 33 nests found in one compartment were overdispersed.

10. Values obtained for route fidelity were usually in the range of 85–100. A single low RF value of 63 may have been caused by recruitment from the marked route. There was considerable internest variation in RF values which did not appear to be associated with the time of year. Observations at the Y-junction showed that RF diminished slightly, but significantly, after a month. However, overall RF to individual trees was 93 during this time. Absence from the routes for more than 14 days had a slight, but significant, effect on forager RF. Exclusion from an aphid tree for three days did not affect the RF of foragers. Although based on low numbers, the data suggest that the following treatments had no effect on RF: anaesthesia with carbon dioxide, chloroform or nitrous oxide, and treatment with the phosphorus-32 internal marking method used in the capture-mark-recapture studies.

11. Observations on foragers paint-marked as honeydew- and prey-carriers showed that these duties were not confined to specific groups of foragers. Carrying behaviour of unknown function constituted 34 percent of returning route traffic in April and was less frequent during the rest of the year. Biometric observations suggested that adult carriers were similar to a random sample taken from the route, while the carried adults were similar to a sample taken from the nest. Of the 100 pairs of AC/CA the carried adult was larger than its respective carrier in only 10 pairs. Carrying behaviour was more frequent (76 percent) during nest moving.

12. Foraging rhythms during four days were studied by making five-minute counts every half-hour from dawn to dusk. The results show that temperature accounts for much of the observed variation in forager numbers. The number of foragers rose linearly from 8.0°C to about 20°C, and reached a maximum at 24°C. Above 27°C ground temperature

the number of foragers declined rapidly. Foraging ceased above 33°C ground temperature.

13. Foragers passed randomly in both directions during observations made in August. Observations on paint-marked individuals suggest that an average return foraging journey lasts 133 minutes, and that this is followed by 103 minutes spent in the nest. Running speed of lugubris is linearly affected by ground temperature, and the response graph is similar to that for polyctena, though different to that reported for aquilonia.

14. Meteorological data suggest an average of 3333 work hours per year ($\simeq$ 139 days) above 8.5°C. Hence a nest with 25 000 foragers (9.7 percent prey-gatherers and 74.5 percent honeydew carriers) collect approximately 2.05 x 10^6 prey items and 76 kg of honeydew per annum. Diptera were the most frequently taken prey items.

15. Forager and colony-size estimates were made by the capture-mark-recapture technique. Forager estimates of five nests (sample marked by paint) ranged from 6906 to 59 594, and colony-size estimates of the same five nests (sample marked by internal phosphorus-32 label and detected by autoradiography of carbon dioxide-anaesthetized ants) ranged from 9797 to 71 052. Colony limits were also studied using radiophosphorus, and the results suggested little internest communication.

16. The most important honeydew sources are aphids of the genus Cinara occurring on various conifers. Cinara pini on Pinus sylvestris and C. piceae on both Picea sitchensis and P. abies are especially important. Observations on C. piceae suggest that this aphid's

colonies are most frequent in a close circle near the lugubris nests. Observations made to see if the aphids affected the tree height near the nest yielded equivocal results. The nest myrmecophiles include three new Irish records. All were synoeketes and no "true guests", or symphiles, have yet been recorded with wood ants in Ireland.

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APPENDIX I

Specimens of *Formica lugubris* in the National Museum, Dublin.

The following specimens of Formica lugubris, all workers, are in the collection of the National Museum, Dublin. Notes from the Museum Accession Book are given in parentheses:

1. Killarney / 151-1905 / rufa fide H.St.J.K.D. / F. lugubris det. C.A. Collingwood.

2. Killarney / 151-1905 /

   (Accession No. 151-1905: given by Royal Society. Killarney, May-June 1905. coll. J.N. Halbert.)

3. Killoughrum, Co. Wexford 110-1896 /

   (Accession No. 110-1896: presented by C.B. Moffat on 31.VIII.1896.)

4. Devils Glen / 8.VI.21 A.W.S. / 126-1921 /

5. Devils Glen / 5.VI.21 / 126-1921 /

   (Accession No. 126-1921: Coll. of Hymenoptera from Cos. Dublin and Wicklow. A.W. Stelfox. May and June 1921. Mostly collected in neighbourhood of Malahide and Rathnew or Wicklow.)

6. Devils Glen Co.WI A.W.S. 30.III.29/

7. Woodford 288-1901 /

8. Woodford 288-1901 / rufa / fide H.St.J.K.D. /

   (Accession No. 288-1901: Coll. J.N. Halbert for Flora and Fauna Committee.)

9. Woodford S.Galway. R.A.P. June 1922 /

10. Russelstown Wood, Kilmacomma, Co. WA July 1927 coll. F.G. Meagher /

APPENDIX II

NEST-SITE VARIABLES

The account of the nest site habitat in 3.3 was based on the data matrix reproduced in this appendix. The values for each nest occupy a single row of the table and the variables are given in this format:

VARIABLE	INTERPRETATION
WOOD	1 = Kilcoran Wood; 2 = Glengarra Wood; 3 = Moore's Wood; 4 = Rossbog Wood; 5 = Boulakennedy Wood; 6 = Galtee Wood; 7 = Shanrahan Wood; 8 = Kilballyboy Wood.
I.D.	Nest identification number.
ALIVE?	1 = alive; 0 = not occupied.
ACTIVE?	1 = active; 0 = not active.
ABAND?	1 = abandoned; 0 = not abandoned.
DIAMETER	Nest diameter in cm.
SPRUCE	1 = present; 0 = absent.
PC	1 = present; 0 = absent.
SP	1 = present; 0 = absent.
LARCH	1 = present; 0 = absent.
TREE HT	Tree height in metres.
CANOPY	Canopy on 1 - 5 scale. (see 3.3)
TREE AGE	Tree age in years.
ASPECT	Aspect in degrees.
SLOPE	Slope in degrees.
ALTITUDE	Altitude in metres.

contd.

VARIABLE	INTERPRETATION	
SOIL pH	Soil pH in pH units.	
SOIL-C	Soil organic carbon in arbitrary units.	
SOIL-H_2O	Soil water as percent of wet weight.	
MOLINIA	Molinia caerulea	All recorded as cover per m^2.
CALLUNA	Calluna vulgaris	
ULEX	Ulex spp.	
ERICA	Erica cinerea	
PTERIDIUM	Pteridium aquilinum	
MOSS	Mosses + liverworts + lichens	
BARE	Bare ground	
VACCINIUM	Vaccinium myrtillus	

