THE BIOLOGY AND ECOLOGY OF MACROMISCHOIDES ACULEATUS (HYMENOPTERA:FORMICIDAE) IN COCOA FARMS IN GHANA

BY

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This is to certify that this thesis has not been submitted for a degree to any other university. It is entirely my own work and all help has been duly acknowledged.

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ABSTRACT

The ecology and biology of *Macromischoides aculeatus* have been studied. The ant was found to be widely distributed in southern Ghana and its distribution overlapped that of the forest zone. In cocoa farms it occurred more commonly and more abundantly in areas with dense shade than in areas of thin shade. Light, predators, Homoptera and food availability were found to influence its distribution. It was found to be largely crepusacular and nocturnal.

M. aculeatus has been found to be antagonistic to other dominant ants in cocoa farms but could occur together with *Crematogaster clariventris* on same trees; this depends on a behavioural mechanism. As a predator it utilizes cocoa capsids and other insects, both living and dead, and feeds too on sugars from extrafloral nectaries or from Homoptera. Mites were found as external parasites and nematode worms as internal parasites.

Colonies were polydomous and largely monogynous. Population changes are discussed. Alate production was periodic and flight activity had a peak between April and May when queens founded colonies independently. Presence of brood was found to stimulate nest building in workers.

It is suggested that since the ant predates cocoa capsids it could be used as a biological control agent by, at least, encouraging its presence through good cultivational practice rather than, as at present, killing it by the use of broad-spectrum insecticides.

1. GENERAL INTRODUCTION

The ant genus Macromischoides was erected by Wheeler (1920) for this species, hitherto placed in Macromischa which is now restricted to the New World. The type locality of M. aculeatus is Gold Coast, that is Ghana, so we are dealing with topotypic material. These ants are confined to the tropical forest zone of West and Central Africa (Wheeler, 1922). In Ghana though no country-wide survey has been conducted, it can be said from the habitat preference they exhibit that the ants are largely confined to the forest regions. They do not exhibit any nest-plant specificity since they occur on large numbers of different plants both wild and cultivated. The most prominent ones among the latter are cocoa, citrus and avocado. Nowadays these ants have become so closely associated with cocoa that one goes to cocoa farms to look for them rather than to the bush. They are tree-dwelling (arboreal) ants that make loose felt nests on the underside of or sandwiched between leaves (Wheeler, 1922). The nests are aggregated and it has been claimed that the queen is found only in one of a large number (Anon, 1947).

The importance of these ants in cocoa farms in Ghana was suggested as early as 1944 by J. Nicol and his research colleagues at the then West African Cocoa Research Institute, Tafo (now Cocoa Research Institute of Ghana, Tafo). They claimed that they had found Macromischoides aculeatus on individual undamaged cocoa trees in badly attacked areas and suggested that the ants were controlling the cocoa capsids through direct predation. Following this discovery they carried out various experiments to employ the ants as biological control agents against the cocoa capsids. They succeeded in a few trials as the following quotation indicates "....The effectiveness of the protection given by Macromischoides aculeatus has recently been illustrated by the severe damage suffered by some trees in the First Progeny Trial which once harboured but later lost the ant." (Anon, 1948). But the overall result was discouraging. The failure is no surprise, since the ecology of the ants as well as of the capsids and of the general environment was then poorly known. Knowledge of these is always very essential in all biological control measures (Smith, 1968).

Subsequent to this attempt, several other entomologists have looked at the problem from time to time. Notable among them are Williams (1954) who associated healthier cocoa with the presence of Macromischoides or Oecophylla. His findings agree quite well with the previous ones of Nicol et al (1944). . Direct evidence of predation was not however obtained until 1965-66, when Marchart and Leston (1969) did radiotracer experiments and made direct field observations to establish beyond all reasonable doubt that the ants do prey on cocoa capsids (Marchart and Leston, 1968, 1969). More recently Collingwood and ZKing (1970) using direct field count methods have also shown that the ants exert considerable predatory pressure on Distantiella theobroma. Moreover, in view of their negative association with mealybug attending ants, especially, Crematogaster spp., it has been suggested that they may help check the spread of swollen shoot virus disease (Leston, personal communications). That Macromischoides aculeatus may be used in direct control measures against cocoa capsids and indirectly against mealybugs is therefore strongly indicated.

Recent progress made in the study of various aspects of the ecology of the cocoa farm, particularly on cocoa capsids and ants gives information which could be developed to give a successful introduction of biological control measures. This is very essential at this time when the chemical approach is gradually failing us. The capsids have developed resistance to some insecticides and Leston (1971) has advocated the use of the red tree ant, Oecophylla longinoda in an integrated control scheme. But better results would perhaps be achieved if Macromischoides aculeatus were used in conjunction with O. longinoda. Although much is already known about the ecology and biology of the latter, virtually nothing is known about the former except for the work noted above.

This consideration has prompted the present investigation, in which the ecology and biology of M. aculeatus are studied together. Topics investigated include distribution in space and time, interrelationships with other ants, food and feeding habits, nests and nesting habits, friends and enemies, colony founding and expansion, and certain aspects of life history.

Section 2. The study area

2. THE STUDY AREA

Preliminary surveys were carried out on the Akwapim Range at Aburi, Mampong, and Adawso. Although the ants occurred in these areas their numbers were too small to constitute a good study population. Moreover the great heights of the trees and therefore of the nests made observations very difficult. These places were therefore abandoned in favour of Tafo, where conditions were found to be more favourable.

General description of the area:

All the observations were made in the plots of the Cocoa Research Institute of Ghana, Tafo. Tafo is in the Eastern Region of Ghana, and lies at latitude 6°17'N and longitude 0°22'W. It is 67 miles from Accra on the Accra-Kumasi road. Taylor (1952) classified it within the Celtis-Triplochiton subdivision of the moist semi-deciduous forests. But on a broader view it is in the Ghana-Guinean bloc of 'moist forest at low and medium altitudes' (Keay, 1959). And according to Church (1957), Tafo has an equatorial type of climate with two equal maxima of peak of rainfall, though it rains every month. The two Wet seasons are March to July and September to October (Wills, 1962). The Dry season falls within December to February and then August. (Walker, 1962; Wills, 1962). The severest period within the dry season is during Harmattan, which occurs around January. Very cool nights and extremely low relative humidity (down to 16% RH.) as well as hazy skies are characteristic of harmattan. (Gibbs, Pickett & Leston, 1968).

Sampling and observation sites:

Sampling and observations were carried out in five plots; C4, C5a, C5b, D14, and H10 (Fig.2.1).

Plot C4: This is a single big plot subdivided into two big blocks and planted with hybrid cocoa. The cocoa trees are of medium height and have very good canopy. The top shade is provided mostly by cultivated trees, for example *Terminalia* spp. There is very little undergrowth and the trees are sprayed regularly. Currently it is being used for experiments on capsid population.

Plot C5a: It is a relatively old plot. The trees are fairly tall in certain areas but those in the observation site are coppiced. The large number of branches per tree of the coppiced cocoa gives them a bushy appearance. Despite the seemingly continuous canopy, there are a few breaks here and there in the canopy. *Terminalia* sp provide the top canopy. The undergrowth is very thick and certain parts of the plot are more or less overgrown with weeds. This plot is now being used for Herbicide experiments.

Plot C5b: A motorable road separates this plot from C5a. The cocoa trees are old and fairly tall. Several trees have been coppiced and these look very bushy. The cocoa canopy is very good in certain parts but extremely poor in others. Top shade is provided by tall *Terminalia* trees. Weeding is not done to ground level. Currently the plot is being used for coppicing and caged experiments.

Plot D14: It is a variety Trial plot with young cocoa of about six years old. The cocoa trees are of medium height and have very good canopy

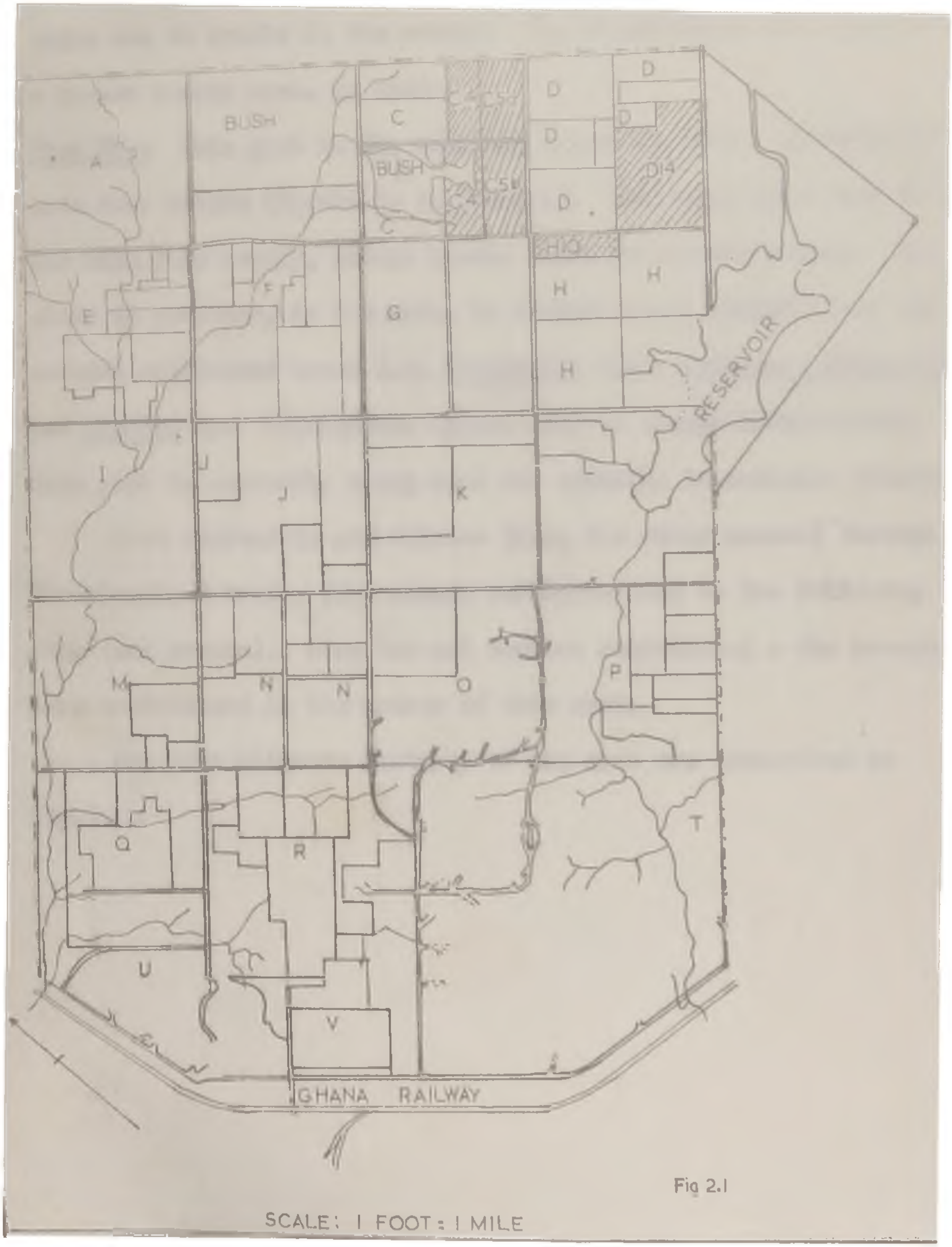


Fig.2.1: A recent map of the Cocoa Research Institute, Ghana, Tafo, showing the study area (cross hatched).

Unlike the other plots, top shade is provided by big, tall forest trees. There is very little undergrowth except in areas receiving light due to breaks in the canopy. The observation site, near to a broken canopy area, is weedy.

Plot H10: This plot is the smallest among the five. It is divided into four blocks (Blocks 1, 2, 3 and 4). The cocoa trees are fairly old with good canopy, though breaks occur in certain places. Top shade is provided, in the main, by forest trees, though there are several cultivated trees i.e. *Terminalia* spp., *Solanum verbascifolium* and *Manihot* sp. Undergrowth occurs only in canopy-broken areas. This plot is currently being used for systemic insecticide trials.

Work started in mid-October (i.e. the rainy season) through December to February (dry season and harmattan) to the following June (wet season). Thus two wet seasons sandwiching a dry season were experienced in the course of this work.

The main climatic features of the area are summarized in Fig.2.2.

Fig 2.2

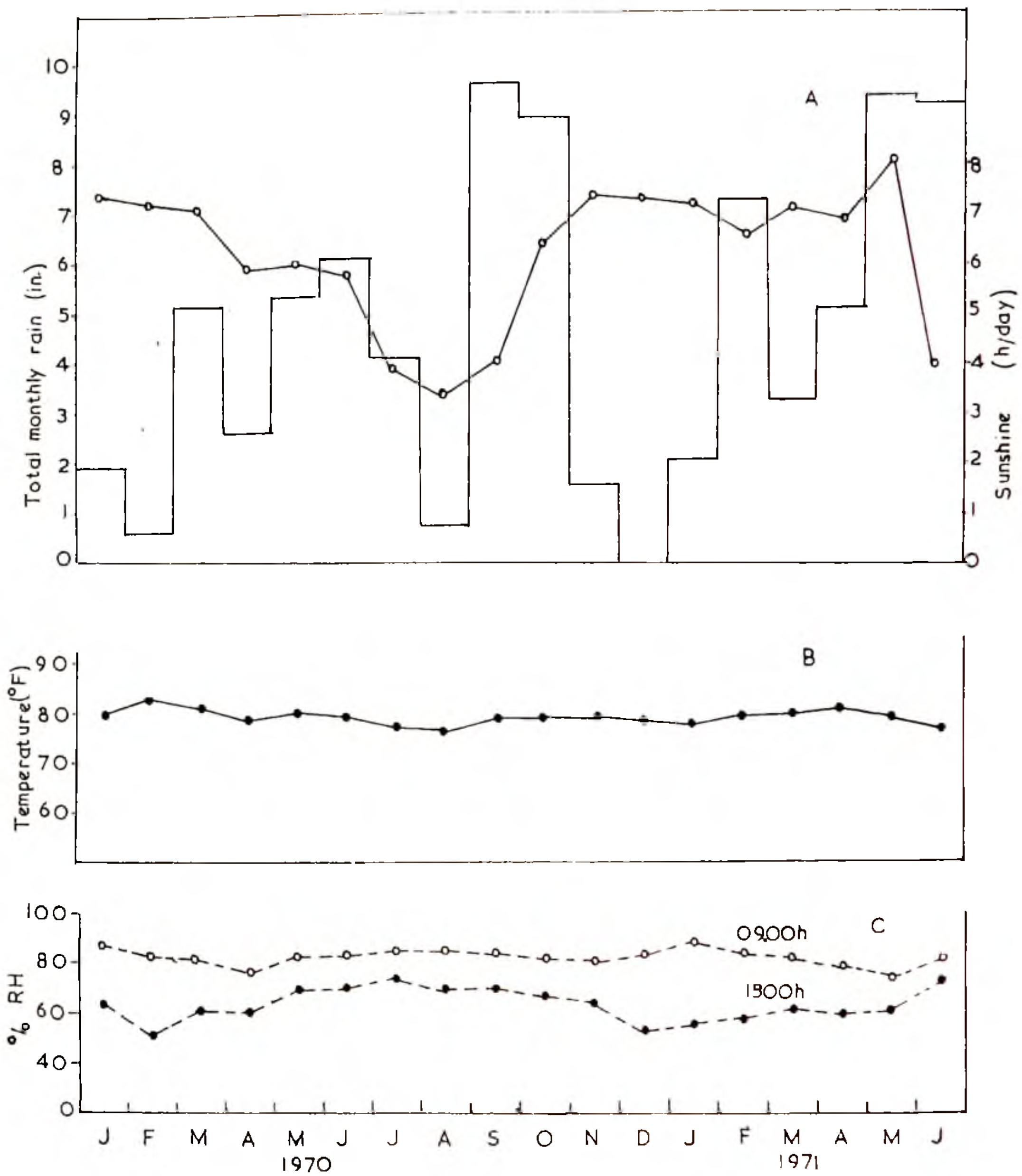


Fig.2.2: Weather data for Tafo during the period of study. A: rainfall (histogram) and sunshine (line); B: temperature; C: relative humidity.

Section 3. Distribution in space.

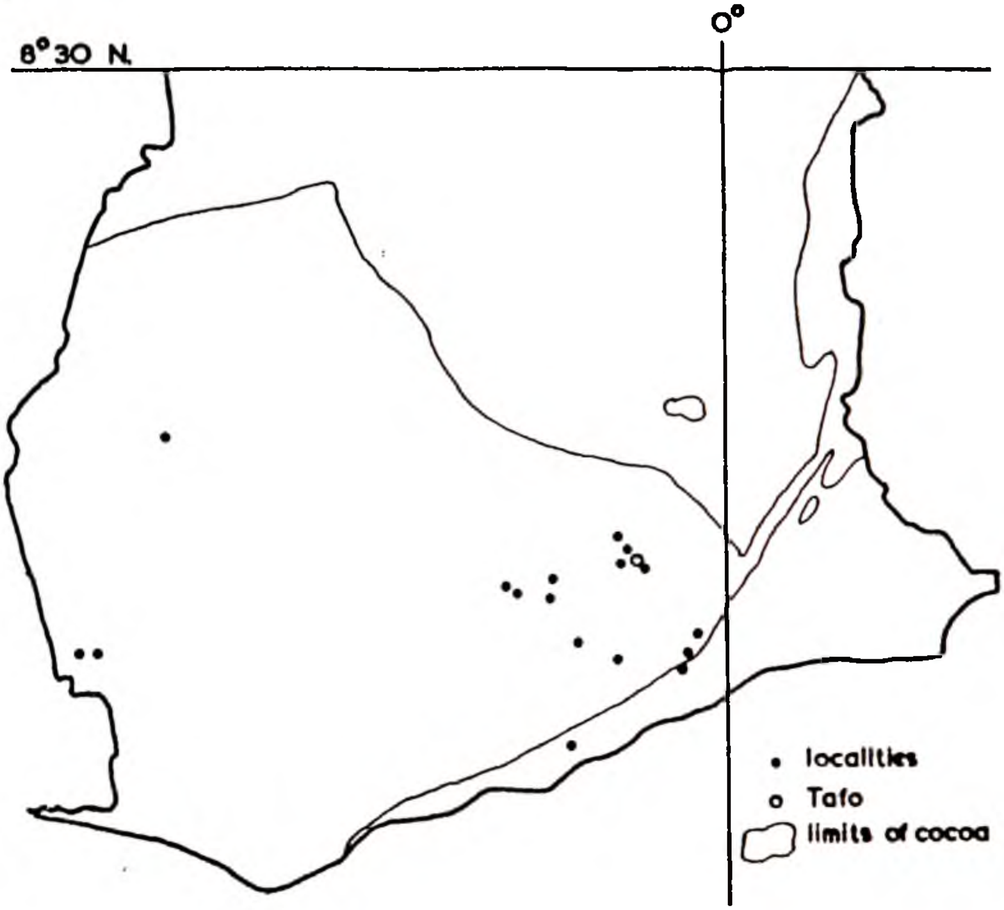
3. DISTRIBUTION IN SPACE

Introduction

Macromischoides aculeatus is confined to the tropical forest zone of West and Central Africa (Wheeler, 1922). In Ghana, surveys so far conducted indicate that it occurs in the forest zones of the Eastern, Western, Brong-Ahafo, Ashanti and Volta regions. Its distribution seems to overlap that of cocoa (Leston: personal communication). Fig.3.1 shows the distribution as known at present.

Wheeler (1922) quoted Lang as saying that *Macromischoides aculeatus* prefers densely leaved trees i.e. good canopy trees. Billes (1946) also claimed that mated females became established more easily on better grown seedlings. Quite recently Collingwood and King (1970) have shown by field scoring that the ants prefer cocoa trees with good canopy. However none of these earlier workers provided maps to substantiate their observations. The present Section aims at mapping specific areas to show the distribution of the ant in relation to different shade regimes and also to other ant species associated with it. Further, an attempt is made to determine colony size, such as the number of nests that constitute a colony, and also colony boundaries. This is done by two main methods: 'acceptance-rejection' and a more sophisticated method using a P^{32} sugar mixture as a radioactive tracer.

Fig 31·



~~100 km~~

Fig.3.1: Distribution of *Macromischoides aculeatus* in southern Ghana.

Materials and method

Mapping:

Mapping was done in three different areas, two in plot H10, and one in plot C4. Four replicates of the radiotracer experiment were carried out in plots H10, C5a, C5b and D14, whilst the 'acceptance-rejection' work was done in plots C5b, C4 and H10.

The area to be mapped was divided into 3 x 3 metre quadrats. The positions of all cocoa and shade trees occurring in each quadrat were accurately indicated on the map and subsequently labelled. Boundaries of different shade regimes were marked to indicate areas with both top shade and good cocoa canopy, good cocoa canopy, top shade only, and poor canopy or open areas. Each tree was then searched for ants of all species and a record made of them. Those which could not be identified on the spot were collected for later identification. All *Macromischoides* nests found on any one tree were labelled. Thus nests found on say tree 4 bore the labels 4a, 4b, 4c etc. Each nest was then removed from the tree with secateurs and enclosed in a small polythene bag, which was in turn put into a bigger polythene bag containing chloroform. They were later opened and a record made of the contents, especially of dealate females. Trees containing other dominant ants i.e. *Oecophylla longinoda* and *Crematogaster stadelmanni* were also noted.

Colony size was crudely determined by using the 'acceptance-rejection' method. This involved transferring workers from one nest to another. Fighting ensued if the workers came from different colonies; if however, they belonged to the same colony, there was no fighting. The ants were transferred by means of a stick which had a band of a grease barrier (Ostico) about two-thirds of the way down its length. Thus the experimenter was safe from attack. The rod was placed against one nest. Ants from this nest climbed on to the stick, and moved up and down beyond the chemical barrier. The stick with the ants was then placed near a second nest. Some workers from the latter nest would climb on to the stick whilst some ants on the stick moved on to the leaf bearing the nest. By this means the ants could be observed at very close quarters both in the nest area as well as on the stick. Record was then made of this.

Radiotracing:

The radioactive work was done with the help of Mr. O.H. Roivainen and his assistant Mr E.O. Agyare. Materials used included 10% sucrose solution and radioactive phosphate (P^{32}). The selected area was mapped to show nest trees and the positions of nests on each tree. All nests were labelled (Fig.3.2). A nest (usually one on a single leaf and a single branch) was selected from any part of the nest aggregation. A post was fixed to the ground with the top part some few inches from the selected nest. A plastic container with a slit in the neck and a perspex plate fitted above the slit was then tied to the post at nest level with aluminium wire as shown in Fig.3.3. The perspex plate was meant to prevent water entering the container

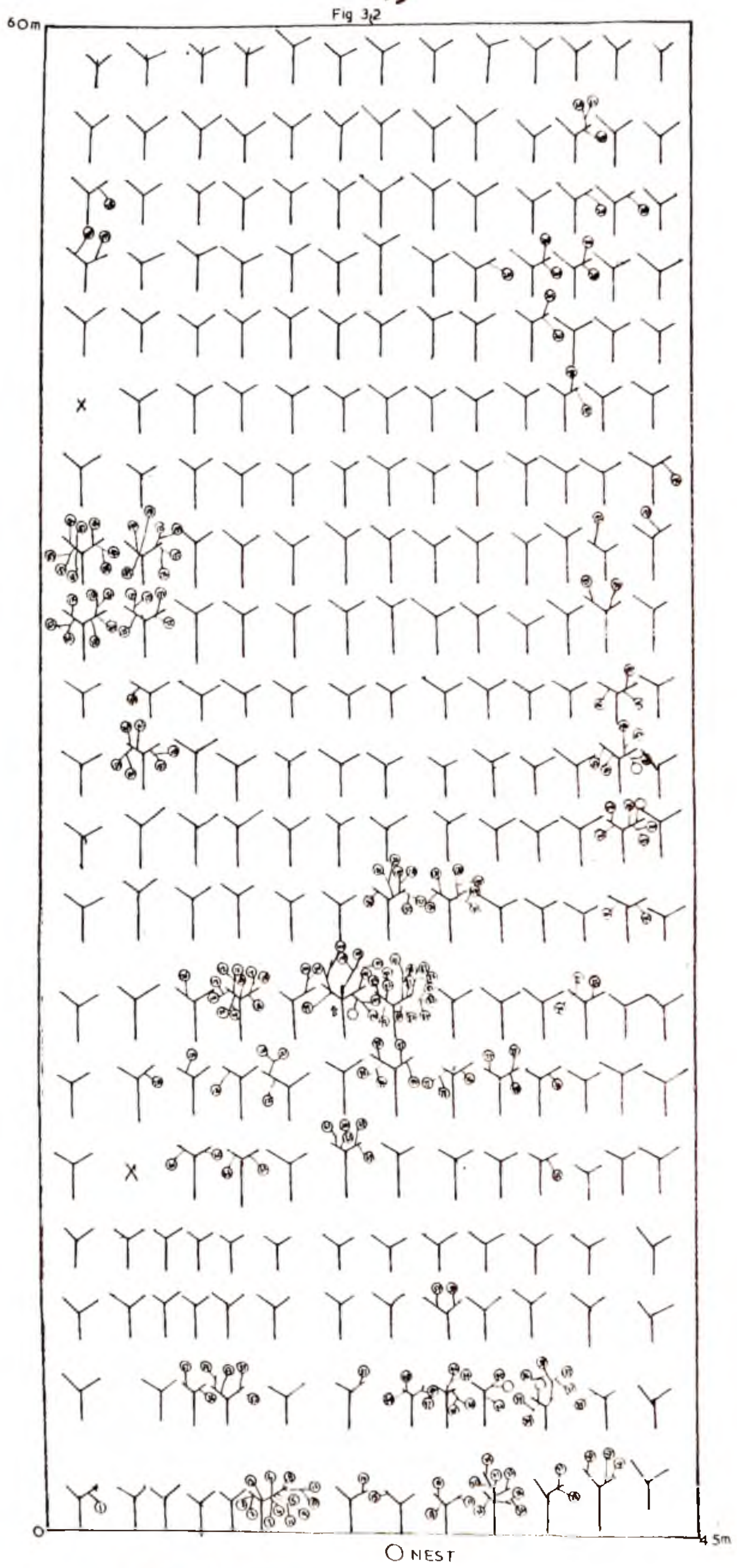


Fig.3.2: Map showing positions of nests on each cocoa tree in Plot C5a, Tafo, 12th April 1971.

SET-UP FOR RADIOISOTOPE EXPERIMENT

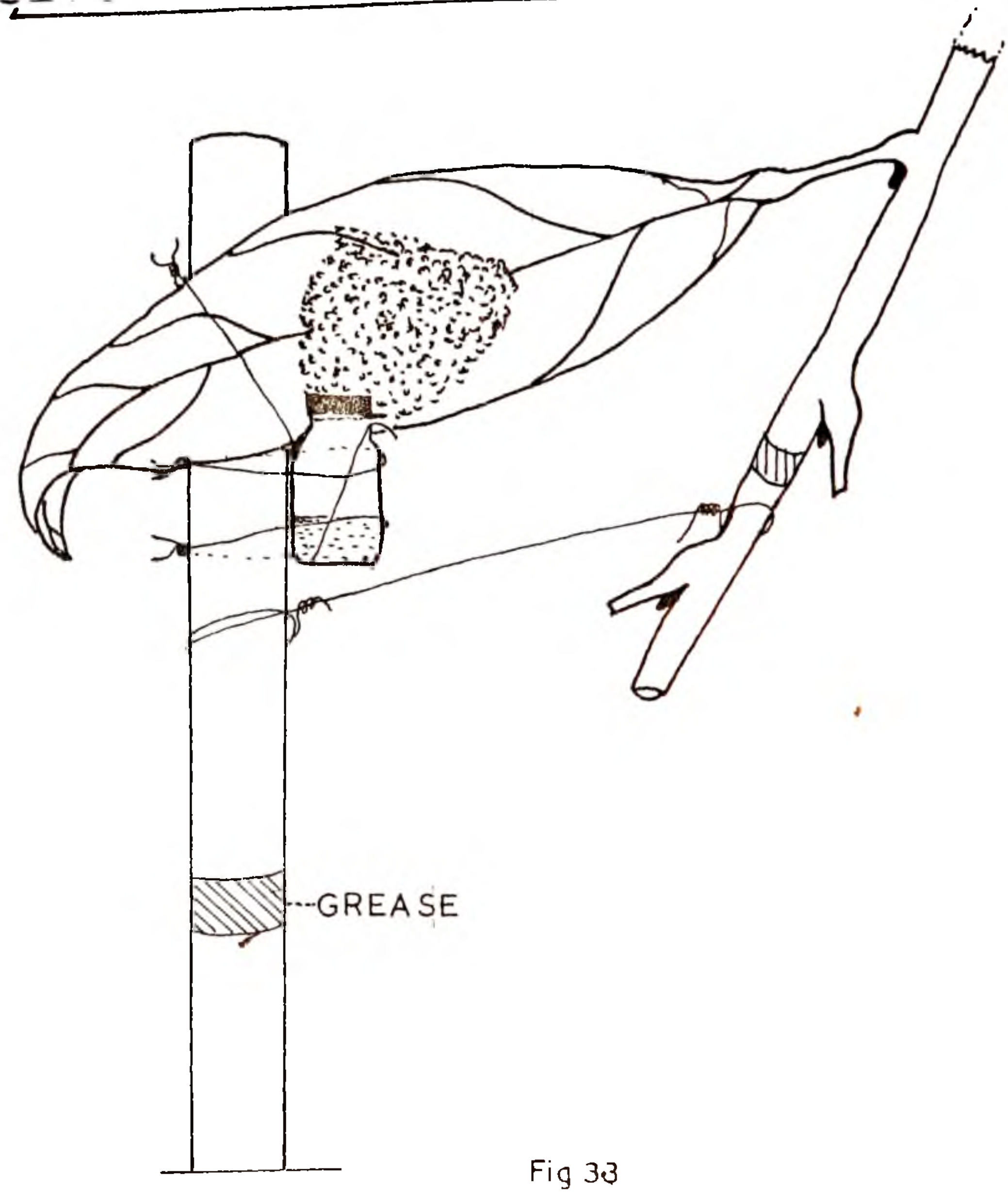


Fig 33

through the slit. $5cm^3$ of the sugar solution was measured into the container. The branch was tied to the post with copper wire thus rendering the arrangement storm-proof. A broad band of grease was applied round the post. $0.09cm^3$ of the radioactive phosphate with an activity of 50 microcuries per millilitre were then gently added to the sugar solution, stirred with a glass rod and the cap of the container was screwed into position. A strip of filter paper was pushed through the slit into the bottom of the container to act as a wick. Lastly the leaf bearing the nest was tied to the post with the aluminium wire. In this way the nest was placed in contact with the container. The ants thus disturbed moved agitatedly, but soon discovered the sugar solution and started feeding on it. Some entered the container while others remained on the filter paper. Each nest was monitored, using a Geiger counter, at 24 h intervals. Monitoring continued until constant counts were obtained in two or three consecutive days. Other insects, particularly ants, found in the area were monitored daily.