WOOD	I.D.	ALIVE?	ACTIVE?	ABANDT	DIAMETER	SPRUCE	PC	SP	LARCH	TREE HT	CANOPY	TREE AGE	ASPECT	SLOPE	ALTITUDE	SOIL PH	SOIL-C	SOIL-H2O	MOLINIA	CALLUNA	ULEX	ERICA	PTERIDIUM	MOSS	BARE	VACCINIUM
1	387a	1	1	0	93	0	1	1	0	7.8	4	30	102	7.0	167	3.9	27.6	64.3	55.3	25.0	0.0	0.3	0.0	0.0	18.3	0.0
1	387b	0	0	0	93	0	1	0	0	8.0	5	30	45	12.0	197	4.2	27.3	54.8	25.8	0.0	0.0	0.0	0.0	19.8	54.5	0.0
1	387d	0	0	0	12	0	1	1	0	6.5	4	30	85	7.0	185	3.9	30.3	72.5	85.3	1.5	0.0	4.3	0.0	4.3	3.0	0.0
1	387e	0	0	1	45	0	1	1	0	6.5	5	30	45	6.8	167	3.7	30.3	70.3	66.0	1.3	0.0	0.3	0.0	17.5	14.8	0.0
1	426a	1	0	0	96	0	0	1	0	6.5	4	34	90	6.0	255	4.7	4.4	30.4	96.7	0.3	0.0	0.0	0.0	2.3	0.0	0.0
1	426b	1	1	0	147	0	1	1	0	6.0	3	34	85	2.5	255	4.0	10.6	57.0	3.5	83.0	0.0	7.8	0.0	2.0	3.8	0.0
1	434a	1	1	0	74	1	1	0	0	10.5	4	32	78	8.0	214	4.1	4.2	41.8	53.8	17.5	0.0	10.0	0.0	0.0	18.8	0.0
1	437a	1	0	0	115	1	0	1	0	7.0	5	32	116	9.0	212	3.9	24.6	54.9	6.8	0.0	0.0	0.0	0.0	0.0	93.2	0.0
1	437b	1	1	0	82	0	1	1	0	4.0	2	32	7	4.2	197	3.9	21.6	66.4	58.5	6.8	0.0	31.8	0.0	0.0	0.0	0.0
1	437c	1	1	0	74	1	1	0	0	4.5	2	32	113	6.2	197	4.4	4.3	41.0	96.5	3.3	0.0	0.0	0.0	0.0	0.0	0.0
1	437d	1	1	0	101	0	1	1	0	12.0	5	32	78	5.2	182	3.8	28.8	73.8	80.8	10.5	0.0	0.5	4.5	1.3	1.3	0.0
1	437e	0	0	1	122	0	1	1	0	12.0	3	32	50	4.2	197	3.9	29.4	66.4	21.7	6.7	0.0	0.0	13.3	0.0	56.3	0.0
1	437e	1	1	0	63	0	1	1	0	12.0	3	32	50	4.2	197	4.0	30.3	74.7	89.3	0.0	0.0	1.7	7.0	0.0	0.0	0.0
1	438a	1	1	0	86	0	1	1	0	9.0	5	32	85	6.5	191	4.0	4.2	25.0	6.5	11.3	0.0	1.5	0.0	0.0	79.5	0.0
1	438b	1	1	0	99	0	1	1	0	9.0	4	32	85	4.2	188	4.3	5.2	30.7	0.5	23.3	0.0	2.3	0.0	0.0	62.8	0.0
1	438c	1	0	0	103	0	1	1	0	10.2	4	32	10	3.2	182	3.8	22.8	59.0	28.0	16.3	0.0	2.0	0.0	3.8	45.0	0.0
1	440a	1	1	0	97	0	0	1	0	6.0	3	32	85	5.0	161	4.0	12.0	56.9	31.3	29.3	12.0	10.3	0.0	0.0	7.5	5.0
1	440b	0	0	1	72	0	1	1	0	12.0	4	32	85	4.2	152	5.4	3.5	30.4	20.3	24.0	0.0	9.5	15.8	7.8	2.5	8.5
1	440c	1	1	0	96	0	0	1	0	11.5	4	32	102	34.0	146	4.4	6.0	38.7	3.0	18.8	0.0	18.8	16.8	7.5	30.0	4.5
1	440d	1	0	0	136	0	1	1	0	13.0	5	32	112	10.0	145	4.0	6.7	42.8	7.8	0.0	25.0	0.0	7.5	11.3	35.0	0.0
1	440e	1	1	0	77	0	1	1	0	9.0	3	32	104	5.0	155	3.7	29.7	66.5	98.8	0.0	0.0	0.5	0.0	0.0	0.0	0.0
1	440f	0	0	1	55	0	0	1	0	5.0	2	32	95	13.0	145	7.1	10.4	43.4	5.3	36.8	1.8	0.5	0.0	11.8	33.0	0.0
1	440f	1	1	0	78	0	1	1	0	5.0	2	32	95	13.0	145	4.4	5.2	36.7	63.3	31.0	2.0	2.0	0.0	0.0	0.0	0.0
1	440g	1	1	0	103	0	1	1	0	7.0	4	32	45	4.5	139	4.0	12.1	50.9	16.3	0.0	1.3	0.0	0.0	0.0	82.5	0.0
1	440h	1	1	0	114	0	1	1	0	9.5	4	32	170	12.5	180	4.3	2.9	15.4	13.0	1.0	10.5	1.8	0.0	3.0	63.8	0.0
1	441a	1	1	0	48	0	1	1	0	7.5	5	30	96	5.0	212	4.5	7.6	37.3	78.5	10.0	0.0	11.3	0.0	0.0	0.0	0.0
1	444b	1	1	0	138	0	1	1	0	13.0	5	117	104	5.3	179	3.9	30.3	71.9	0.0	0.0	0.0	0.0	24.5	2.8	0.0	72.8
1	444c	0	0	1	28	0	0	1	0	7.5	3	17	85	3.0	139	4.1	30.3	64.1	26.0	2.0	1.3	0.0	60.0	0.0	44.8	17.8
1	444d	1	0	0	91	1	0	0	0	7.5	4	17	85	6.5	127	4.1	23.1	52.7	28.3	0.0	0.0	0.0	0.0	1.3	67.0	2.8
1	447a	1	1	0	61	0	1	0	0	8.2	4	22	95	2.0	206	4.3	27.9	49.8	66.8	7.0	16.3	0.0	10.0	0.0	0.0	0.0
1	449a	1	1	0	107	0	0	1	0	7.5	5	22	107	12.0	189	4.4	6.1	25.9	38.3	0.0	0.0	0.0	30.0	2.5	25.8	0.0

WOOD	I.D.	ALIVE?	ACTIVE?	ARAND?	DIAMETER	SPRUCE	PC	SP	LARCH	TREE HT	CANOPY	TREE AGE	ASPECT	SLOPE	ALTITUDE	SOIL PH	SOIL-C	SOIL-H_2O	MOLINIA	CALLUNA	ULEX	ERICA	PTERIDIUM	MOSS	BARE	VACCINIUM
1	449b	1	1	0	101	0	1	1	0	7.7	4	22	144	9.0	189	3.7	26.4	59.3	50.5	19.0	12.5	0.0	0.0	2.5	15.5	0.0
1	449c	1	1	0	37	0	1	1	0	7.5	4	22	180	26.0	200	4.5	29.4	57.8	75.5	0.0	15.0	0.0	0.0	1.3	3.8	0.0
1	451a	1	1	0	105	0	0	1	0	12.6	4	29	169	12.6	115	3.8	25.8	40.8	21.0	2.5	28.8	0.0	30.8	0.0	37.8	0.0
1	451b	1	1	0	111	0	1	1	0	10.5	4	29	141	5.5	118	3.8	12.1	64.5	15.0	0.0	40.0	6.3	0.0	14.8	24.0	0.0
1	451h	1	1	0	97	0	1	1	0	9.0	4	29	194	6.5	179	3.7	30.3	59.1	64.5	0.0	8.8	0.0	1.8	0.0	2.5	0.0
1	451c	1	1	0	94	0	1	1	0	10.0	4	29	169	4.0	124	3.7	11.4	50.1	41.0	0.0	71.3	0.0	1.3	4.0	8.8	0.0
1	451e	1	1	0	115	0	0	1	0	7.5	4	29	175	14.5	115	4.0	29.7	67.2	1.5	0.0	0.0	0.0	0.5	0.0	98.0	0.0
1	451d	1	1	0	97	0	1	1	0	13.5	5	29	156	7.0	106	4.4	4.8	16.9	5.9	3.0	0.0	0.0	0.0	0.0	88.0	0.0
1	451f	1	1	0	113	0	1	1	0	10.0	4	29	158	7.2	112	3.5	26.4	61.8	53.8	0.0	25.3	0.0	0.0	15.0	27.3	0.0
1	451g	0	0	0	91	0	1	1	0	12.0	5	29	158	8.2	109	4.0	27.9	61.1	40.8	0.0	10.5	0.0	0.0	32.8	23.5	0.0
1	451i	1	1	0	90	0	1	1	0	8.0	3	29	164	10.8	115	3.9	30.3	55.2	27.8	1.3	60.0	0.5	7.5	0.5	12.0	0.0
1	452a	0	0	1	74	0	0	1	0	10.0	3	117	136	8.8	112	5.2	8.2	41.8	11.5	0.0	17.5	0.3	10.8	4.0	0.0	0.0
1	452a	1	1	0	79	0	0	0	1	4.0	3	12	112	9.5	112	4.3	30.0	72.3	8.8	0.0	0.0	0.0	39.9	0.0	40.1	0.0
1	452b	1	1	0	47	0	0	1	0	11.0	4	117	136	3.2	124	4.8	5.9	28.2	4.7	64.0	6.0	5.0	0.0	0.0	16.0	0.0
1	452c	1	1	0	51	0	0	1	1	13.5	4	117	138	7.0	182	4.7	4.9	22.3	1.3	33.1	0.0	32.0	0.8	1.6	6.3	0.0
1	452d	1	1	0	126	0	0	1	0	15.0	5	117	206	10.0	115	5.6	5.0	28.4	0.0	9.8	0.0	0.0	0.3	5.0	24.0	0.0
1	453c	1	1	0	39	1	0	0	1	4.5	3	26	158	7.2	145	4.1	30.0	51.4	94.5	0.0	0.0	2.3	1.0	2.0	0.0	0.0
1	453d	1	1	0	46	1	0	0	1	7.2	3	12	169	11.2	133	4.1	11.8	45.2	93.7	0.0	1.7	0.9	1.0	2.5	0.0	0.0
1	455a	1	1	0	27	0	1	1	0	7.5	4	22	136	3.0	85	4.4	5.2	28.7	88.0	3.7	2.3	0.0	0.0	5.7	0.3	0.0
1	455b	1	1	0	87	0	1	1	0	7.5	3	22	175	3.2	85	4.2	10.4	54.5	25.3	28.8	9.3	5.0	0.0	0.0	31.8	0.0
1	455	0	0	1	70	0	0	1	0	7.5	4	22	175	4.0	85	4.2	5.5	28.8	35.0	0.0	42.7	0.3	0.0	0.0	19.3	0.0
1	455d	1	1	0	88	0	0	1	0	6.5	4	22	180	5.0	85	4.2	6.7	44.1	40.0	0.0	7.8	0.0	0.0	9.8	14.8	0.0
1	455e	1	0	0	84	0	0	1	0	9.4	4	5	180	1.8	85	4.2	30.0	67.3	2.8	0.0	0.0	0.0	52.0	0.0	0.0	0.0
1	455f	1	1	0	87	0	1	1	0	5.5	3	22	186	1.0	85	3.9	5.5	49.2	63.8	9.0	17.5	8.0	0.0	0.0	0.0	0.0
1	455g	1	1	0	76	0	1	1	0	4.0	2	22	186	4.0	85	4.1	6.1	44.6	44.0	3.5	21.3	25.0	0.0	0.0	0.0	0.0
1	455h	1	1	0	62	0	1	1	0	3.5	2	22	180	1.0	85	3.9	10.5	61.2	56.8	2.5	0.0	31.3	0.0	1.3	3.8	0.0
1	455i	1	1	0	48	0	1	1	0	6.0	3	22	192	4.0	85	3.7	9.0	64.1	53.3	5.0	5.0	36.3	0.0	0.3	0.0	0.0
1	456a	1	1	0	66	1	0	1	0	7.7	5	18	180	4.2	85	5.1	7.7	36.3	33.0	0.0	15.3	1.5	1.8	15.0	24.8	0.0
1	456b	1	1	0	111	1	0	0	0	6.0	4	18	180	4.0	85	3.8	30.3	61.5	14.8	18.5	49.3	0.0	0.3	5.8	40.3	2.5
1	456c	1	1	0	86	1	0	1	0	6.4	4	18	180	2.0	85	6.4	8.6	41.0	45.8	14.5	2.0	0.0	58.8	0.0	13.8	0.0
1	456d	0	0	0	97	1	0	0	0	6.0	3	18	176	0.5	85	4.2	12.0	53.9	17.3	24.5	0.0	0.0	3.8	10.5	0.0	0.0
1	456e	1	1	0	107	1	0	1	0	6.0	4	18	176	3.9	85	3.8	29.1	65.9	74.3	16.7	0.0	0.0	0.0	6.7	0.0	0.0
1	457a	1	1	0	124	0	1	1	0	6.7	4	18	166	5.0	85	4.0	10.6	40.8	16.0	0.5	5.0	0.0	59.0	0.0	27.0	0.0

WOOD	I.D.	ALIVE?	ACTIVE?	ABANDT	DIAMETER	SPRUCE	PC	SP	LARCH	TREE HT	CANOPY	TREE AGE	ASPECT	SLOPE	ALTITUDE	SOIL pH	SOIL-C	SOIL-H2O	MOLINIA	CALLUNA	ULEX	ERICA	PTERIDIUM	MOSS	BARE	VACCINIUM
1	458e	1	1	0	98	0	0	1	0	7.0	3	28	107	3.8	115	4.4	29.7	66.5	3.8	15.0	0.0	0.0	20.0	0.0	41.3	20.8
2	902a	1	1	0	113	1	1	0	0	9.0	5	39	144	8.7	149	4.1	8.5	34.6	2.0	0.0	0.0	12.5	3.8	3.3	73.8	0.0
2	902b	0	0	1	97	0	1	1	0	9.5	5	39	169	5.0	149	5.6	0.7	20.1	0.3	2.5	0.0	20.5	0.0	0.3	51.8	0.0
2	902c	1	1	0	145	1	1	0	0	9.5	5	39	156	3.0	149	4.4	2.0	20.2	7.0	0.0	0.0	0.0	0.0	12.0	80.0	0.0
2	902d	1	1	0	89	1	0	1	0	11.0	5	39	205	4.0	122	4.3	3.1	24.5	51.3	0.0	0.0	0.0	0.0	0.0	27.3	1.7
2	903a	1	1	0	56	0	0	0	0	1.0	1	8	156	6.2	137	6.0	8.0	42.9	0.3	0.0	0.0	0.0	55.0	0.0	38.0	0.0
2	904b	1	0	0	107	1	0	0	0	9.0	5	40	195	5.5	183	4.7	7.0	32.1	2.0	0.0	0.0	0.0	0.0	0.0	89.0	0.0
2	905c	1	1	0	66	0	0	1	0	10.5	5	45	119	9.0	168	6.4	5.9	36.0	32.7	0.0	0.0	0.0	31.7	0.0	65.0	0.0
2	910a	1	1	0	77	0	0	1	0	9.5	5	25	208	10.0	168	5.1	2.3	26.2	50.3	6.3	15.0	0.3	0.0	0.0	7.5	0.0
2	910b	0	0	0	105	0	0	1	0	8.5	5	25	248	8.0	162	3.9	12.2	69.9	0.0	0.0	0.0	0.0	57.5	0.0	42.0	0.0
2	910c	1	0	0	129	0	0	1	0	9.3	5	25	275	17.0	152	4.2	9.6	46.5	0.0	0.0	0.0	0.0	0.0	0.0	77.0	2.0
2	911a	1	1	0	66	1	0	1	0	9.2	4	25	85	6.2	152	5.1	3.8	24.1	0.0	0.0	0.3	0.0	0.0	1.5	71.5	0.0
2	931a	1	1	0	49	1	1	0	0	3.0	1	10	142	4.8	155	4.2	5.3	31.1	20.3	53.0	2.5	1.3	0.0	13.8	2.5	0.0
2	931b	1	1	0	84	1	1	0	0	3.0	1	10	197	4.2	155	4.3	10.3	28.9	98.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0
2	931c	1	1	0	55	1	1	0	0	2.0	1	10	180	6.8	168	4.4	4.3	19.6	35.5	19.0	4.0	7.3	0.0	1.3	21.3	0.3
2	931d	1	1	0	82	1	1	0	0	3.0	2	10	158	4.0	177	4.6	2.8	14.9	70.8	10.3	10.0	0.0	0.0	0.0	8.0	0.0
2	931e	1	1	0	37	1	1	0	0	5.0	2	10	192	5.0	168	4.1	5.4	22.8	59.3	29.0	1.3	4.5	0.0	0.0	5.0	0.0
2	931f	1	1	0	42	1	1	0	0	3.0	1	10	192	4.0	168	4.3	3.4	23.8	72.5	16.5	0.0	1.5	0.0	3.3	5.0	0.0
2	932a	0	0	1	68	0	0	0	0	3.0	1	9	264	8.0	201	4.1	17.7	50.8	9.5	3.0	8.3	0.0	0.0	15.8	40.5	2.5
2	932a	1	1	0	25	0	0	0	0	3.0	1	9	264	8.0	201	5.6	6.1	43.3	0.0	7.3	24.0	0.3	0.0	20.0	24.3	0.5
2	933a	1	1	0	15	1	0	0	0	0.5	1	10	197	7.0	216	4.4	6.0	39.6	47.0	30.3	0.0	20.0	0.0	0.5	0.0	0.0
2	933b	1	1	0	28	1	1	0	0	3.0	2	10	212	6.8	186	3.7	25.2	52.6	32.3	60.8	4.0	0.0	0.0	0.5	0.0	0.0
2	933c	1	1	0	24	1	1	0	0	3.0	2	10	212	6.8	189	4.2	8.4	36.5	21.5	43.5	0.0	5.8	0.0	15.3	8.8	0.0
2	933d	0	0	1	37	1	1	0	0	3.0	2	10	212	6.8	192	4.1	8.3	39.9	15.5	50.8	25.0	8.8	0.0	0.8	0.0	0.0
2	934a	1	1	0	44	1	1	0	0	3.0	2	8	186	5.8	229	4.1	7.2	60.5	30.3	55.0	0.0	8.0	0.0	0.3	0.0	0.0
2	934b	1	1	0	21	1	0	0	0	2.0	2	8	164	30.0	235	3.7	26.1	57.9	7.3	60.8	1.3	5.8	0.0	0.0	30.0	0.0
2	934c	1	1	0	85	0	1	1	0	7.5	4	37	214	7.0	247	3.7	8.3	47.1	84.8	0.0	0.0	0.3	0.0	2.5	12.3	0.0
2	935a	1	1	0	38	1	1	0	0	3.0	2	10	200	2.5	262	3.8	5.9	24.4	51.5	39.0	0.0	5.5	0.0	0.0	2.5	0.0
2	935b	1	1	0	41	1	1	0	0	4.0	3	10	197	6.2	259	4.8	11.3	45.7	64.0	29.0	0.0	6.8	0.0	0.0	0.0	0.0
2	936a	1	1	0	38	1	1	0	0	4.0	3	8	208	10.8	244	3.9	2.8	22.5	33.4	4.5	5.0	42.1	0.0	1.3	13.8	0.0
2	936b	1	1	0	23	1	1	0	0	5.0	3	8	208	4.0	238	4.3	9.6	51.1	77.8	8.5	0.0	8.8	0.0	2.3	1.0	0.0
2	936d	1	1	0	35	1	1	0	0	4.0	2	8	24	6.2	256	4.3	7.0	30.6	83.3	5.0	0.0	6.8	0.0	0.5	3.0	0.0
2	936c	1	1	0	28	1	1	0	0	4.0	3	8	164	7.0	250	4.6	4.6	20.5	0.3	56.5	2.5	20.8	0.0	2.0	5.0	0.0