Results

i. Mapping

The results of mapping are shown in figures 3.4 - 3.6. They indicate that the ants show a preference for shaded areas. Tables 3.1 and 3.2 give the figures for the various surveys. A chi-squared test of the presence or absence of the ants in the different shade regimes showed that the results were highly significant.

Fig.3.4: Distribution of M. aculeatus and O. longinoda in relation to different shade regimes in plot C.4. Tafo, 14th November 1970

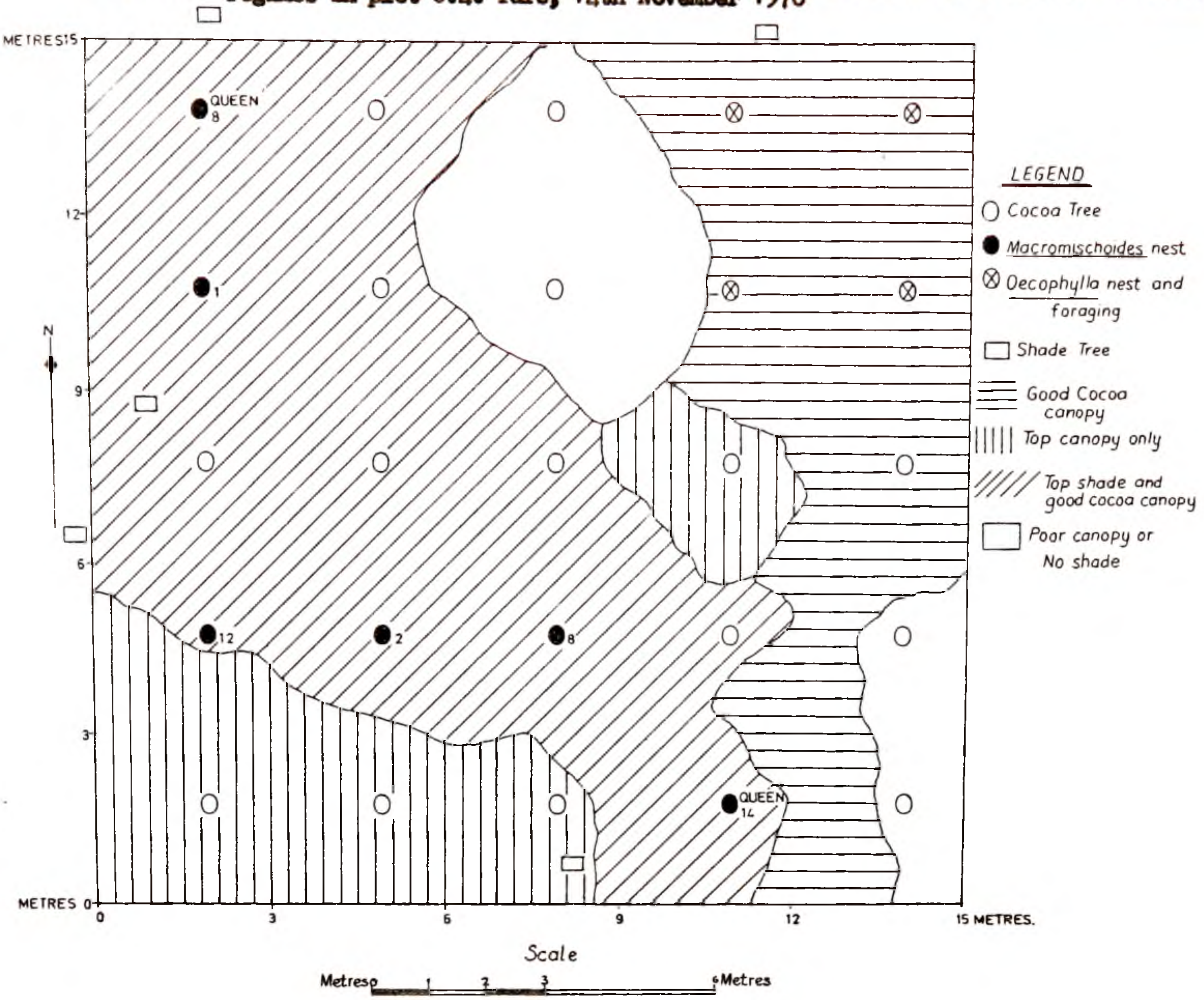
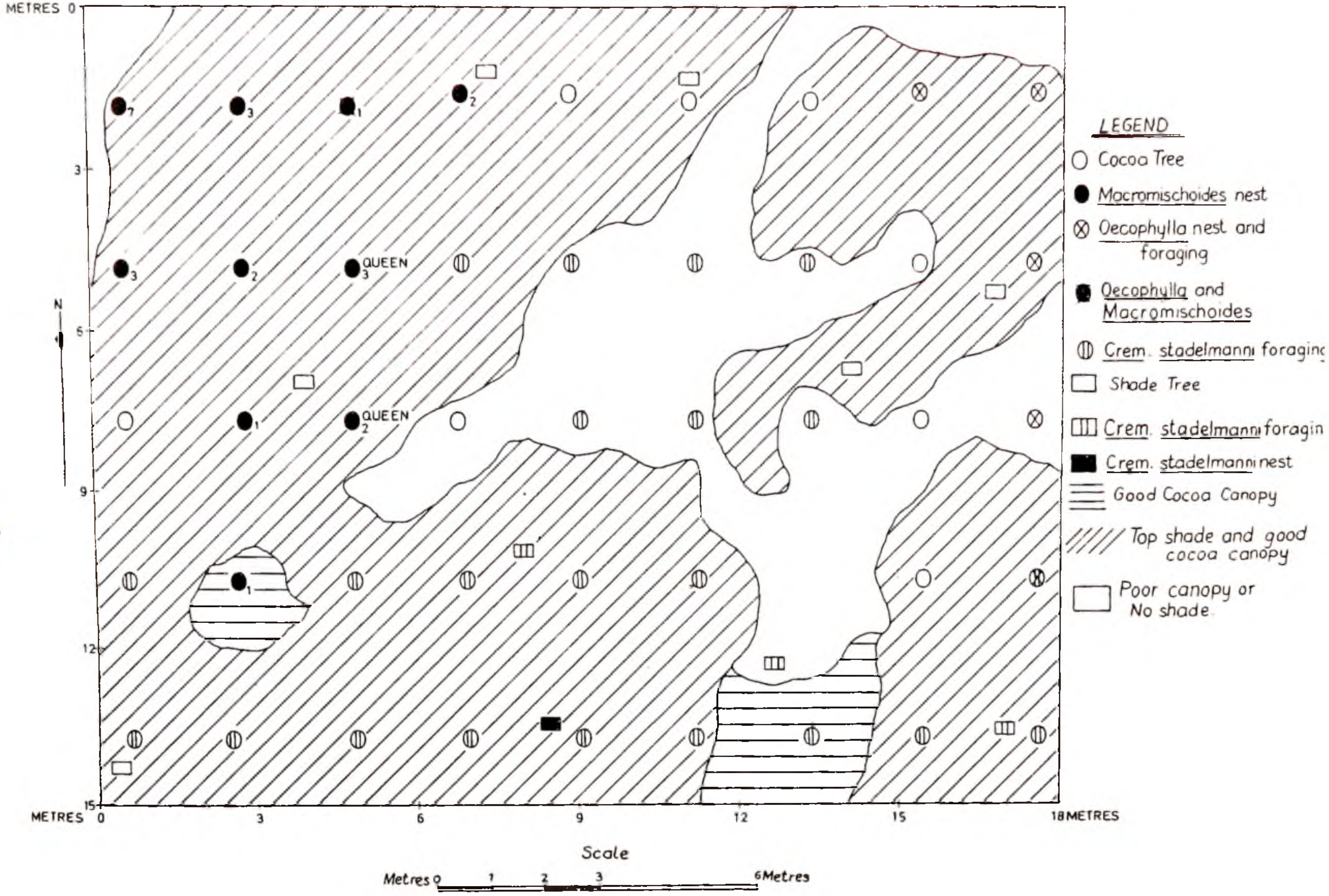


Fig.3.5: Distribution of M. aculeatus and other dominant ants in relation to different shade regimes in plot H10b$_3$, Tafo , 15th November, 1970



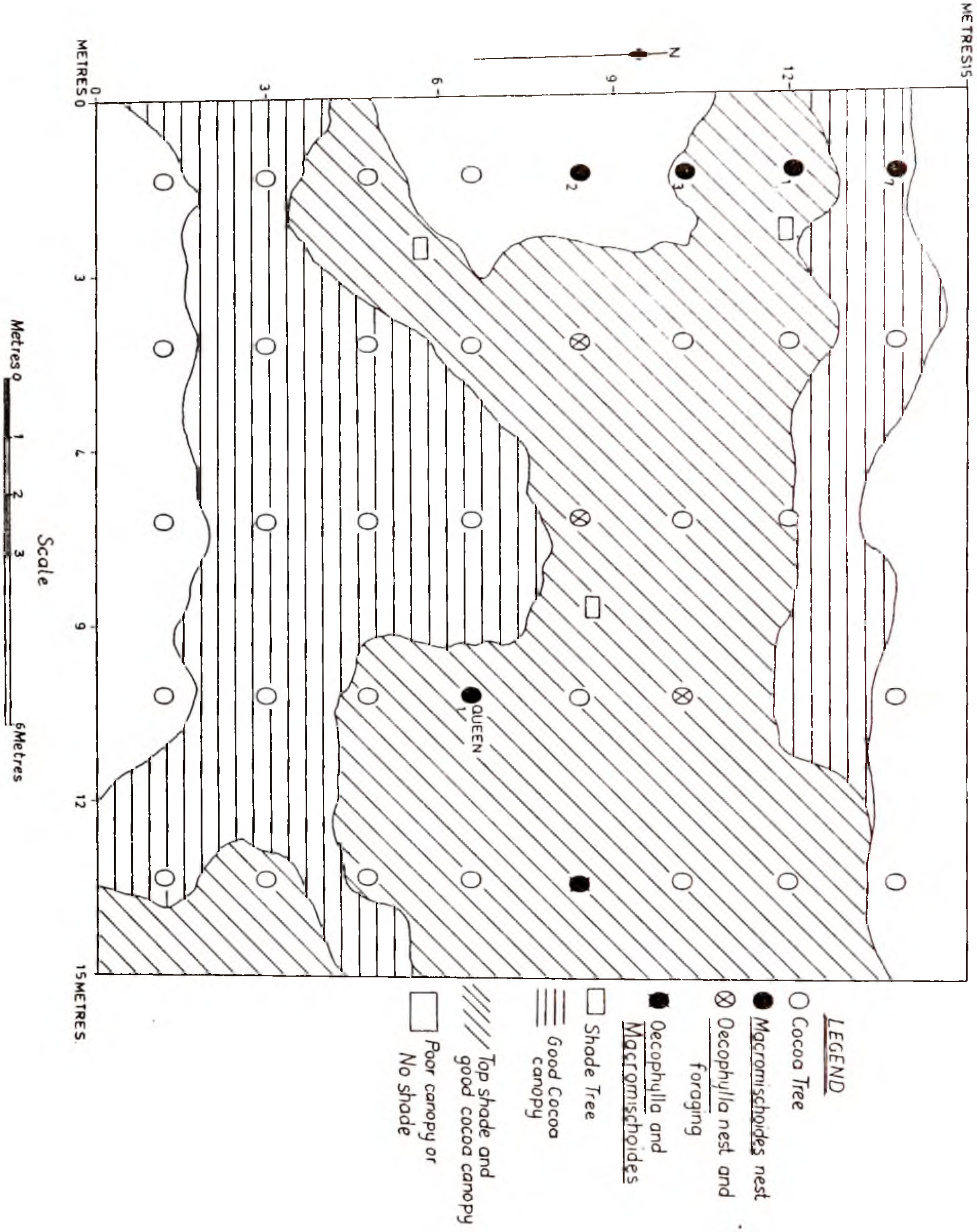


Fig.3.6: Distribution of *M. aculeatus* and *O. longinoda* in relation to different shade regimes in plot $\mathrm{H1Gb}_4$, Tafo, Nov. 1970

Table 3.1

Distribution of *Macromischoides* in different shade regimes in Plots H10 and C4.

Plot		Top shade and good cocoa canop	Good cocoa canopy	Poor cocoa canopy or no shade	Totals
H10B	Total No. of trees	20	10	8	38
	Trees with *Macro*	4	1	1	6
	Total No. of nests	6	7	2	15
H10B	Total No. of trees	33	2	10	45
	Trees with *Macro*	9	1	-	10
	Total No. of nests	24	1	-	25
C4	Total No. of trees	12	5	3+2 seedling	22
	Trees with *Macro*	6	-	-	6
	Total No. of nests	45	-	-	45

Table 3.2

Occurrence of *Macromischoides* under different shade regimes

Macromischoides	No. of tree under top shade plus good cocoa canopy	No. of tree under good cocoa canopy	No. of tree under poor canopy or no shade	Total
Present	19	2	1	22
Absent	46	15	22	83
Total	65	17	23	105
% of trees with *Macro*	29.2	11.7	4.5	20.9
% of trees with *Macro* as compared to total trees	18.0	1.9	0.9	

$\chi^2 = 42.02$ Degress of freedom = 1 $P \angle 0.1$

ii. Radioisotope experiments:

The results of the radiotracer experiment are shown in Figs. 3.7 - 3.9 and Tables 3.3 - 3.5. They show colony boundaries and indicate that there are "no-man's-lands" between colonies. They provide further information on colony sizes. Table 3.5 shows the rate of spread of the radioactive sugar. This will be discussed under 'Daily activity patterns, foraging and food' in Section 5.

Discussion

The results of the mapping prove beyond all reasonable doubt that the ants prefer areas with dense shade, i.e. those with both top shade and good cocoa canopy. 86.3% of the total number of trees with *Macromischoides* occurred in this area. The next preferred areas are those having good cocoa canopy (9.1%). The least preferred areas are those with either poor cocoa canopy or no shade at all (5.6%). Incidentally this least preferred area is where *Oecophylla longinoda* abounds. Results of several laboratory experiments seem to substantiate the field observations. In the laboratory the ants always retreated into dark corners of stools and tables to nest. Only on four occasions did they manage to construct half-finished nests on cocoa seedlings in the open in the laboratory. However, when placed in a dark room they constructed a nest on top of a metal bar. Thus light intensity is a major factor that influences choice of nesting site. Another factor worth considering is the greater leaf area of good canopy cocoa which offers better opportunity for

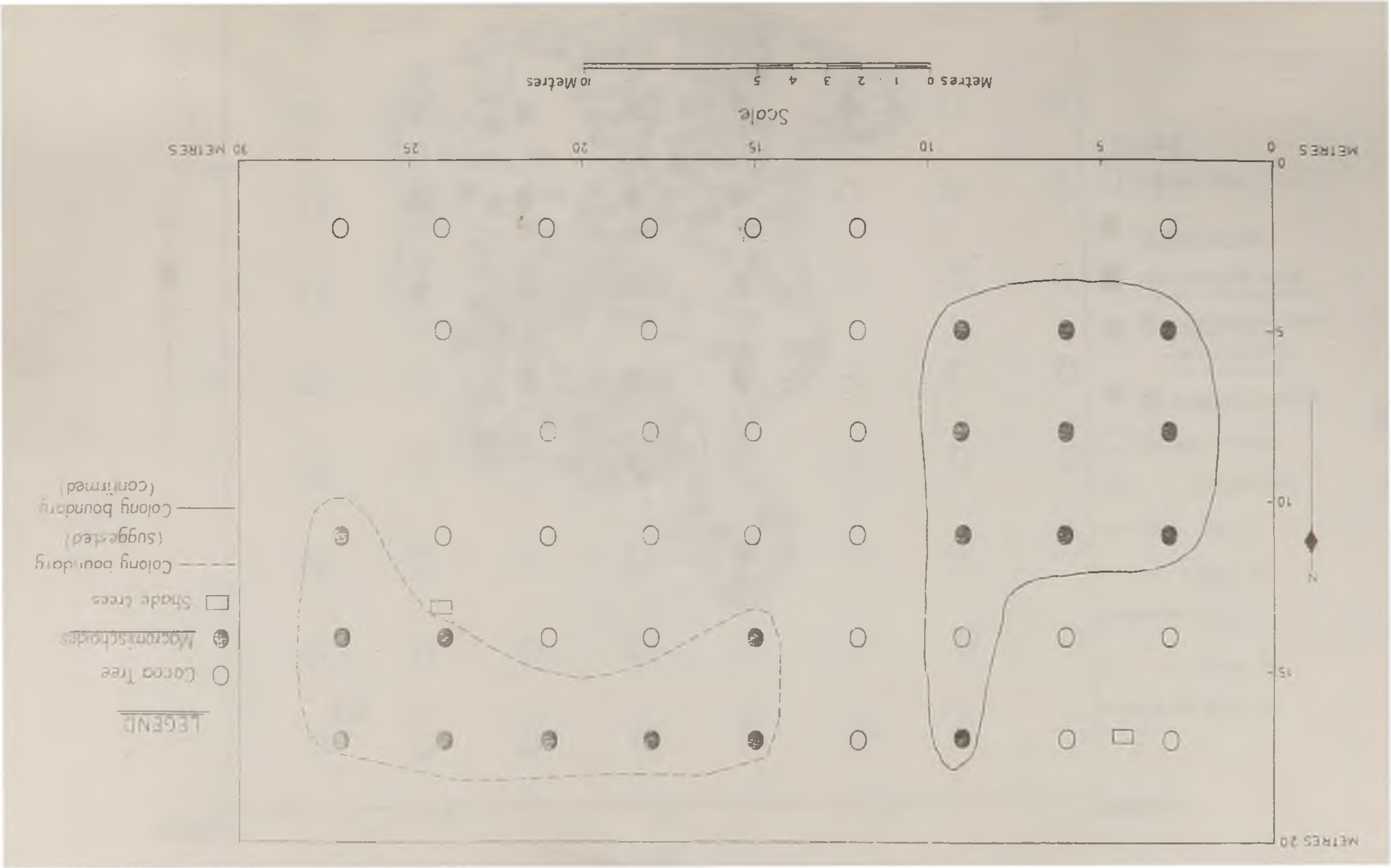


Fig.3.7: Demarcation of colony boundaries of *M. aculeatus* using radioactive sugar, Tafo, C5b, Tafo, 19th - 29th March 1971.

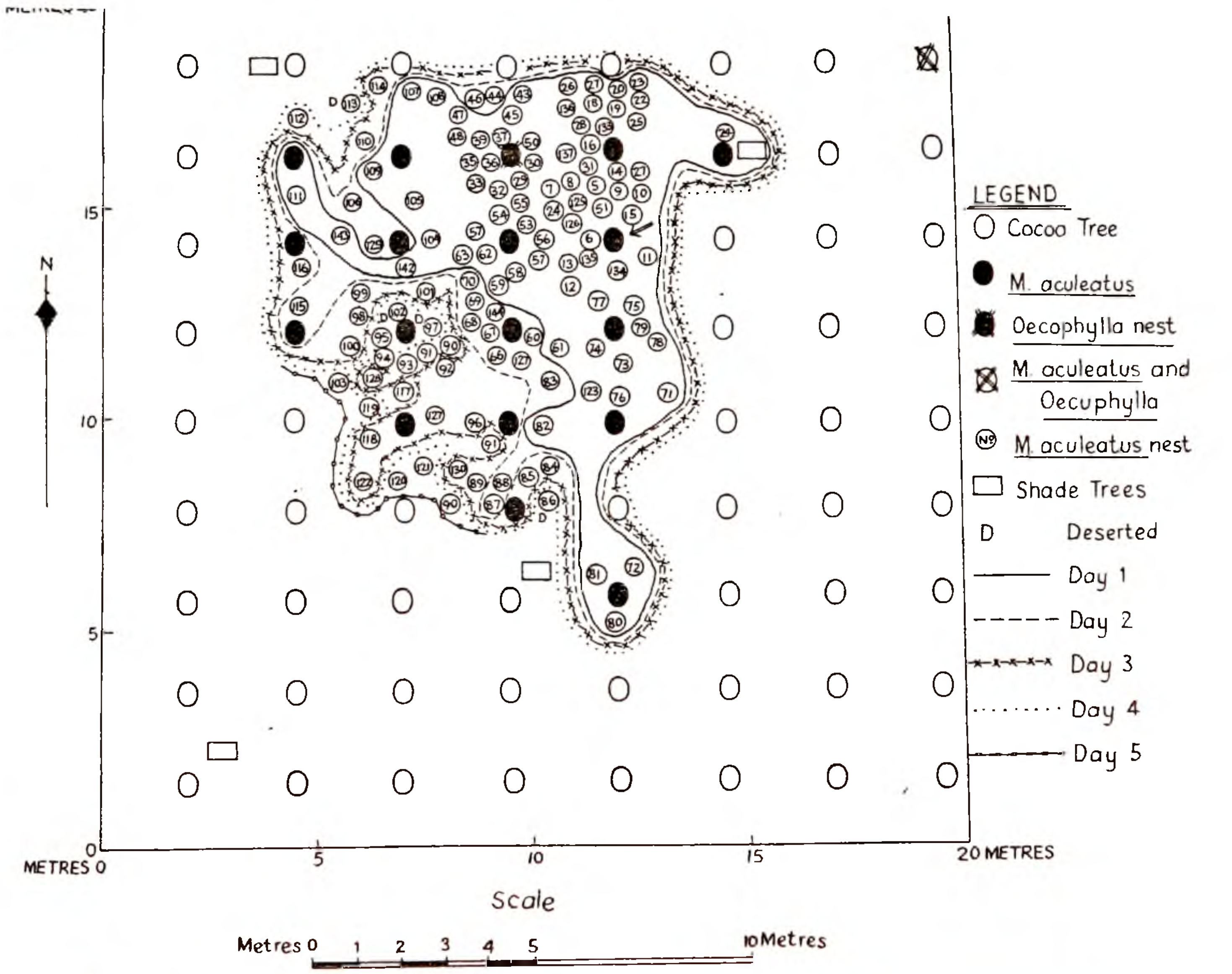


Fig.3.8: The rate of spread of radioactive sugar in a *M. aculeatus* colony in plot H10b, 19th - 29th March 1971. The arrow indicates the point of introduction of P32 sugar.

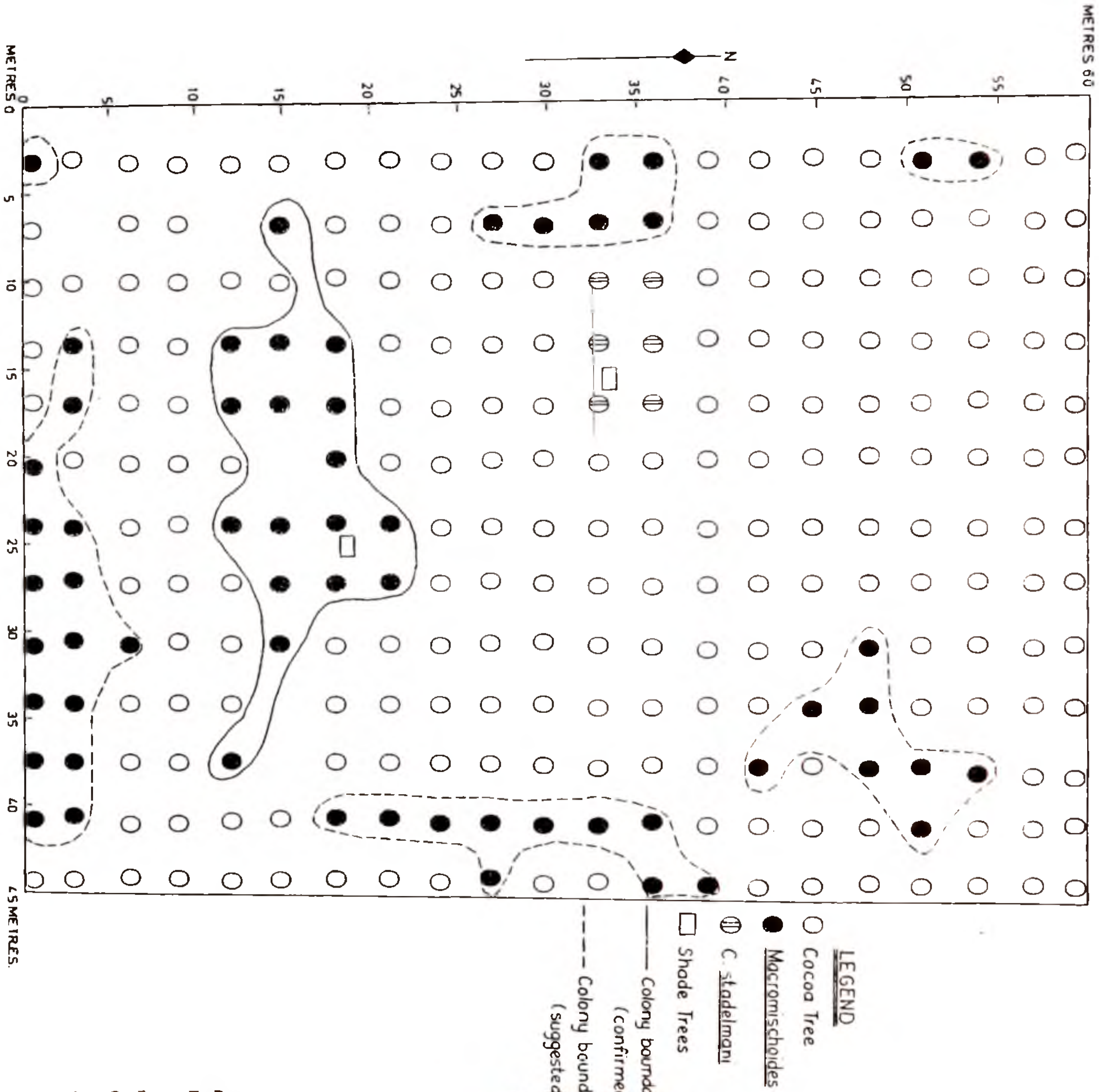


Fig.3.9: Colony boundaries of *M. aculeatus* in plot C5a, Tafo, 13th - 15th April, 1971

Table 3.5

Summary of radioactive test results

Plot	C5a	C5b	D14	H10
Total number of nests	224	77	56	144
Number of nest radioactive	74	38	54	140
Rate of spread in days	1	3	3	5

Table 3.4

Rate of spread of radioactive sugar. Trial 2

Date	No. of nest R. active in C5a
17.iv.71	74
18.iv.71	74
19.iv.71	74
22.iv.71	74
25.iv.71	74

Table 3.3

Rate of spread of the radioactive sugar. Trial 1

Date	No. of nests R. active in C5b	No. of nests R. active in H10	No. of nests R. active in D14
19.iii.71	37	92	-
20.iii.71	36	107	47
21.iii.71	38	127	53
22.iii.71	38	135	53
23.iii.71	38	140	54

alighting and for nesting sites to mated females (Billes, 1946). It is also likely that shaded cocoa trees experience less violent storms than unshaded ones. Thus ant nests in this area may be saved from storm-damage, a factor thathas been recently found to cause mass deaths to both Oecophylla and Macromischoides (Leston, personal communication). Storm-damage will be particularly high in Macromischoides which constructs nests sandwiched between leaves, since the storm can easily force the leaves apart. Once the ants fall to the ground, they become disorientated and their behaviour profoundly upset. They therefore perish by either predation or deprivation.

The maps could not define accurately colony size and colony boundaries. The radiotracer experiment achieved this in a very clear cut way. The limit of the radioactivity is the limit of a colony, since only ants from the same colony have an access to the radioactive sugar. Colony boundaries could thus be drawn with ease and the number of radioactive nests found within the demarcated area constituted the size of the colony. Colony sizes were found to be very variable indeed. By the 'acceptance-rejection' method three colonies were found to contain 2, 36 and 47 nests respectively while four colonies containing 38, 53, 74 and 140 nests respectively were identified with the radiotracer. The number of nests may depend on the age of a colony, since a colony is founded by a single queen. Obviously more mature colonies will have more nests than incipient ones. Other factors however, such as shade regimes, food availability and predators may greatly influence the size of the colony. According to Wheeler (1922) several hundreds of nests may be found on a single plant in the Congo forests. If his observation is correct, then colonies may contain several thousands of nests. The number of nests per tree in our cocoa farms is, however, very small, the highest number observed so far being twenty-three. Although actual colony size may be small the ants cover a wide area due to the small number of nests per tree. From a practical viewpoint this is an advantage, in that the ants can by this means protect many cocoa trees from capsid attack, and moreover will not hamper farm work, such as harvesting of cocoa.