WOOD	I.D.	ALIVE?	ACTIVE?	XBAND?	DIAMETER	SPRUCE	F.C.	S.P.	LARCH	TREE HT	CANOPY	TREE AGE	ASPECT	SLOPE	ALTITUDE	SOIL PH	SOIL-C	SOIL-H2O	MOLINIA	CALLUNA	ULEX	ERICA	PTERIDIUM	MOSS	BARE	VACCINIUM
2	936e	1	1	0	91	1	1	0	0	4.0	3	8	22	6.5	290	4.3	5.0	37.2	5.8	48.5	9.3	24.3	0.0	0.8	9.5	0.0
2	937b	1	1	0	27	1	1	0	0	3.0	3	8	216	7.2	290	4.5	2.8	26.1	4.8	29.0	0.0	51.0	0.0	1.3	7.5	0.0
2	937a	0	0	1	32	1	1	0	0	3.0	2	8	216	7.2	290	4.2	3.4	24.3	3.8	6.5	0.0	40.8	0.0	12.5	18.5	0.0
2	937c	1	1	0	22	1	1	0	0	4.0	3	8	216	7.2	290	4.1	7.3	43.7	11.0	0.0	13.8	35.0	0.0	17.8	22.5	0.0
2	937d	1	1	0	35	1	1	0	0	4.0	2	8	50	9.2	290	3.8	6.1	35.9	24.5	16.0	7.5	24.0	0.0	0.0	2.5	0.5
2	938a	1	1	0	139	1	0	0	0	9.5	5	31	228	6.2	256	3.7	28.8	66.1	25.5	0.0	0.0	0.0	0.0	0.0	63.3	1.0
2	938b	1	1	0	75	0	1	1	0	15.0	5	31	244	7.0	290	4.1	26.4	68.8	39.0	7.8	17.0	2.5	0.0	0.0	18.0	9.0
2	938c	1	1	0	98	1	1	0	0	4.0	4	31	280	8.0	293	3.6	27.9	62.7	25.5	0.0	0.0	0.0	0.0	0.0	63.3	2.0
3	250a	1	1	0	127	0	0	1	0	5.5	4	27	345	17.0	207	4.2	7.3	49.3	25.0	48.0	0.0	0.3	0.0	7.5	0.3	14.8
3	252a	1	1	0	48	0	1	1	0	5.5	4	28	50	6.0	189	4.0	30.3	77.4	3.3	77.0	0.0	2.3	0.0	15.3	0.0	3.3
3	253a	1	1	0	15	0	1	1	0	2.0	2	28	50	6.0	189	3.9	12.0	66.8	3.8	39.8	0.0	2.0	0.0	52.8	0.0	2.5
3	256a	1	1	0	82	0	0	1	0	13.5	5	42	312	1.9	177	3.9	10.7	46.1	0.3	0.0	0.0	0.0	0.0	5.3	71.0	23.3
3	256b	1	1	0	109	0	0	1	0	9.5	4	42	319	7.2	183	4.0	6.6	43.1	0.0	0.0	0.0	0.0	0.0	5.0	82.0	11.8
3	257a	1	1	0	139	0	1	1	0	7.5	3	42	327	6.3	220	4.0	25.2	61.2	17.5	0.0	0.0	0.3	0.0	4.0	30.8	0.3
3	258a	1	0	0	74	0	1	1	0	7.5	5	42	26	6.2	137	4.3	5.3	27.0	11.3	33.8	16.3	11.8	0.0	12.0	15.0	0.0
3	259b	0	0	1	136	0	0	1	0	8.2	5	42	2	6.5	177	4.2	27.6	71.6	48.3	0.0	0.0	0.0	0.0	22.0	15.8	0.0
3	259b	0	0	1	31	0	0	1	0	8.2	5	42	310	1.9	175	3.6	22.5	62.1	23.8	7.5	0.0	0.0	0.0	62.3	6.3	0.3
3	259b	1	1	0	25	0	0	1	0	8.2	5	42	310	1.9	175	3.9	25.5	74.4	32.5	0.0	0.0	0.0	0.0	13.8	12.0	26.3
3	259a	1	1	0	11	0	1	0	0	4.0	2	22	26	6.2	137	4.2	7.0	30.3	12.5	55.0	0.0	10.0	0.0	6.3	16.3	0.0
3	262a	1	1	0	108	1	0	1	0	11.0	5	39	339	12.9	280	4.1	9.2	60.9	49.3	12.5	0.0	0.0	0.0	3.8	8.8	9.5
3	264a	1	1	0	64	0	0	1	0	12.7	5	42	346	5.0	137	4.2	10.2	54.1	4.0	0.0	0.0	1.3	0.0	0.0	62.0	26.3
3	264b	0	0	1	75	0	1	0	0	3.0	3	20	45	3.5	152	3.9	7.4	32.8	63.3	8.8	43.8	0.0	0.0	4.0	0.0	0.0
3	264c	1	1	0	122	0	0	1	0	10.5	4	42	342	3.3	137	4.5	8.9	43.3	37.3	5.0	0.0	2.8	0.0	5.0	0.0	50.0
3	264b	1	1	0	63	0	1	0	0	3.0	3	20	45	3.5	152	4.3	10.0	38.2	30.0	17.5	22.5	11.3	0.0	0.0	18.8	0.0
3	265b	0	0	0	95	0	1	0	0	11.5	5	41	76	8.4	177	4.4	8.5	51.4	68.3	14.0	3.3	6.7	0.0	2.0	0.0	0.0
3	266a	1	1	0	96	0	1	0	0	7.5	4	39	30	8.0	280	3.7	21.6	60.0	42.0	9.5	0.0	0.3	0.0	25.5	16.8	8.5
3	267e	0	0	1	95	0	1	1	0	10.0	5	39	297	10.8	305	5.7	12.0	51.0	36.5	2.5	0.0	0.0	0.0	1.8	60.3	0.0
3	267a	1	1	0	103	1	1	0	0	10.0	5	39	297	8.3	311	4.0	30.0	72.2	30.5	14.8	0.0	1.0	0.0	4.0	27.0	3.5
3	267d	0	0	1	92	0	1	1	0	8.0	4	39	308	16.5	311	4.3	4.2	24.0	33.5	21.3	0.0	0.0	0.0	38.8	5.0	0.3
3	267c	0	0	0	152	0	1	1	0	6.0	3	39	347	5.0	311	3.9	30.3	73.7	0.0	30.0	0.0	7.8	0.0	61.5	0.0	1.8
3	267d	0	0	0	57	0	1	1	0	6.0	4	39	347	5.0	311	3.7	11.5	44.2	0.0	0.0	0.0	6.3	0.0	33.3	60.5	0.0
3	267b	1	1	0	58	0	1	1	0	6.0	4	39	297	11.5	311	3.9	24.0	71.2	2.5	3.8	0.0	12.8	0.0	53.3	26.0	1.5
3	268a	1	0	0	103	1	0	0	0	15.0	5	42	360	7.5	162	5.2	5.6	40.3	4.0	0.0	2.5	0.0	42.3	0.3	9.8	0.0