Thus this work has shown that the ants nest mainly in well-shaded areas, that they are polydomous, and colonies are separated by free zones. Other findings such as number of queens per colony, rate of spread of P^{32} and relationship with other ants will be discussed subsequently.

Section 4. Seasonal population patterns.

4. SEASONAL POPULATION PATTERNS

Introduction

Periodicity of brood and adult workers and of sexual caste production of ants in temperate regions is a common phenomenon which has been reported in many cases, for example *Leptothorax* sp. by Headley (1943) and *Myrmica* sp. by Brian (1957). Brian (1957) explains that periodicity is inevitable if the life cycle of any ant is long compared with an annual climatic cycle.

In the tropics, seasonal changes in ant populations have also been reported. Ledoux (1949, quoted by Sudd, 1967) reports that though *Oecophylla longinoda* produces sexuals throughout the year in West Africa, they are more common just at the end of the rains in November. Gibbs and Leston (1970) working at Tafo, Ghana, however found the peak of *O. longinoda* alate female liberation between March and May. They also demonstrated periodicity in alate female production in *Odontomachus haematodus*.

Periodicity has not however been explicitly demonstrated in *M. aculeatus*. It can, nevertheless, be inferred from Lang's (quoted by Wheeler, 1922) statement that nests of *M. aculeatus* in the Congo, "sometimes" contained brood and winged individuals but "often" only a few workers or were empty. Billes *et al* (1946) working at Tafo noted the period of emergence of foundress queens between April and May. Apart from these casual observations no effort has been made to demonstrate the changes in the population in relation with the seasons.

The present study aims at investigating the changes in the population of M. aculeatus during the period of sampling from October 1970 to June 1971. This includes period of oviposition, changes in adult worker and worker brood populations, sexual production and population changes. An attempt will also be made to relate the population changes to the seasons as classified by Gibbs and Leston (1970).

Methods

Sampling times: Initially, from 14th October to 23rd November 1970, sampling was done at weekly intervals. This was, however, changed to fortnightly for the rest of the sampling period.

Sampling sites: Preliminary surveys were conducted to select fairly large nest aggregates since before the radioisotope experiment it was not easy to delimit colony boundaries. Thus it was not certain whether two or three nest-aggregates found in the same area belonged to one colony or different colonies. Sampling was therefore done in different nest aggregates partly due to this initial uncertainty about colony boundaries and also the smallness of the nest-aggregates. Two or three samplings in one area resulted in complete collapse of the nest aggregate. It was then necessary to move on to the next nest-aggregate and so on. Sampling was made in PH10, Blocks 1-4 and from two nest-aggregates in Plot C5a.

Sampling method: In collecting the nests, a polythene bag, measuring 30cm x 38cm was pushed half-way up a nest and held there with the mouth open. Then, with the pair of secateurs, the petiole was cut so that the leaf bearing the nest fell into the bag. The mouth of the bag was quickly held together and tied with the rubber band. By this means few or none of the agile workers was lost. When however the nest was at such a place that the bag could not be held under it, the leaf petiole was simply cut with the secateurs and dropped into the already-open bag. A few workers were sometimes lost by this method. Prior to cutting the nest a label written in pencil on a piece of paper was dropped into the bag. This bore the tree and nest numbers. Any first tree sampled on any particular date was labelled 'A'. Similarly the first nest on tree A was designated A1. Thus three nests on tree A were labelled A1, A2 and A3. Tree A of a particular date might or might not be tree A the following or subsequent sampling periods. The nests collected were packed into a bigger polythene bag, tied with a rubber band and conveyed to the laboratory.

In the laboratory the ants were killed with ethyl acetate, chloroform, Carnoy's fluid or occasionally carbon dioxide. Each bag was then opened, nest taken out and contents emptied on a large sheet of white paper. The nest was then examined under a dissecting microscope for any food remains, inquilines, or predators. The different castes and developmental stages were sorted into different petri-dishes with a forceps. A small quantity of 70% alcohol in the petri dish facilitated larval and egg sorting. These together with the nests were examined under the microscope together with the debris left after separation of the ants. Any parasites, inquilines, or food remains collected were put into 70% alcohol and labelled.

Counting: Since the ants were small and numbers obtained very large, at times running into thousands, counting was done in calibrated tubes. One hundred workers, or larvae or pupae were counted into flat-bottomed perspex tubes and marked. The rest of the tube was calibrated upon this first mark. An egg-measuring tube was also made, but it was designed to count in thousands. Queens, alate males and females, reproductive larvae and pupae were actually counted. Worker pupae and larvae were counted if their number was small. Record was then made of the various numbers obtained.

Results

The data for the population counts are given in Table 4.1. Figure 4.1 shows the graph of the mean number of workers and worker brood per nest per week or fortnight. It also contains information on oviposition and times when queens were obtained in the different sampling sites. This figure indicates that worker brood was present almost throughout the sampling period, and, with but a few fluctuations, mean adult worker population remained more or less steady throughout the period. There was however a marked drop in October,

Table 4.1

Tafo, H10b$_4$, 14.X.70

No. of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae			Larvae		Eggs
						Workers	Females	Males	Works	Reprod.	
1	A1	1,600	-	1	-	100	-	-	5	-	3,100
2	A2	250	-	-	-	4	-	-	3	-	-
3	A3	250	-	-	-	-	-	-	18	-	-
4	A4	50	-	-	-	-	-	-	2	-	-
5	A5	200	-	-	-	-	-	-	6	-	-
6	B1	50	-	-	-	-	-	-	-	-	-
7	B2	700	-	-	-	-	-	-	58	-	-
8	C1	15	-	-	-	-	-	-	-	-	-
9	C2	150	-	-	-	-	-	-	-	-	-
10	D1	300	-	-	-	100	-	-	55	-	-
11	D2	250	-	-	-	11	-	-	43	-	-
12	D3	200	-	-	-	8	-	-	54	-	-
Total		4015	-	1		223	-	-	244	-	3,100
		401.5		0.08		18.5			20.3		258.3
	SD										
	SE										

Table 4.1 (continued)

Tafo, H1Ob$_4$ 21.1.70

No. of Nest	Nest No.	Workers	Alate Females	Dealate Females	Alate Males	Pupae Workers	Pupae Females	Pupae Males	Larvae Workers	Larvae Reprod.	Eggs
1	A1	50	-	-	-	5	-	-	23	-	-
2	A2	600	-	1	-	250	-	-	127	-	2500
3	A3	600	-	3	-	50	-	-	230	-	4800
4	A4	200	-	-	-	40	-	-	5	-	15
5	A5	200	-	-	-	10	-	-	11	-	- -
6	B1	400	-	-	-	300	-	-	100	-	-
7	B2	350	-	-	-	400	-	-	43	-	-
8	C1	700	-	-	-	200	-	-	150	-	- -
9	C2	200	-	-	-	50	-	-	60	-	-
10	D1	200	-	-	-	4	-	-	3	-	20
11	D2	100	-	-	-	20	-	-	-	-	-
12	D3	13	-	-	-	-	-	-	-	-	-
13	E	150	-	-	-	5	-	-	12	-	-
14	F	200	-	-	-	100	-	-	90	-	-
15	G	250	-	-	-	10	-	-	37	-	-
16	H2	250	-	-	-	30	-	-	60	-	-
17	I1	3	-	-	-	-	-	-	-	-	-
18	I2	250	-	-	-	-	-	-	90	-	-
19	I3	100	-	-	-	21	-	-	25	-	-
		4816	-	4	-	1495			1066		7335
	$\bar{x}$	253.47		0.21		78.68			56.10		386.0
	SD										
	SE										

Table 4.1 (continued)

Fafo HMOb$_4$ 28.X.70

No. of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae Workers	Pupae Females	Pupae Males	Larvae Workers	Larvae Reprod.	Eggs
1	A1	480	-	-	-	100	-	-	60	-	-
2	B1	100	-	-	-	2	-	-	10	-	-
3	B2	800	-	-	-	700	-	-	150	-	-
4	B3	800	-	1	-	10	-	-	100	-	3000
5	B4	300	-	-	-	80	-	-	12	-	-
6	C	100	-	-	-	13	-	-	12	-	-
7	I	100	-	-	-	9	-	-	2	-	-
8	1	60	-	-	-	-	-	-	-	-	-
9	2	400	-	-	-	25	-	-	100	-	-
10	3	200	-	-	-	40	-	-	35	-	-
11	4	500	-	-	-	50	-	-	53	-	-
12	F	600	-	-	-	150	-	-	552	-	-
13	G	100	-	-	-	-	-	-	4	-	-
		4460	-	1	-	1179			600		3000
	$\bar{x}$	343.07		0.07		90.69			46.15		230.76
	D										
	SE										

Tafo, $H10b_4$, 2.XI.70

Nol of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae			Larvae		Eggs
						Worker	Females	Males	Workers	Reprod.	
1	A1	500	-	-	-	300	-	-	300	-	-
2	A2	50	-	-	-	30	-	-	100	-	-
3	B1	200	-	-	-	200	-	-	20	-	-
4	B2	180	-	1	-	100	-	-	8	-	150
5	C	150	-	-	-	100	-	-	70	-	-
6	D	40	-	-	-	4	-	-	10	-	-
7	E	100	-	-	-	150	-	-	14	-	-
8	F	250	-	-	-	150	-	-	40	-	-
9	G	180	-	-	-	3	-	-	5	-	-
10	H1	50	-	-	-	1	-	-	4	-	-
11	H2	250	-	-	-	50	-	-	40	-	-
		1950		1		1588			711		150
	$\bar{x}$	177.27		0.09		144.36			64.6		13.63
	SD										
	SE										

Table 4.1 (continued)

Tafo, H10b$_4$, 2.XI.70

Nol of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae			Larvae		Eggs
						Worker	Females	Males	Workers	Reprod.	
1	A1	500	-	-	-	300	-	-	300	-	-
2	A2	50	-	-	-	30	-	-	100	-	-
3	B1	200	-	-	-	200	-	-	20	-	-
4	B2	180	-	1	-	100	-	-	8	-	150
5	C	150	-	-	-	100	-	-	70	-	-
6	D	40	-	-	-	4	-	-	10	-	-
7	E	100	-	-	-	150	-	-	14	-	-
8	F	250	-	-	-	150	-	-	40	-	-
9	G	180	-	-	-	3	-	-	5	-	-
10	H1	50	-	-	-	1	-	-	4	-	-
11	H2	250	-	-	-	50	-	-	40	-	-
		1950		1		1588			711		150
	$\bar{x}$	177.27		0.09		144.36			64.6		13.63
	SD										
	SE										

Table 4.1 (continued)

Tafo, H10b$_3$, 17.XI.70

No. of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae Workers	Pupae Females	Pupae Males	Larvae Workers	Larvae Reprod.	Eggs
1	A1	100	-	-	-	50	-	-	6	-	-
2	A2	400	-	-	-	100	-	-	100	-	-
3	A3	280	-	-	-	40	-	-	20	-	-
4	A4	300	-	-	-	9	-	-	200	-	-
5	A5	60	-	-	-	-	-	-	2	-	-
6	A6	400	-	-	-	300	-	-	180	-	-
7	A7	1100	-	-	-	200	-	-	100	-	-
8	A8	250	-	-	-	6	-	-	50	-	-
9	A9	300	-	-	-	800	-	-	500	-	-
10	A10	350	-	-	-	200	-	-	150	-	300
		3540				1705			1308		300
	$\bar{x}$	354				170.5			130.8		30.0
	D										
	SE										

Table 4.1 (continued)

Tefo, H10b$_1$ & b$_3$, 23.XI.70

No. of Nest	Nest No.	Workers Females	Alete Females	Delate Females	Alete Male	Pupae			Larvae		Eggs
						Workers	Females	Males	Workers	Reprod.	
1	A1	1200	-	-	-	900	-	-	600	-	-
2	A2	600	-	-	-	200	-	-	200	-	-
3	B1	1000	-	-	-	400	-	-	200	-	-
4	B2	100	-	-	-	100	-	-	90	-	-
5	C1	250	-	-	-	-	-	-	20	-	-
6	C2	40	-	-	-	-	-	-	1	-	-
7	C3	7	-	-	-	-	-	-	-	-	-
8	C4	10	-	-	-	-	-	-	-	-	-
9	C5	40	-	-	-	4	-	-	1	-	-
10	C6	200	-	-	-	300	-	-	13	-	-
11	C7	20	-	-	-	-	-	-	-	-	-
12.	C8	120	-	-	-	-	-	-	24	-	-
13	C9	400	-	-	-	40	-	-	100	-	-
14	C10	400	-	-	-	10	-	-	150	-	-
		4387				1954			1379		
	$\bar{x}$	313.35				139.57			98.50		

Table 4.1 (continued)

Tafo, H10b$_1$ & b$_3$ 7.XII.70

No. of Nest	Nest No.	Workers	Alate Females	Dealate Females	Alate Males	Pupae Workers	Pupae Females	Pupae Males	Larvae Workers	Larvae Reprod.	Eggs
1	A1	450	-	-	-	250	-	-	84	-	-
2	A2	1000	-	-	-	100	-	-	32	-	-
3	A3	800	-	-	-	200	-	-	180	-	-
4	B1	750	-	-	-	175	-	-	150	-	-
5	B2	400	-	-	-	38	-	-	95	-	-
6	C1	900	-	-	-	30	-	3	70	21	-
7	C2	300	-	-	-	23	1	3	38	12	-
8	C3	180	-	-	-	1	-	-	8	-	-
9	C4	300	-	-	-	27	7	9	23	15	-
10	C5	40	-	-	-	10	-	2	5	-	-
11	C6	200	-	-	-	100	2	1	9	7	-
12	D1	1100	-	-	-	30	2	1	55	15	-
13	D2	300	-	-	-	1	-	-	- -	-	-
14	D3	280	-	-	-	-	-	-	22	-	-
15	D4	150	-	-	-	18	2	1	8	7	-
16	D5	300	-	-	-	120	6	15	27	14	-
		7450				1123	20	35	806	91	
	$\bar{x}$	465.62				70.18	1.25	2.18	50.37	5.68	

Table 4.1 (continued)

Tafo, H10b_1 & b_3 21.XII.70

No. of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae Workers	Pupae Females	Pupae Males	Larvae Workers	Larvae Reprod.	Eggs.
1	A1	500	-	-	-	150	-	-	95	-	-
2	A2	400	-	-	-	150	-	-	130	-	-
3	A3	50	-	-	-	30	-	-	5	-	-
4	B1	950	-	-	-	250	-	-	100	-	-
5	B2	550	-	-	-	200	-	-	150	-	-
6	C1	1000	1	-	1	150	2	4	4	7	-
7	C2	300	3	-	1	350	9	41	-	14	-
8	C3	100	3	-	-	10	5	8	-	-	-
9	C4	7	-	-	-	-	-	-	-	1	-
10	C5	3	-	-	-	-	-	-	-	-	-
11	C6	400	7	-	4	150	7	20	1	-	-
12	C7	500	-	-	-	20	-	7	-	2	-
13	C8	1300	5	-	4	300	13	56	5	8	-
14	C9	1600	23	-	1	200	7	46	8	34	-
15	C10	400	2	-	1	100	2	17	6	6	-
		7700	44		12	2060	45	199	504	72	
	$\bar{x}$	513.3	2.9		0.80	137.3	3.0	13.26	33.6	4.80	

Table 4.1 (continued)

Tafo, H10b$_1$ & b$_3$, 4.I.71

No. of Nests	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae Workers	Pupae Females	Pupae Males	Larvae Workers	Larvae Reprod.	Eggs
1	A1	250	-	-	-	120	-	-	48	-	-
2	B1	20	-	-	-	-	-	-	-	-	-
3	B2	450	-	-	-	400	-	-	250	-	-
4	B3	80	-	-	-	11	-	-	-	-	-
5	C	1400	-	-	-	300	-	-	380	-	-
6	D1	200	-	-	1	8	-	1	-	-	-
7	D2	250	1	-	13	14	-	-	-	-	-
8	D3	600	7	-	4	1	-	5	-	-	-
9	D4	300	20	-	32	8	2	8	- -	-	-
10	D5	100	2	-	1	2	-	2	-	-	-
		3650	30		51	864	2	16	678	-	-
	$\bar{x}$	365.0	3.0		5.1	86.4	0.2	1.6	67.8		

Table 4.1 (continued)

Tefo, H10b_1 & b_3, 18.I.71

No. of Nests	Nest No.	orkers	Alate Females	Delate Females	Alate Males	Pupae Workers	Pupae Females	Pupae Males	Larvae Workers	Larvae Reprod.	Eggs
1	A1	800	-	-	-	50	-	-	400	-	-
2	A2	1600	-	-	-	500	-	-	350	-	-
3	B1	50	-	-	-	2	-	-	1	-	-
4	B2	900	-	2	-	5	-	-	60	-	2500
5	C1	600	2	-	24	- -	-	-	-	-	-
6	C2	100	-	-	1	- -	-	-	-	-	-
7	D1	300	2	-	8	-	-	-	-	-	-
8	D2	180	2	-	-	-	-	-	-	-	-
9	E1	400	22	-	101	1	-	5	-	-	-
10	E2	250	-	-	4	-	-	-	-	-	-
11	E3	300	4	-	19	1	-	-	-	-	-
12	E4	200	9	-	35	-	1	2	-	-	-
13	D1	400	8	-	17	-	-	1	-	-	-
14	D2	50	-	-	-	-	-	-	-	-	-
		6130	49	2	209	559	1	8	811	-	2500
	$\bar{x}$	437.8	3.5	0.14	14.9	23.99	0.07	0.57	57.92	-	178.5

Table 4.1 (continued)

Tafo, H10b$_1$ & b$_3$, I.II.71

No. of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae			Larvae		Eggs
						Workers	Females	Males	Workers	Reprod.	
1	A1	250	-	-	-	-	-	-	20	-	-
2	B2	600	-	-	-	600	40	11	90	64	-
3	B2	50	-	-	-	-	-	-	-	-	-
4	B3	450	-	-	-	100	-	-	30	5	-
5	B4	200	-	-	-	8	-	-	5	-	-
6	B5	500	-	-	-	300	3	2	35	11	-
7	B6	500	-	-	-	100	5	1	100	40	-
8	C1	480	-	-	-	15	6	3	20	36	-
9	C2	600	-	-	-	200	45	18	30	90	-
10	C3	400	-	-	-	150	18	14	24	30	-
11	D1	90	-	-	-	-	-	-	-	-	-
12.	D2	300	-	-	-	-	-	-	-	-	-
13	D3	900	3	-	2	- -	-	-	-	-	-
14	D4	500	-	-	-	-	-	-	-	-	-
15	E1	20	-	-	-	-	-	-	-	-	-
16	E2	400	-	-	-	-	-	-	-	-	-
17	E3	100	-	-	-	-	-	-	-	-	-
18	F1	900	1	-	1	-	-	-	-	-	-
19	F2	1500	1	-	-	-	-	-	-	-	-
20	F3	50	1	-	-	-	-	-	-	-	-
		8790	6	-	3	1473	117	49	354	276	
	$\bar{x}$	439.5	0.30		0.15	73.65	5.85	2.45	17.7	13.8	

Table 4.1 (continued)

Tafo, H10b$_1$ & b$_2$, 15.II.71

No. of Nest	Nest No.	Workers	Alate Females	Dealate Females	Alate Males	Pupae			Larvae		Eggs
						Workers	Females	Males	Workers	Reprod.	
1	A1	600	-	-	1	250	83	108	9	3	-
2	A2	300	-	-	-	14	4	13	16	6	-
3	B1	1600	1	-	2	200	138	232	74	68	-
4	B2	700	35	-	14	130	73	184	65	84	-
5	C1	1300	-	-	-	-	-	-	-	-	-
6	C2	100	-	-	-	-	-	-	-	-	-
7	C3	200	-	-	-	-	-	-	-	-	-
8	C4	80	-	-	-	-	-	-	-	-	-
9	D1	50	-	-	-	-	-	-	-	-	-
10	D2	200	-	-	-	-	-	-	-	-	-
11	E1	50	-	-	-	-	-	-	-	-	-
		5180	36		17	594	298	537	164	161	
	$\bar{x}$	470.9	3.27		1.54	54.0	27.09	48.81	14.90	14.63	

Table 4.1 (continued)

Tafo, H10b$_2$,a b I.III.71

No. of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae			Larvae		Eggs
						Workers	Females	Males	Workers	Reprod.	
1	A1	400	12	-	33	25	45	188	63	150	-
2	A2	250	5	-	18	31	20	53	15	68	-
3	A3	450	14	-	22	50	68	191	32	72	-
4	B1	400	3	-	18	28	35	80	95	103	-
5	C1	550	9	-	36	145	40	92	89	57	-
6	C2	200	6	-	83	12	25	6	19	18	-
7	C3	350	8	-	66	19	28	4	33	21	-
8	C4	380	6	-	39	68	54	18	45	94	-
9	D1	450	11	-	56	46	15	32	16	85	-
		3430	74		371	424	330	664	407	668	
	$\bar{x}$	381.11	8.22		41.2	47.11	36.6	73.77	45.22	74.2	

Table 4.1 (continued)

Tafo, H10b$_2$, 15.III.71

No. of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae			Larvae		Eggs
						Workers	Females	Males	Workers	Reprod.	
1	A1	400	20	-	42	35	12	33	72	14	-
2	A2	250	48	-	35	27	8	14	30	18	-
3	A3	600	75	-	160	38	25	83	88	75	-
4	B1	450	54	-	132	16	4	39	42	23	-
5	B2	380	38	-	73	20	9	45	18	25	-
6	C1	500	35	-	120	43	15	73	65	13	-
7	C2	200	6	-	83	12	6	21	19	18	-
8	C3	450	25	-	94	33	18	33	45	23	-
9	D1	500	13	-	115	35	18	45	43	166	-
10	D2	350	8	-	66	19	9	28	33	21	-
		4080	322		920	278	124	414	455	246	
	$\bar{x}$	408.0	32.2		92.0	27.8	12.4	41.4	45.5	24.6	
	SD										
	SE										

Table 4.1 (continued)
Tafo, $H10b_2$, 29.III.71

No. of Nest	Nest No.	Workers	Alate Females	Dealate Females	Alate Males	Pupae Workers	Pupae Females	Pupae Males	Larvae Workers	Larvae Reprod.	Eggs
1	A1	500	8	-	34	15	25	88	81	19	-
2	A2	300	12	-	30	4	3	17	53	20	-
3	A3	550	15	-	60	2	20	78	28	5	-
4	B1	300	4	-	20	6	1	7	43	14	-
5	B2	450	7	-	21	24	20	44	85	15	-
6	B3	500	10	-	54	45	17	195	92	98	-
7	C1	400	13	-	25	30	25	150	29	68	-
8	C2	400	6	-	6	2	1	3	46	44	-
9	C3	300	2	-	53	4	13	70	59	25	-
10	D	250	7	-	64	3	24	69	25	15	-
		3950	84		367	135	152	721	541	323	
	$\bar{x}$	395.0	8.4		36.7	13.5	15.2	72.1	54.1	32.3	
	SD										
	SE										

Table 4.1 (continued)

Tafo, C5a, 13.IV. 71

No. of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae Workers	Pupae Females	Pupae Males	Larvae Workers	Larvae Reprod.	Eggs
1	A1	250	7	-	35	5	-	1	24	-	-
2	A2	600	1	-	8	5	2	9	53	10	-
3	B1	300	2	-	43	4	-	16	17	1	-
4	C1	400	4	-	130	4	1	8	42	6	-
5	C2	200	1	-	145	3	-	-	9	-	-
6	C3	400	23	-	176	30	[illegible]	2	52	14	-
7	C4	400	19	-	60	6	-	7	14	-	-
8	C5	200	17	-	39	83	18	41	23	-	-
9	C6	1200	144	-	302	100	24	72	40	5	-
		3950	218	-	938	240	43	156	274	36	
	$\bar{x}$	438.8	24.2		104.2	26.6	4.7	17.3	30.4	4.0	
	SD										
	SE										

Table 4.1 (continued)

Tafo C5a, 26.IV.71

No. of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae			Larvae		Eggs
						Workers	Females	Males	Workers	Reprod.	
1	A1	300	7	-	50	11	1	6	18	6	-
2	A2	150	2	-	60	13	-	16	3	-	-
3	A3	200	-	-	28	35	2	37	13	-	-
4	A4	500	7	-	49	25	14	102	62	4	-
5	B1	300	5	-	155	19	8	41	12	-	-
6	B2	450	4	-	75	17	2	13	14	-	-
7	C	550	19	-	63	15	-	-	108	12	-
8	D1	350	3	-	154	13	42	235	18	2	-
9	D2	250	4	1	7	25	-	-	35	-	600
10	D3	400	33	-	344	50	15	90	20	-	-
		3450	84	1	985	223	84	540	303	18	600
	$\bar{x}$	345.0	8.4	0.1	98.5	22.3	8.4	54.0	30.3	1.8	60.0
	SD										
	SE										

Table 4.1 (continued)

Tafo, C5aI, 10.V.71

No. of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae			Larvae		Eggs
						Workers	Females	Males	Workers	Reprod.	
1	A1	150	2	-	1	4	1	15	-	-	-
2	A2	400	10	-	84	8	3	22	-	-	-
3	A3	20	1	-	-	1	1	-	-	-	-
4	A4	500	15	-	115	9	10	77	2	-	-
5	B1	30	2	-	16	7	7	21	-	-	-
6	B2	30	6	-	14	7	5	2	-	-	-
7	C1	700	8	-	79	8	4	26	-	-	-
8	C2	1100	25	-	115	20	17	82	-	-	-
9	D1	1300	25	-	206	30	10	94	-	-	-
10	D2	45	13	-	24	7	4	31	-	-	-
		4275	107		654	101	60	370	2		
	$\bar{x}$	427.5	10.7		65.4	10.1	6.0	37.0	0.2		
	S.D										
	S.E										

Table 4.1 (continued)

Tafo, C5aI 25.V.71

No. of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae Workers	Pupae Females	Pupae Males	Larvae Workers	Larvae Reprod.	Eggs.
1	A1	10	-	-	-	-	-	-	-	-	-
2	A2	250	-	-	-	-	-	-	-	-	-
3	B1	200	-	-	-	-	-	-	-	-	-
4	B2	250	11	-	70	-	-	-	-	-	-
5	B3	100	2	-	11	-	-	-	-	-	-
6	C1	600	-	-	-	8	-	-	-	-	-
7	C2	50	1	-	1	-	-	-	-	-	-
8	C3	180	5	-	2	-	-	-	-	-	-
9	C4	600	21	-	36	-	-	-	-	-	-
10	D1	900	37	-	254	-	-	-	-	-	-
		3140	77		374	8					
	$\bar{x}$	314.0	7.7		37.4	0.8					
	SD										
	SR										

Table 4.1 (continued)

Tafo, C5a II, 7.VI.71

No. of Nest	Nest No.	Workers	Alate Females	Delate Females	Alate Males	Pupae			Larvae		Eggs
						Workers	Females	Males	Workers	Reprod.	
1	A1	25	1	-	—	4	-	-	-	-	-
2	B1	475	3	-	-	69	-	-	-	-	-
3	C1	1200	1	-	1	35	-	-	-	-	-
4	D1	900	2	-	7	150	-	-	-	-	-
55	D2	300	5	-	4	-	-	-	-	-	-
6	D3	40	2	-	1	10	-	-	-	-	-
7	E1	350	3	-	8	13	-	-	-	-	-
8	E2	50	-	-	6	4	-	-	-	-	-
		3340	17		27	285	-	-	-	-	-
	$\bar{x}$	417.5	2.1		3.4	35.6	-	-	-	-	-
	SD										
	SE										

Table 4.1 (continued)

Tafo, G5a II, 30.VI.71

No. of No.	Nest No.	Workers	Alate Females	Dealate Females	Alate Males	Pupae Workers	Pupae Females	Pupae Males	Larvae Workers	Larvae Reprod.	Eggs
1	A1	300	4	-	2	51	-	-	4	-	-
2	A2	100	-	-	4	10	-	-	2	-	-
3	B1	400	2	-	16	200	-	-	15	-	-
		800	6		22	261			21		
	$\bar{x}$	233.3	2.0		7.3	87.0			7.0		
	SD										
	SE										