WOOD	I.D.	ALIVE?	ACTIVE?	ABAND?	DIAMETER	SPRUCE	PL	SP	LARCH	TREE HT	CANOPY	TREE AGE	ASPECT	SLOPE	ALTITUDE	SOIL PH	SOIL-C	SOIL-H2O	MOLINIA	CALLUNA	ULEX	ERICA	PTERIDIUM	MOSS	BARE	VACCINIUM
3	269d	1	1	0	25	0	0	1	1	9.5	4	39	336	8.5	247	7.7	3.1	23.4	21.3	22.3	0.0	0.0	0.0	2.8	37.0	0.0
3	270a	1	1	0	94	1	1	0	0	4.0	3	7	345	8.0	165	4.4	5.8	29.8	89.3	6.7	0.3	0.3	0.0	0.0	3.3	0.0
3	270b	0	0	1	67	0	1	1	0	2.5	2	7	341	8.8	146	3.8	30.0	71.0	14.3	2.5	47.5	17.5	0.0	7.0	11.3	0.0
3	270c	0	0	1	78	0	0	1	0	7.4	4	7	341	4.2	143	4.4	5.3	35.8	37.5	16.3	0.0	8.8	0.0	13.0	33.3	0.0
3	270b	1	1	0	96	0	1	1	0	2.5	2	7	341	8.8	146	3.9	29.1	73.2	4.8	79.5	1.3	0.5	0.0	4.8	5.0	0.0
3	270d	0	0	0	158	0	0	1	0	9.4	5	42	246	7.0	171	4.1	4.3	38.3	75.0	10.0	0.0	2.5	0.0	4.0	3.8	0.0
3	271a	1	1	0	72	0	0	1	0	9.5	5	41	320	8.0	207	4.4	3.7	25.8	49.0	22.8	12.8	5.8	0.0	1.5	0.0	0.0
3	272a	1	1	0	56	0	1	1	1	8.4	5	39	325	6.0	256	5.0	4.1	31.6	44.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	273a	0	0	0	153	0	0	1	0	9.5	5	41	336	11.8	186	3.8	30.3	67.8	7.5	0.0	0.0	18.6	0.0	28.8	0.0	44.9
3	273b	0	0	0	132	0	0	1	0	8.8	5	41	345	8.5	171	4.0	29.4	64.0	7.0	12.5	0.0	0.0	0.0	15.5	50.0	0.0
3	273c	1	1	0	106	0	1	1	0	4.0	3	7	330	10.0	152	3.8	12.1	51.0	15.0	20.0	31.5	14.3	0.0	0.0	18.5	0.0
3	273d	1	1	0	83	0	1	1	0	4.0	4	41	330	10.0	146	4.3	6.8	47.0	16.8	43.5	37.0	2.5	0.0	0.0	0.0	0.0
3	273e	1	1	0	89	1	1	0	0	5.0	4	41	24	8.0	171	3.8	11.5	45.2	48.5	21.5	0.0	7.5	0.0	0.0	22.5	0.0
3	273f	1	1	0	89	0	0	1	0	6.7	4	41	50	4.8	165	4.0	10.1	47.6	57.8	25.0	0.0	4.8	0.0	0.0	12.5	0.0
3	273g	1	0	0	48	0	0	1	0	7.0	4	41	342	7.5	146	3.7	5.3	25.3	35.0	27.5	13.8	10.0	0.0	0.0	13.8	0.0
3	273i	1	1	0	66	1	1	1	0	7.0	4	7	336	8.0	140	4.3	1.8	18.2	30.5	6.8	51.3	11.5	0.0	0.0	0.0	0.0
3	273j	1	0	0	142	0	0	1	0	11.8	5	41	354	13.8	128	4.1	9.4	69.2	19.3	1.5	0.0	2.0	0.0	16.3	56.3	4.0
3	274a	1	1	0	84	0	0	1	0	6.0	4	41	333	5.0	213	5.9	6.5	27.5	10.3	40.5	0.0	21.3	0.0	0.0	19.0	0.0
3	276a	1	0	0	113	1	0	0	0	13.4	5	40	348	6.2	198	3.6	29.7	63.7	21.3	0.0	0.0	0.0	0.0	36.3	42.3	0.0
3	276b	0	0	0	129	0	1	1	0	13.4	5	40	336	13.0	198	3.5	30.0	58.7	4.8	0.0	0.0	0.0	0.0	15.0	80.3	0.0
3	276c	0	0	0	115	0	1	1	0	15.2	5	40	347	7.0	220	3.7	27.6	59.1	6.5	0.0	0.0	0.0	0.0	23.8	67.0	0.0
3	276d	0	0	0	111	0	1	1	0	13.4	5	40	336	7.0	207	3.6	20.1	52.8	0.8	0.0	0.0	0.0	0.0	31.8	63.8	0.0
3	276e	0	0	0	115	0	0	1	0	8.0	4	40	42	10.0	207	4.0	10.4	45.4	8.3	40.3	0.0	0.0	0.0	20.0	29.3	0.0
3	280a	1	1	0	32	0	1	1	0	6.0	4	40	27	9.0	195	4.1	4.4	41.8	56.0	26.0	0.0	4.5	0.0	7.5	0.0	0.0
3	280b	0	0	0	59	0	0	1	0	12.0	5	40	32	6.2	195	3.9	24.9	52.7	26.0	3.8	0.3	0.0	0.0	76.3	24.8	18.8
3	280c	0	0	0	124	0	0	1	0	14.0	5	40	39	5.0	195	3.7	26.7	60.0	28.3	11.7	0.0	0.0	0.0	10.0	43.3	0.0
3	280d	1	1	0	128	0	0	1	0	8.7	4	40	7	12.5	143	4.0	30.0	72.3	15.0	21.3	20.0	7.8	0.0	0.0	55.8	0.0
3	280e	0	0	1	103	0	0	1	0	7.8	4	40	7	10.8	146	3.8	30.6	71.2	6.0	8.3	0.0	1.0	0.0	2.8	82.0	0.0
3	280f	1	1	0	68	0	1	1	0	15.2	5	40	47	8.2	152	3.7	30.3	64.8	19.0	27.8	0.0	2.5	0.0	27.8	0.0	23.0
3	280g	1	0	0	106	0	1	1	0	11.7	5	40	47	6.0	152	5.6	20.1	61.1	30.0	0.0	0.0	6.8	0.0	53.3	10.0	0.0
3	280h	0	0	1	38	0	0	1	0	8.5	4	41	16	6.5	162	6.0	4.6	31.4	4.0	0.0	27.5	2.5	0.0	65.3	10.0	0.0
3	280e	1	1	0	38	0	0	1	0	7.8	4	40	7	10.8	146	4.4	30.0	69.2	10.5	43.5	0.0	3.8	0.0	41.0	0.0	0.0
3	280h	0	0	1	24	0	0	1	0	8.5	4	41	16	6.5	162	4.6	4.3	30.6	8.8	28.0	0.0	0.0	0.0	29.5	10.3	0.0

WOOD	I.D.	ALIVE?	ACTIVE?	ABAXIAL?	DIAMETER	SPRUCE	PC	SP	LARCH	TREE HT	CANOPY	TREE AGE	ASPECT	SLOPE	ALTITUDE	SOIL pH	SOIL-C	SOIL-H2O	MOLINIA	CALLUNA	ULEX	ERICA	PTERIDIUM	MOSS	BARE	VACCINIUM
3	283b	1	1	0	47	0	0	1	0	8.5	4	41	16	6.5	162	6.1	5.2	24.7	5.0	25.3	1.3	0.5	0.0	8.8	32.3	0.0
3	284a	1	0	0	205	1	0	0	0	13.5	5	39	50	7.8	412	3.7	29.7	78.7	0.0	0.0	0.0	0.0	0.0	1.8	98.3	0.0
3	284b	0	0	1	93	1	0	1	0	8.0	4	39	85	9.0	423	4.1	4.7	41.0	58.8	7.5	0.0	0.0	0.0	3.8	29.8	0.0
3	284b	1	0	0	23	1	0	1	0	8.0	4	39	85	9.0	412	4.1	7.3	41.3	44.6	26.3	0.0	0.0	0.0	19.5	7.4	0.0
3	285a	1	1	0	96	0	1	1	0	14.0	5	40	360	8.0	152	5.6	3.4	26.0	7.0	6.3	2.8	2.0	0.0	2.0	51.0	0.0
3	285b	1	1	0	88	0	1	1	0	11.8	5	40	22	7.0	155	6.6	3.8	25.0	39.8	0.0	0.0	22.5	0.0	0.3	32.0	0.0
3	286a	1	1	0	115	0	1	1	0	15.0	5	40	336	8.2	159	5.4	11.9	36.6	45.5	0.0	5.0	0.0	0.0	0.8	65.8	0.0
3	288a	1	1	0	115	0	0	1	0	9.3	5	42	119	8.0	177	6.9	4.9	28.8	20.8	8.8	0.0	6.3	0.0	10.5	34.0	7.5
4	109a	1	1	0	72	0	1	1	0	9.0	5	47	60	4.8	183	6.3	6.1	32.9	72.3	0.0	0.0	0.0	0.0	0.0	2.3	0.0
5	943a	1	0	0	85	0	1	0	0	4.0	5	9	172	8.4	131	3.9	12.0	56.8	48.7	38.3	8.3	2.0	0.0	5.7	0.0	0.0
6	776a	1	1	0	105	0	1	1	0	5.0	4	27	57	10.6	213	3.9	30.0	66.8	0.0	14.6	0.0	14.6	0.0	0.0	28.3	38.3
6	778a	1	0	0	85	0	0	1	0	7.5	4	27	85	19.5	198	4.1	29.7	67.9	0.0	0.0	0.0	0.0	2.5	0.0	25.3	24.6
7	002a	1	1	0	127	0	1	1	0	17.0	5	44	22	8.0	97	4.2	24.9	44.7	42.8	0.0	0.8	1.3	0.0	1.3	24.3	24.8
7	020a	0	0	0	103	0	0	1	0	16.0	5	45	18	3.5	85	4.0	10.9	34.4	0.7	0.0	0.0	0.0	0.0	53.3	21.7	2.7
8	560a	1	1	0	76	1	1	0	0	2.0	1	6	5	22.8	213	4.0	31.2	65.1	0.0	1.0	0.0	0.0	46.9	5.3	46.9	0.0
8	578a	1	1	0	113	1	0	1	0	6.0	3	36	291	7.0	305	4.0	15.3	62.4	0.0	8.8	0.0	0.3	56.3	1.3	20.3	54.3
8	576a	0	0	1	74	0	0	1	0	3.5	3	38	28	24.0	274	3.9	27.6	71.7	0.0	48.5	0.0	15.3	3.5	3.8	5.0	10.3
8	576b	1	1	0	141	0	0	1	0	5.0	4	38	28	22.5	274	3.8	28.8	66.9	0.0	1.8	0.0	1.0	9.0	0.0	13.8	73.5
8	576c	1	1	0	97	0	0	1	0	6.5	4	38	327	19.0	284	3.8	21.3	76.9	0.0	9.3	0.0	1.3	8.3	54.8	0.0	23.5
8	576d	0	0	1	81	0	0	1	0	6.5	4	38	327	19.0	290	4.3	12.0	58.0	0.0	0.5	0.0	1.0	22.0	13.0	5.0	0.0
8	576e	1	1	0	137	0	0	1	0	8.0	5	38	327	15.8	296	4.2	9.5	39.7	0.0	22.5	0.0	0.0	25.0	32.8	2.5	1.0

APPENDIX III

AN ANT COUNTER FOR WOOD ANT ROUTES

The ant counter described here was developed in co-operation with Mr V. Neff, of the Department of Biochemistry. Although it was not used in this project, some of the ideas may have other applications.

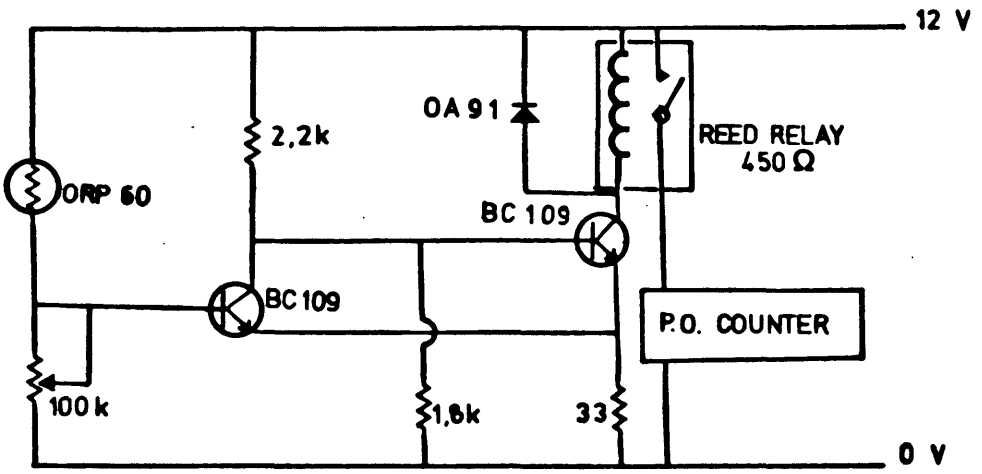
As pointed out in 4.4.1, an ant counter, or a calibratable recorder of some sort, is required to obtain long-term activity records of wood ants. DeBruyn and Kruk-deBruin (1972) used pitfall traps with a time changing mechanism, which was limited to changing the traps every two hours. However a photocell circuit seemed to offer better possibilities of more frequent counts.

Siddorn (1962) and Stradling (1968) have used photocell counters successfully to count the foragers from laboratory colonies of ants, and Dibley and Lewis (1972) designed a counter which gave records for up to 80 days on leafcutter-ant trails in Trinidad. The present circuit is a modified form of that used by Stradling (1968), and is similar to the circuit used by Dibley and Lewis (1972) and another suggested by Long (1968) for counting revolutions of wind vanes.

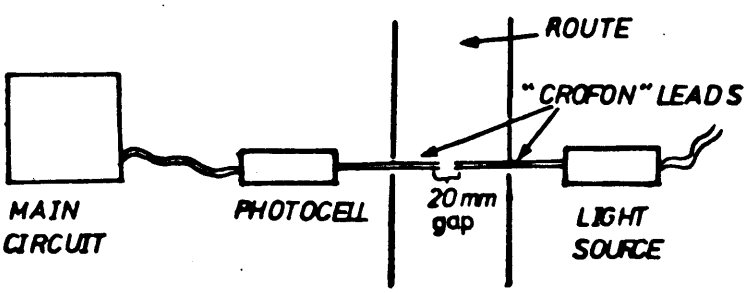
The circuit used is given in appendix figure 1. All the components are readily available and inexpensive. The "P.O. counter" is a British Government-surplus telephone counter and it is necessary to purchase a few to obtain one of suitable coil resistance (more than 200 ohm). This circuit worked well under laboratory conditions using a flashlight bulb as a light source.

Under field conditions, it was necessary to place the light receptor and light source so that passing ants broke the light beam. Since flat surfaces were necessary, a number of boards were placed across suitable routes at different nests. The ants were slow to accept these and some of the "bridges" were circumvented by the ants. However a few "bridges" already in use by ants were suitable, and one of these on route 1 of nest KC-440g (nest C in chapter 4; see plate 5, and section 4.4.1) was used to test the ant counter.

The counter and light source was powered by two 6 V rechargeable cells. The set-up for field use is shown in appendix figure 2. The light source was enclosed in a sealed container and a light-conducting lead (CROFON 1610 manufactured by Fibre Optics Suppliers, P.O.Box 702,



Appendix figure 1: Circuit diagram of the ant counter.



Appendix figure 2: Diagram of the ant counter in position.

London W10 6SL) was used to form the light beam on one side of the ant route. The light beam was carefully alligned with another CROFON lead to the photocell, also contained in a separate sealed container. Each time the light beam was broken a count was registered. Best results were obtained by shading the light leads from direct sunlight with a black polythene sheet. This did not disturb the ants. A maximum gap of 15-20 mm between the light source and receptor leads was possible with the present circuit. The ants were guided through the beam by funnel-shaped baffles, which were coated with FLUON to prevent the ants from climbing over them.

The counter was calibrated on route 1 of KC-440g and run on 5.X.1974 in conjunction with the day's observations described in 4.4.1. Consequently direct comparison is possible between electronically counted (continuous for the entire observation) and observer counted (a five-minute count of ants in both directions every half-hour) foraging traffic.

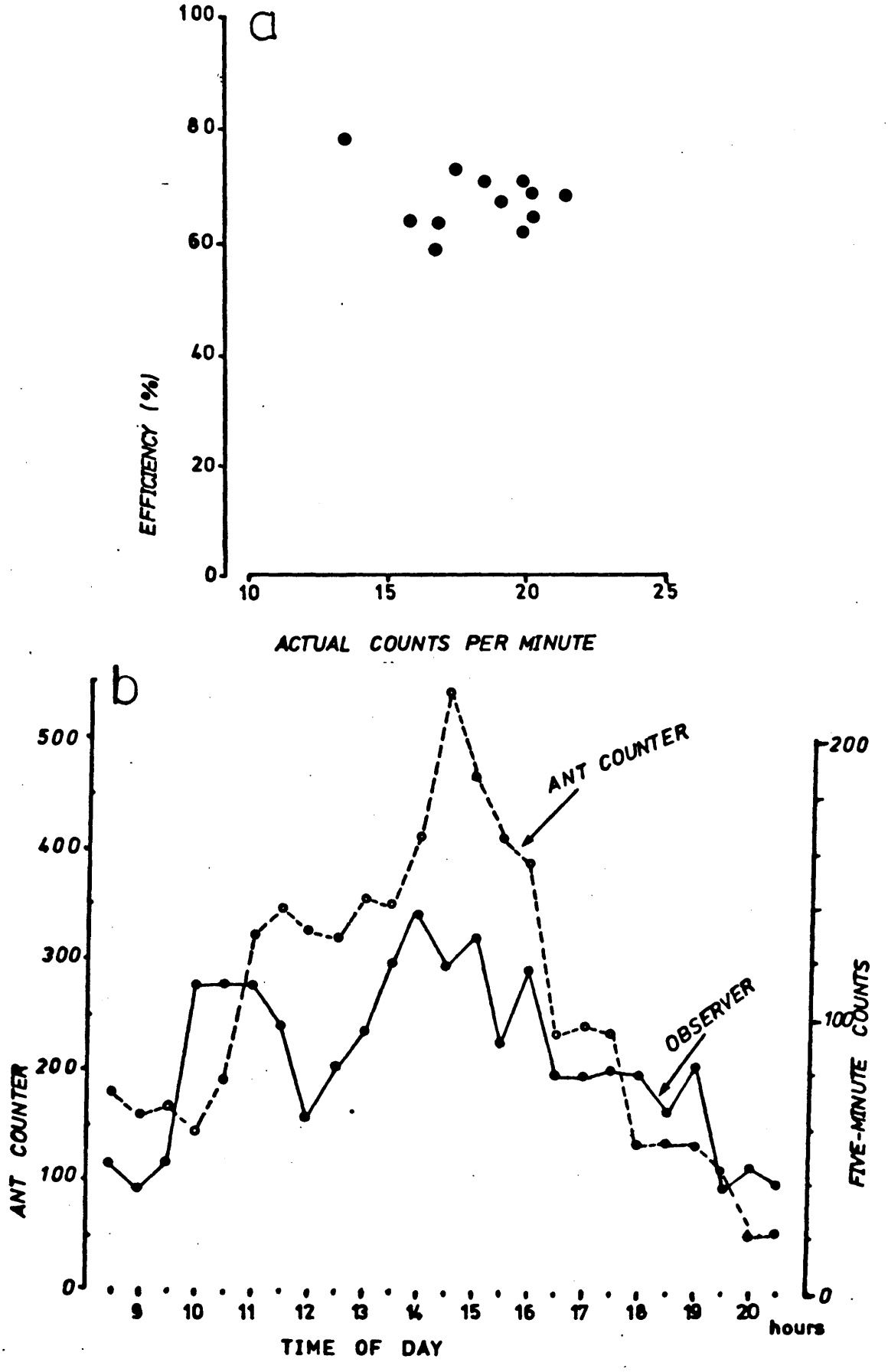
The calibration of the counter is given in appendix figure 3a. The percent efficiency was calculated as

$$\frac{\text{number counted by the ant counter}}{\text{actual number}} \times 100$$

In each case the observer counted the actual number of ants passing while the counter registered 100. At the traffic rates shown, the counter was quite consistent and recorded about 70 percent of passing traffic.