Fig 4.1

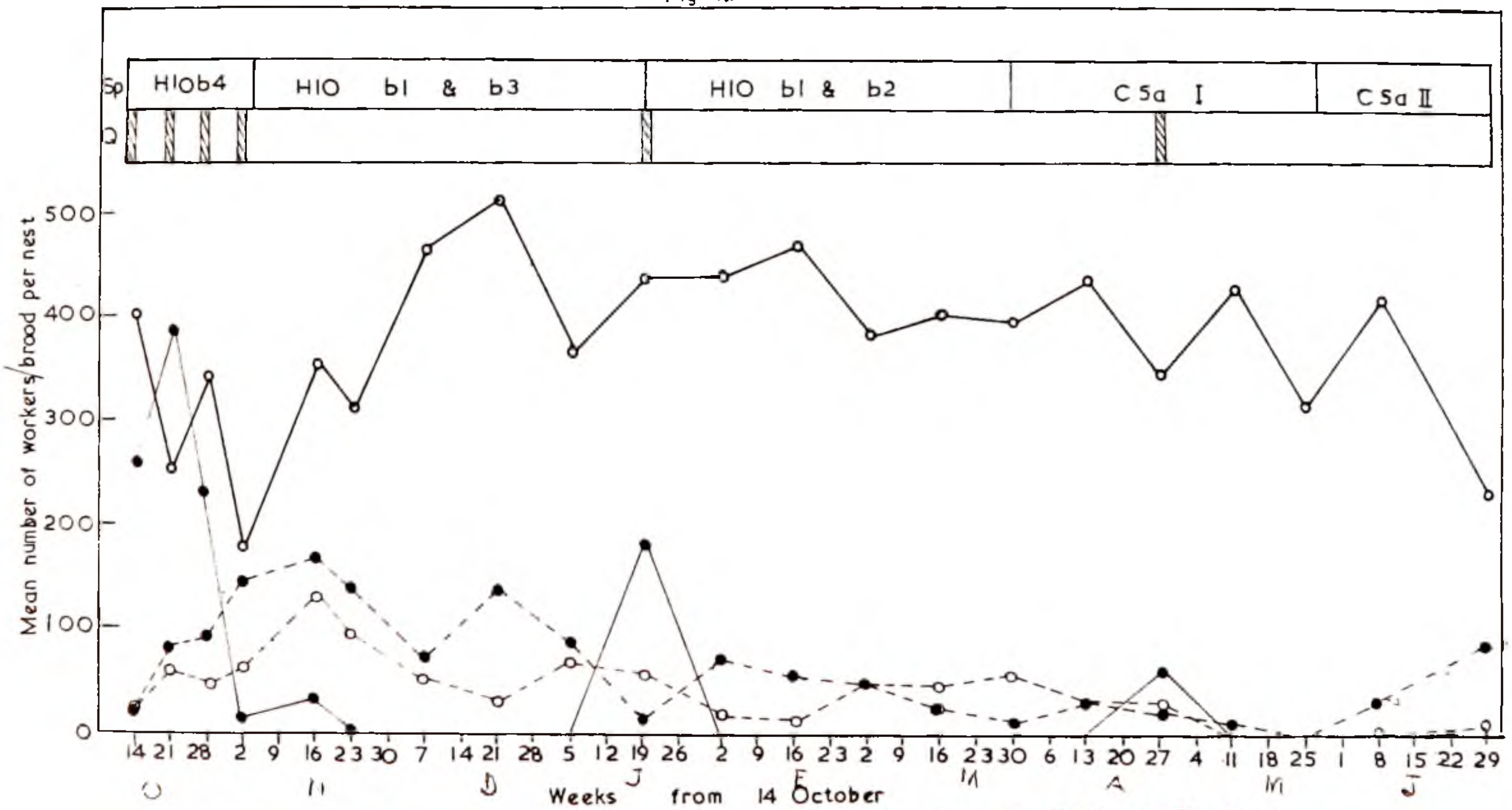


Fig.4.1: Seasonal distribution of workers and worker-brood of *M. aculeatus*. (o——o, adult workers; ●-----●, worker pupae; o-----o, worker larvae; ●——●, eggs). Sp: Sampling plots; Q: cross hatching indicates dealate queen found in destructive sampling.

followed by a steady build-up to a peak in December, then a slight drop in January after which the population was maintained at a nearly steady level, until it started fluctuating widely in May with a sharp drop in June.

Pupae alternate, more or less, with adults. Pupal production started at a high peak between October and December but declined gradually till it reached nearly zero in May. With a few discrepancies, larvae alternated with pupae. Fig. 4.1 shows also that large numbers of eggs were obtained in October, very few in November and fairly large numbers in January and May. In all nine queens were collected. Six of these were obtained in plot H10b4, one in H10b1 and b2, and two in C5a. With the exception of H10b1 and b3, eggs were obtained each time a queen was found.

Fig. 4.2 shows the seasonal changes in sexual caste population. It demonstrates a strong periodicity. Sexual caste production started in December, reached a maximum between March and May, and declined nearly to zero in June. Build-up of both adult and immature sexual individuals was usually followed by a sharp decline in their numbers.

Initially alate females were more abundant than males. Female population growth was gradual and drawn-out as compared with the more or less exponential build-up of males. Thus very soon the males outnumbered the females by varying ratios, but at the peak it is about 4:1.

Male and female pupae alternated with male and female adults respectively. Larvae also alternated with pupae.

Fig 4.2

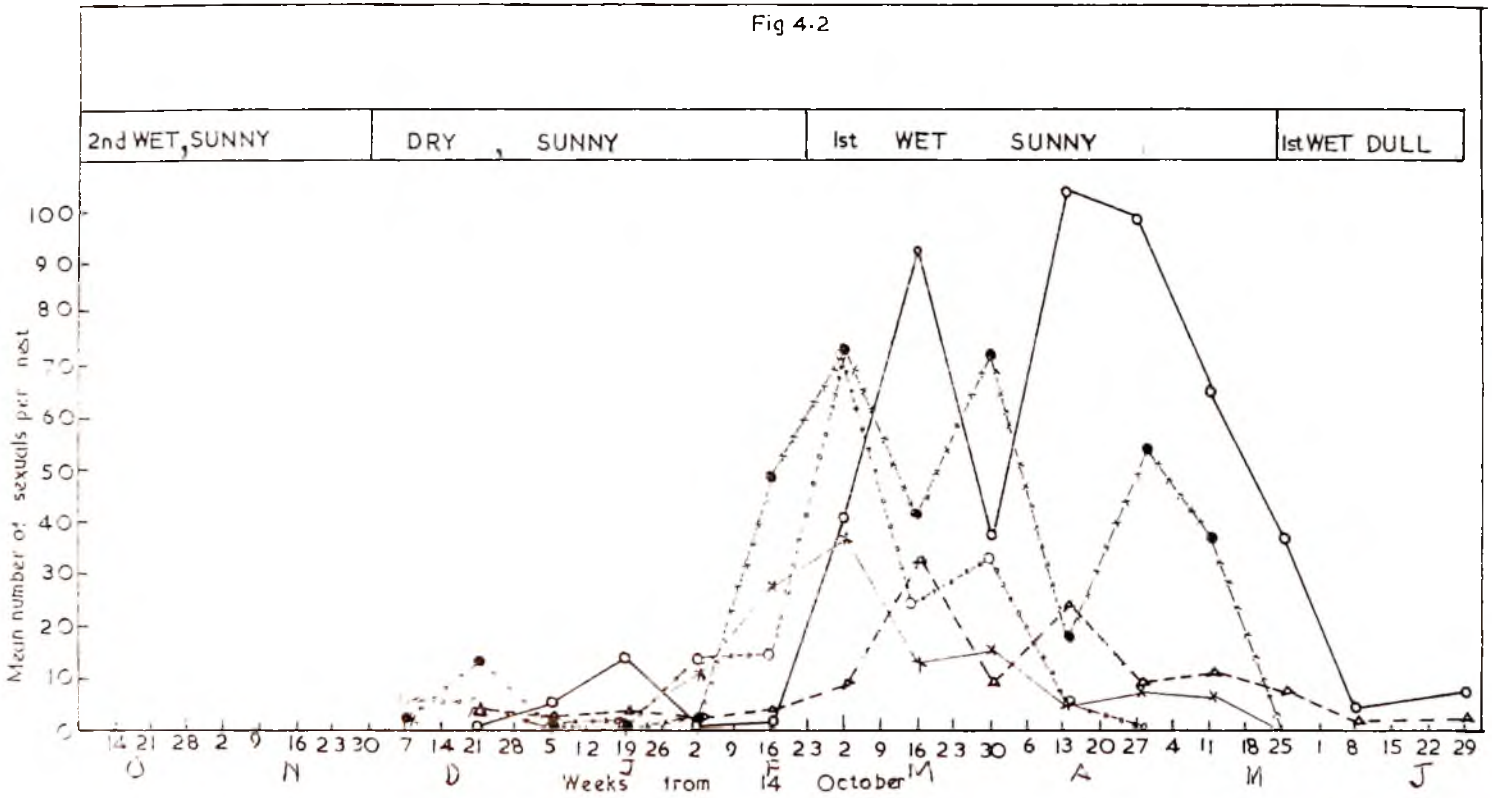


Fig.4.2: The seasons; and seasonal distribution of alates and sexual-brood of *M. aculeatus*. (o—o—o, alate males; △—△—△, alate females; x—x—x, male pupae; •-x-•-x-•, female pupae; o...o...o, male and female larvae).

The greatest production of sexuals was in the first Wet sunny season, but their development started earlier in the first Dry sunny season.

Discussion

The results demonstrate a periodicity in sexual caste production beyond all reasonable doubt. The present finding that sexuals have a peak between March and May agrees with Bille's (1946) earlier observation. This period falls within the first wet, sunny season of Gibbs and Leston's classification. The large flush that occurs early in this season may produce large leaves which may be retained for eight or nine months. Since according to Nicol (1944) the size and the retention period of leaves are major factors that determine colonization of *M. aculeatus* this season would be an ideal one. Moreover the large range of insects (Gibbs and Leston, 1970) available during this season will ensure an abundant food supply for the developing and developed sexuals as well as their attendant workers. Further, considering the fact that the ants are largely markedly photophobic, the first wet, dull season which immediately follows sexual production, development and liberation, will afford them more hours of activity, since cloud cover is maximal during this season. The wide fluctuations in adult alate populations may denote flight periods.

Worker caste population was maintained at a relatively high level throughout the sampling period. This is understandable, for the worker must be there to prepare for the advent of the sexuals and when they arrive the workers are still needed to nurse and feed them. Any large decline in their numbers will therefore affect the entire colony adversely. It is interesting that unlike the adult worker population, worker brood numbers dropped with the production of sexuals, but were maintained at low levels nearly throughout the period.

The fact that eggs were not obtained throughout the sampling period does not necessarily mean that oviposition is periodic. Since Macromischoides is largely monogynous removal of the queen from a colony early during the sampling period would mean that no more eggs would be obtained in subsequent collections. If it had been possible to identify the queen's nest and leave it uncut or had the sampling method not been destructive a different result might have been obtained.

It is interesting that the eggs laid early in the sampling period developed only into workers, except at the beginning of the first dry sunny season in December when sexuals were produced. Schneirla (1957) found a similar situation in the genus Eciton, a New World Dorylinae. Gibbs and Leston (1970) have suggested that the high temperatures in the dry sunny season might 'accelerate' the development of sexual larvae of Oecophylla longinoda. This may, perhaps, be the explanation for the production of sexual brood of Macromischoides in the dry season.

In view of the destructive nature of sampling and the fact that I moved from one colony to another as necessary, no valid or meaningful inferences can be made on brood population fluctuations from the graphs.

So far it has not been possible to determine the duration of all the different larval instars in the laboratory. Nor, unfortunately, can much be learnt from Figs.4.1 and 4.2 about this subject.

Section 5. Diurnal activity pattern, food and foraging habits.

5. DIURNAL ACTIVITY PATTERN, FOOD AND FORAGING HABITS

Introduction

Works on ant diurnal activity, food andforaging habits are now very numerous. The few to be mentioned include the works of Duncan-Weatherley (1953), Ayre (1958) and Leston (1968) on daily activities of different ant species. Notable among the workers on ant foraging or hunting are Brian (1955), Vowlès (1955) and Wallis (1964). Lange ((1960 cited by Sudd, 1967), Chauvin et al (1961) and Wallis (1962) have also worked on food traffic among ants. Works on scent trails and trail laying by Carthy (1951), Wilson (1959) and Sudd (1967) are also well-known. There are, however, no data on this matter specifically referring to Macromischoides aculeatus. The present study attempts to provide information on this subject.

Ants are well known to have fluctuating peaks of activity. Some species may have one peak of activity in 24 h, which may be either in the day or during the night; others may have two or several peaks a day.

Several attempts have been made to determine the environmental factors that directly or indirectly influence this activity pattern. Some authors have gone even further to suggest that there is an innate rhythm of activity. Cloudsley-Thompson (1953) and Pittendrigh and Bruce (1957) claim that the activity rhythms in Periplaneta and Drosophila respectively are temperature dependent.

In *Formica subnitens*, Ayre (1958) found that light and humidity were the significant factors but he could not differentiate their effect from temperature and atmospheric pressure since they were all interrelated under field conditions. Another worker, such as Schneirla (1944) has linked activity patterns with the presence or absence of brood-eggs, larvae and pupae. The presence of brood, he claims, always causes high activity in a colony, since the brood acts as a drain on food reserves of the colony. Wheeler (1910) just called the responsible stimulus 'hunger', and claimed that it was one of the main stimuli to increased activity.

In this study the possible meteorological factors, such as air temperature, relative humidity, and light intensity as well as other environmental factors, i.e. presence or absence of predators that may influence daily activity pattern have been examined.

Materials and methods

Ten nests were selected randomly from a colony and labelled A, B, C .....J. Census points were established about one foot away from the nest on the branch bearing the nest. All connections with the nest other than the selected census point were severed. These preparations were made a day previous to the day of counting. Hourly counts were made of all ants passing the census point during a period of five minutes using a tally counter. Atmospheric temperature and relative humidity were recorded with a'Moisture content meter' and light intensity with "Weston Master V" exposure meter.

Continuous 24 h counts were made. Three replicates were made on different dates and in different plots or blocks; one during the dry season and two in the wet season. To investigate the influence of other dominant ants on the activity pattern, one 24-h count was made in plot D14, where _Macromischoides aculeatus_ and _Crematogaster clariventris_ occurred together on the same trees. The results of the activity counts and observations on food and foraging habits are given below.

Results and observations

Activity pattern: The results of the activity counts are given in Tables 5.1 - 5.5, and Figs. 5.1 - 5.5. They indicate that the ants are mainly crepuscular and nocturnal in their activity. In the absence of _Crematogaster clariventris_ activity starts at about 15.00 hours rising to a peak at 17.00 hours and may continue either steadily throughout the night (Fig.5.1), or show a steady decline (Fig.5.2). Peak activity was found to be very variable. In one case it was between 17.00 and 18.00 hours. (Fig.5.1) whilst in another it fell between 18.00 and 23.00 hours (Figs.5.2 and 5.3). The period of low activity was between 09.00 hours to 15.00 hours. This coincides with periods of high temperatures and light intensities, and low relative humidities. Activity build-up usually followed a rise in relative humidity and fall in atmospheric temperature and light intensity (Figs. 5.1 - 5.3).