The record produced by the counter, and that of the observer is given in appendix figure 3b, where it can be seen that quite similar trends are evident (the counter data in this figure was not corrected by the calibration factor). However, when darkness fell, it was evident that the foragers were attracted to the light beam and, by walking backwards and forwards, produced spurious results. An attempt to introduce a red filter to the light source, since ants are insensitive to red light, was not successful due to the limits of the circuit, and this problem was not overcome.

APPENDIX REFERENCES are included with the references of the main text.



Appendix figure 3: (a) The efficiency of the ant counter; (b) the number of foragers on route 1, nest C, 5.X.1974 as monitored by the ant counter and by an observer.

APPENDIX IV

MAPS OF THE STUDY AREA

MAPS:

The maps accompanying this thesis are folded in a pocket on the inside of the back cover.

MAP 1

Map of the South Tipperary district, with the boundaries of the Forest and Wildlife Service woodlands shown in heavy line. The woods mentioned in the text can be located by the following numbers:

1, Ballinacourty; 2, Rossbog; 3, Moore's; 4, Ballydavid; 5, Kilcoran; 6, Boulakennedy; 7, Glengarra; 8, Galtee; 9, Kilballyboy; 10, Shanrahan. (Scale 1:63 360)

MAPS 2, 3, 4

Maps of the study woods showing the nests known up to autumn 1975. Compartment numbers are given. Nests known prior to 1974 have been allocated a letter and were included in the nest site survey of chapter 3.

Map 2: Moore's Wood;
Map 3: Kilcoran Wood;
Map 4: Glengarra Wood.

(scale 1:10 560)

PLATE 1

A. The Formica rufa record in the Haliday MS Catalogue of Irish Insects. The text reads "common near Clara - Wicklow & its hills by the river, farside A.F. Annamoe. Rossbehy W.Cl. coll.". The symbol ⊕ means Haliday considered the species as "certainly Irish".

B. Sunning clusters of Formica lugubris on nest MW-268a, spring 1974.

C. Adult-carrying behaviour of Formica lugubris. AC = adult carrier, and CA = carried adult (see overlay).

A

fusca ⊕ z

fuliginosa ⊕ ha

emarginata? ⊕ z Sandymount.

flava ⊕ z

rufa ⊕ common - near Clara - Wicklow
& its hills by the river, forside
Annamoe. Rosebery Wkly coll. A. F.
T. Cl. C.S.L.

viridula Nyl. ⊕ Hothouses.

B



C



PLATE 2

A, B, C Three of the five nests whose total foragers and colony size were estimated using the capture-mark-recapture technique. (Scale = 0.5 m)

A. nest F (KC-457a)

B. nest G (KC-441a)

C. nest H (KC-452a)

A



B



C



PLATE 3

A, B Two of the five nests whose total forager and colony size were estimated using the capture-mark-recapture technique. (Scale = 0.5 m)

A. nest J (GG-936b)

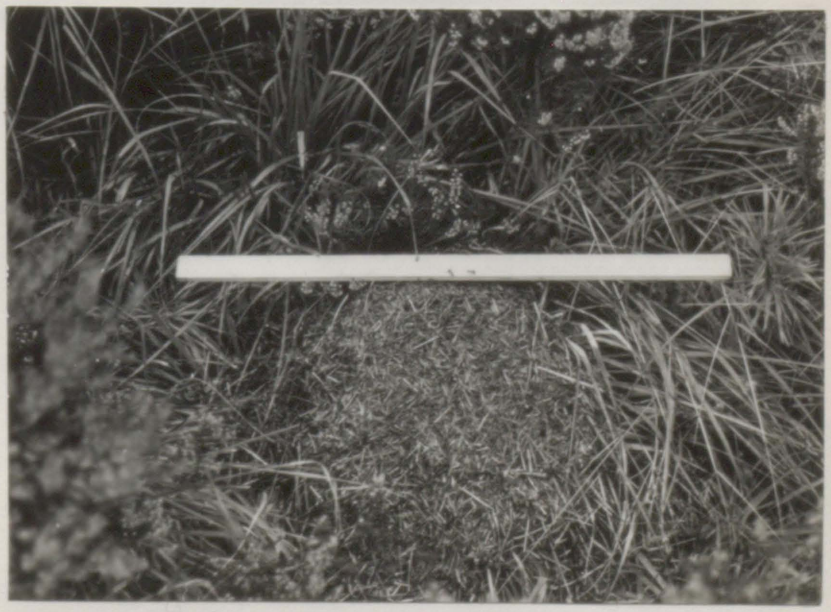
B. nest I (GG-936d)

C *Formica lugubris* attending *Cinara pini* on a young shoot of *Pinus sylvestris*.

A



B



C



PLATE 4

A. Formica lugubris attending Cinara piceae on the main stem of a young Picea sitchensis.

B. The same, close-up.

A



B



PLATE 5

A. Formica lugubris attending Cinara kochiana on Larix decidua.

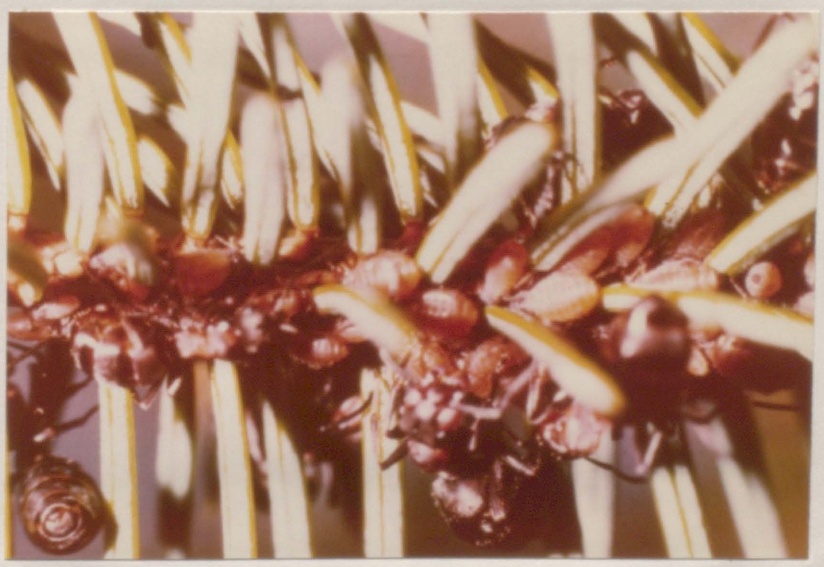
B. Formica lugubris attending Cinara pilicornis on a young shoot of Picea sitchensis.

C. The census point, CP, on route 1 of nest C (KC-440g). The route runs at the base of the wire fence. The ant counter (1) and temperature recorder (2) are shown in position.

A



B

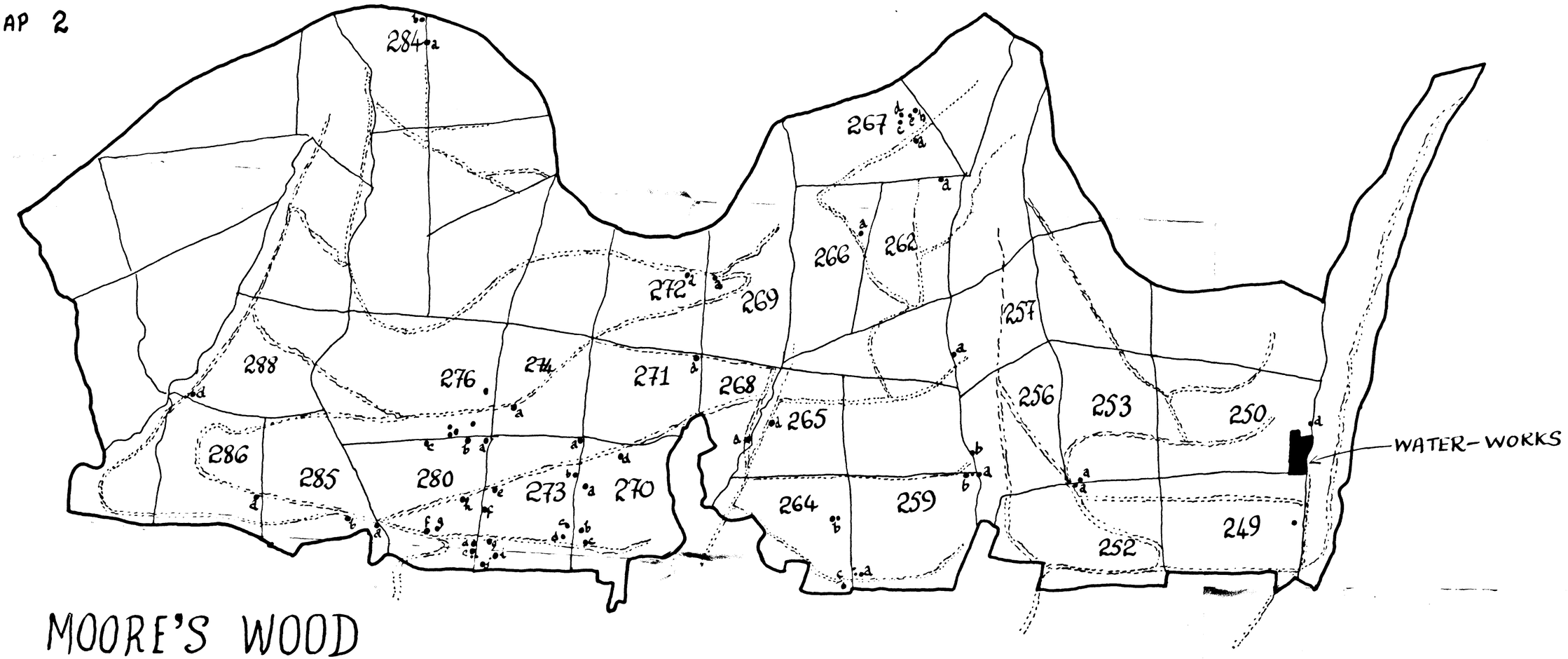


C




10
9
6
7
8
5
6
4
3
2
1

MAP 2



MOORE'S WOOD

SCALE 1: 10560

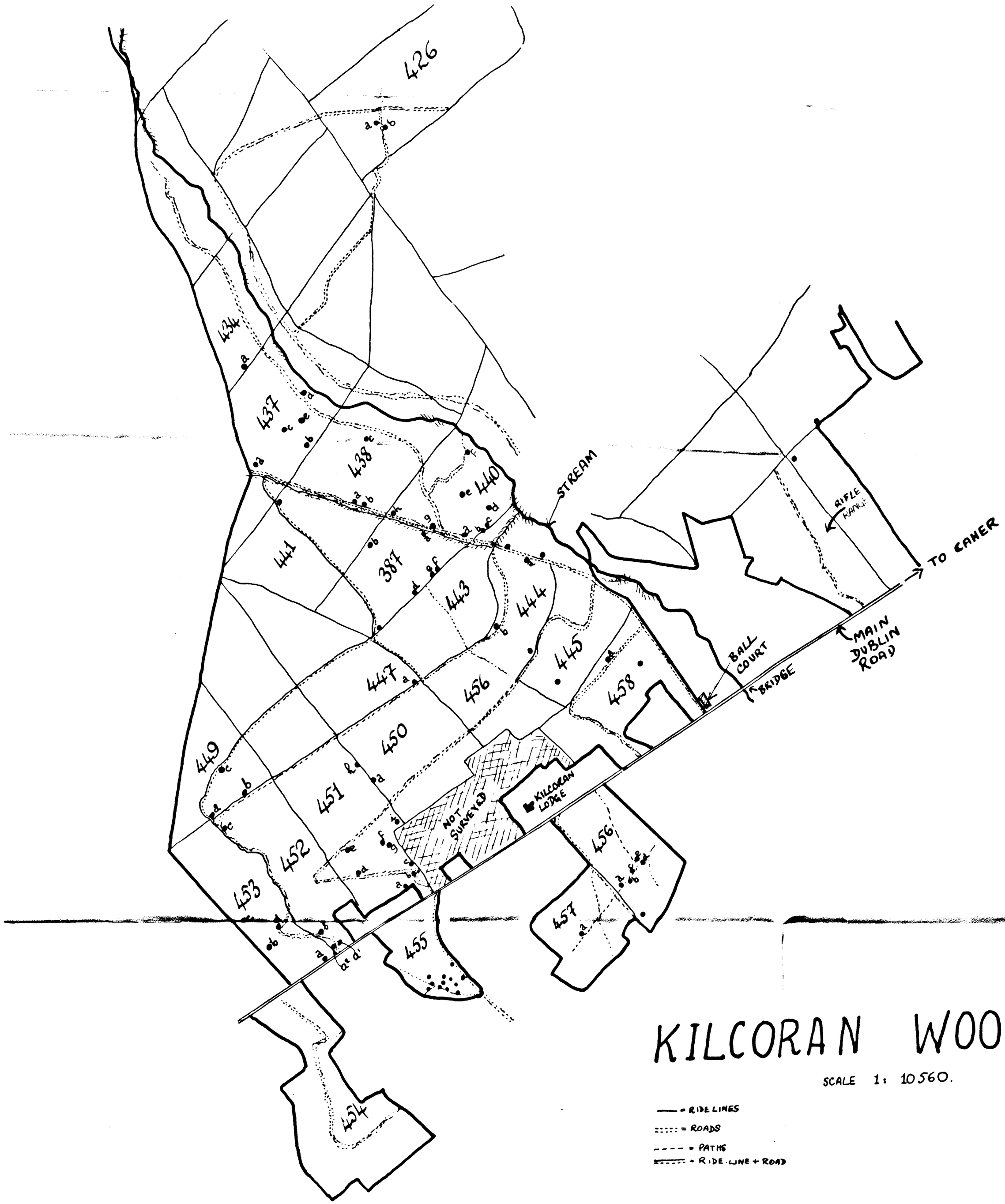
—— = RIDE LINES

= ROADS

- - - - - = PATHS

= RIDE LINE + ROAD

MAP 3



KILCORAN WOOD.

SCALE 1: 10560.

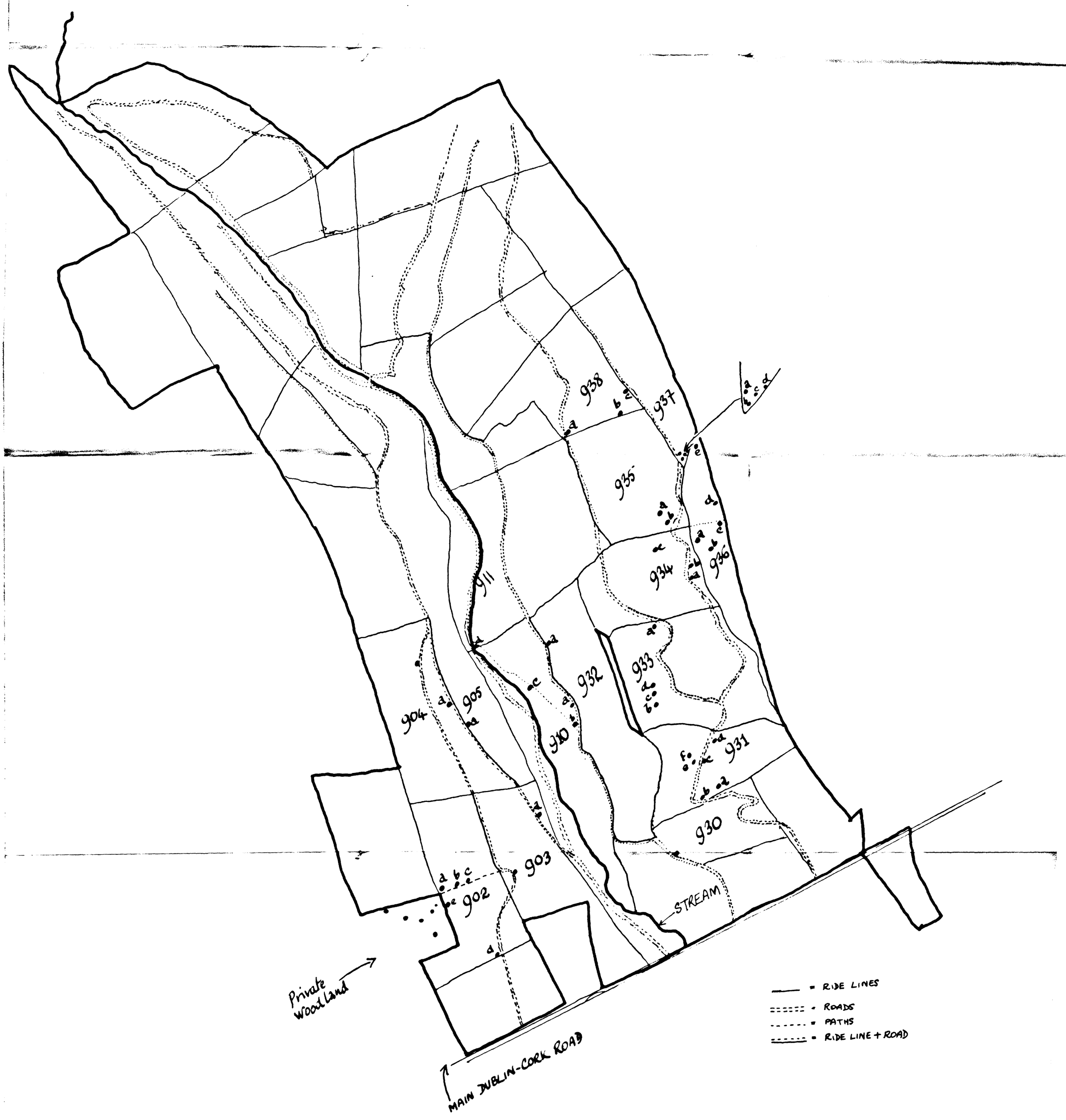
—— = RIDE LINES

::::: = ROADS

- - - - = PATHS

=:=:= = RIDE LINE + ROAD

MAP 4


938
937
935
934
936
911
933
932
931
904
905
910
930
903
902
STREAM
Private woodland
MAIN DUBLIN-CORK ROAD
= RIDE LINES
= ROADS
= PATHS
= RIDE LINE + ROAD