There is a change in this activity pattern in presence of _Crematogaster clariventris_. Unlike the _clariventris_ free areas

Table 5.1

Macromischoides count 14.xii.71

Time	Nests										Total	Weather	
	A	B	C	D	E	F	G	H	I	J		Temp. oF	Hum. %
7.00	38	0	84	28	152	0	6	0	0	37	245	73	100
8.00	26	0	74	13	38	0	0	0	1	13	165	75	100
9.00	8	0	29	16	20	0	1	0	1	3	78	79	100
10.00	5	0	10	1	3	0	0	0	0	7	26	83	100
11.00	13	0	80	0	14	0	8	1	1	7	124	88	82
12.00	6	0	17	7	9	0	0	4	14	8	65	90	70
13.00	9	0	20	5	10	0	1	0	0	14	59	93	70
14.00	4	0	6	2	36	0	0	2	0	5	55	91	78
15.00	10	0	8	8	1	0	0	0	0	3	30	90	80
16.00	6	0	12	29	134	0	2	6	0	47	236	82	86
17.00	19	0	249	71	123	0	6	9	0	51	594	79	100
18.00	39	8	155	50	219	2	5	41	1	36	556	75	100
19.00	51	0	45	28	155	3	3	20	1	10	316	73	100
20.00	111	0	54	35	119	0	18	3	1	6	347	72	100
21.00	87	1	81	29	93	3	42	0	2	14	352	70	100
22.00	131	7	105	14	90	2	30	6	1	22	408	70	100
23.00	94	1	60	73	96	4	44	4	5	5	386	70	100
24.00	40	2	85	40	87	4	90	0	0	0	348	70	100
1.00	79	10	72	36	80	4	54	2	1	23	361	70	100
2.00	90	2	86	21	124	4	90	0	20	16	453	72	100
3.00	72	16	41	28	143	4	70	2	0	41	417	71	100
4.00	49	0	15	25	73	6	137	3	42	6	356	71	100
5.00	51	6	57	32	185	15	16	5	6	13	426	70	100
6.00	64	15	71	8	150	6	37	3	0	18	372	71	100
Total	1102	68	1516	599	2154	47	660	111	97	405	6759		

Table 5.2

Macromischoides count, 14.xii.71

Time	Nests											Weather	
	A	B	C	D	E	F	G	H	I	J	Total	Temp. °F	Hum. %
9.00	0	3	17	14	12	2	3	0	5	12	58	79	100
10.00	0	3	17	3	14	2	2	0	7	9	57	83	100
11.00	4	11	7	4	1	2	30	0	1	28	88	88	82
12.00	1	1	1	0	0	0	5	0	2	10	20	90	70
13.00	4	2	21	1	0	0	10	0	2	8	48	93	70
14.00	2	0	0	0	0	0	7	0	1	31	41	91	78
15.00	2	0	0	0	0	0	3	0	16	101	122	90	80
16.00	25	29	32	22	31	10	12	0	20	105	286	82	86
17.00	110	104	84	32	100	69	42	18	54	162	785	79	100
18.00	114	99	115	89	85	89	41	70	46	158	875	75	100
19.00	89	119	50	67	58	62	50	87	25	116	732	73	100
20.00	113	97	87	50	47	56	53	76	32	99	710	72	100
21.00	95	128	84	94	42	80	47	71	21	92	756	70	100
22.00	74	75	68	83	36	58	51	62	6	57	570	70	100
23.00	104	76	52	47	22	61	34	85	10	60	551	70	100
24.00	89	50	70	81	59	80	73	72	12	63	649	70	100
1.00	109	79	24	53	56	74	10	76	8	77	566	70	100
2.00	73	117	64	38	61	39	16	89	6	62	565	72	100
3.00	81	65	69	94	53	56	43	74	10	54	599	71	100
4.00	34	62	31	40	10	47	32	58	7	65	386	71	100
5.00	62	69	115	88	26	86	24	46	19	57	592	70	100
6.00	57	126	75	91	7	64	13	42	11	41	526	71	100
7.00	43	104	40	32	14	19	6	45	12	48	363	71	100
8.00	14	114	28	17	9	20	9	38	10	53	312	73	100
Total	1308	1533	1151	1040	743	976	616	1009	343	1568	10287		

Table 5.3

Macromischoides counts 20.iv.71

Time	Nests										Total	Weather		
	A	B	C	D	E	F	G	H	I	J		Temp. °F	Hum. %	Light
8.00	12	6	32	47	1	2	4	7	0	0	111	88.2	100	7.6
9.00	0	0	9	7	4	1	1	0	0	0	22	84.0	89.6	8.5
10.00	8	0	9	1	0	0	1	0	0	0	19	83.0	86.0	9.2
11.00	1	0	2	1	0	0	0	1	0	0	5	91.8	81.0	9.4
12.00	0	0	26	0	0	0	0	0	0	0	26	93.4	77.0	9.8
13.00	0	0	1	0	0	1	1	0	0	0	3	93.3	77.1	9.2
14.00	1	0	0	0	0	0	0	0	0	0	1	92.8	77.4	9.0
15.00	0	0	0	0	0	0	0	49	9	0	58	82.9	98.7	7.6
16.00	35	9	7	21	3	7	0	5	2	0	89	82.6	100	7.2
17.00	1	5	3	18	3	7	1	98	13	6	155	78.1	100	2.0
18.00	50	36	74	30	11	104	11	135	26	79	556	74.0	100	0
19.00	93	30	56	43	21	14	0	88	44	29	418	74.0	100	0
20.00	62	43	91	20	26	115	D	95	61	40	553	74.0	100	0
21.00	95	51	106	24	58	88	E	96	20	42	580	74.0	100	0
22.00	82	36	163	36	52	40	S	101	20	46	576	74.0	100	0
23.00	82	34	116	27	45	124	E	108	19	41	596	74.0	100	0
24.00	55	46	76	17	21	135	R	94	10	24	478	72.0	100	0
1.00	63	45	98	11	22	85	T	79	13	25	441	72.0	100	0
2.00	60	64	71	53	26	106	E	102	20	37	539	72.0	100	0
3.00	82	30	66	17	20	90	D	85	17	25	432	72.0	100	0
4.00	86	28	29	19	7	148		93	22	31	463	72.0	100	0
5.00	55	30	87	20	5	66		86	17	13	379	72.0	100	0
6.00	31	24	81	2	4	39		50	6	10	247	73.0	100	0
7.00	19	18	76	0	0	15		15	20	0	163	74.0	100	0
Total	973	535	1253	414	329	1187	19	1387	339	448	6886			

Table 5.4

Macromischoides counts 23.iv.71

Time	Nests											Weather		
	A	B	C	D	E	F	G	H	I	J	Total	Temp. oF	Hum. %	Light
8.00	6	1	1	0	0	4	1	4	0	0	17	80.5	94.4	7.7
9.00	0	0	0	0	0	2	1	5	1	0	9	85.6	83.2	8.4
10.00	0	0	0	0	0	0	0	2	0	0	2	90.5	75.6	8.9
11.00	0	0	0	0	0	0	0	0	0	0	0	90.5	71.5	9.6
12.00	0	0	0	0	0	0	0	0	0	0	0	90.0	70.0	9.1
13.00	0	0	0	0	0	0	0	0	0	0	0	90.0	68.2	8.6
14.00	0	0	0	0	0	0	0	0	0	0	0	91.3	67.3	8.5
15.00	0	0	0	0	0	0	0	0	1	1	2	90.5	69.7	8.0
16.00	0	0	0	0	0	0	0	0	0	0	0	89.3	74.9	7.9
17.00	1	0	0	0	1	0	0	2	2	0	6	85.7	82.4	2.5
18.00	6	4	2	0	21	8	0	23	10	61	135	82.8	89.3	0
19.00	29	6	33	1	59	61	16	61	54	42	362	80.8	99.0	0
20.00	13	7	40	0	40	40	25	38	98	47	348	79.4	100	0
21.00	4	44	30	0	31	26	43	43	77	57	355	78.0	100	0
22.00	40	68	49	3	39	37	20	40	61	69	426	76.2	100	0
23.00	19	68	84	0	91	34	12	21	122	65	516	75.0	100	0
24.00	24	84	46	21	114	20	7	18	114	64	512	74.0	100	0
1.00	24	61	75	6	71	32	16	14	115	51	465	74.0	100	0
2.00	9	84	62	5	94	44	27	46	132	64	567	74.0	100	0
3.00	16	45	58	4	68	25	14	81	82	61	454	74.0	100	0
4.00	29	66	42	12	73	38	14	20	90	55	439	72.2	100	0
5.00	36	172	38	16	136	30	4	23	52	22	529	72.0	100	0
6.00	8	62	4	0	39	24	2	14	6	3	162	72.8	100	6.5
7.00	4	8	4	0	3	7	0	6	1	0	33	75.8	100	8.1
Total	268	780	568	68	880	432	202	461	1018	662	5339			

Table 5.5

Macromischoides count 23.iv.71

Time	A	B	C	D	E	F	G	H	I	J	Total	Temp. °F	Hum. %	Sat Def.	Light
8.00	1	0	0	0	15	3	0	1	0	1	21	80.5	94.4		7.7
9.00	0	0	0	0	2	2	0	0	0	0	4	85.6	83.2		8.4
10.00	0	0	0	0	1	0	0	0	0	0	1	90.5	75.6		8.9
11.00	0	0	0	0	0	0	0	0	0	0	0	90.5	71.5		9.6
12.00	0	0	0	0	0	0	0	0	0	0	0	90.0	70.0		9.1
13.00	0	0	0	0	0	0	0	0	0	0	0	90.0	68.2		8.6
14.00	0	0	0	0	0	0	0	0	0	0	0	91.3	67.3		8.5
15.00	0	0	0	0	0	0	0	0	0	0	0	90.5	69.7		8.0
16.00	0	0	0	0	0	0	0	0	0	0	0	89.3	74.9		7.9
17.00	0	0	0	0	0	0	0	3	0	0	3	85.7	82.4		2.5
18.00	0	6	0	2	3	24	4	3	24	9	75	82.8	89.3		0
19.00	18	8	9	59	25	29	4	8	28	29	217	80.8	99.0		0
20.00	8	65	122	86	55	80	10	13	90	67	596	79.4	100		0
21.00	8	10	59	39	39	71	19	8	23	91	367	78.0	100		0
22.00	5	33	119	57	42	43	15	10	72	33	429	76.2	100		0
23.00	11	124	110	62	29	58	25	13	83	21	536	75.0	100		0
24.00	2	213	131	93	30	72	27	19	72	62	721	74.0	100		0
1.00	7	285	214	66	28	62	24	5	74	52	617	74.0	100		0
2.00	8	85	159	48	31	38	40	14	81	30	534	74.0	100		0
3.00	3	99	168	38	54	41	11	13	112	72	598	74.0	100		0
4.00	3	146	143	28	36	62	23	11	86	78	616	72.2	100		0
5.00	8	143	155	43	12	47	7	5	40	53	513	72.0	100		0
6.00	0	4	20	4	7	6	3	3	10	14	71	72.8	100		6.5
7.00	1	1	3	4	4	10	6	1	1	0	28	75.8	100		8.1
Total	83	1222	1412	629	400	648	218	130	776	612	6147				

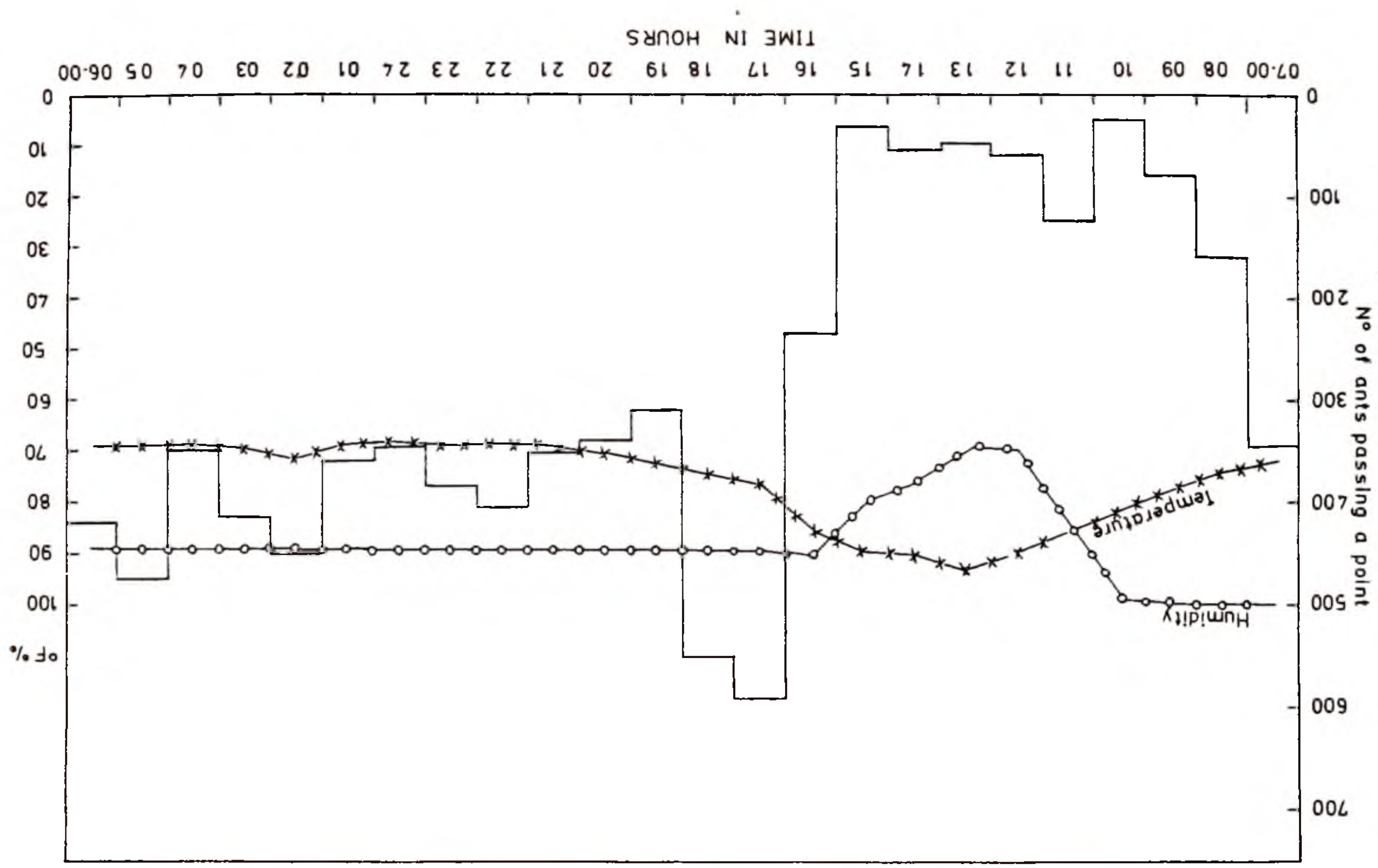


Fig.5.1: <u>Macromischoides</u> activity counts in plot H10b., Tafo 14th December 1970.
Left hand scale (1,3 - a); light in units (Weston Master V exposure meter)
Right hand scale (0,10 - 100) temperature in °F; R.H. percent.

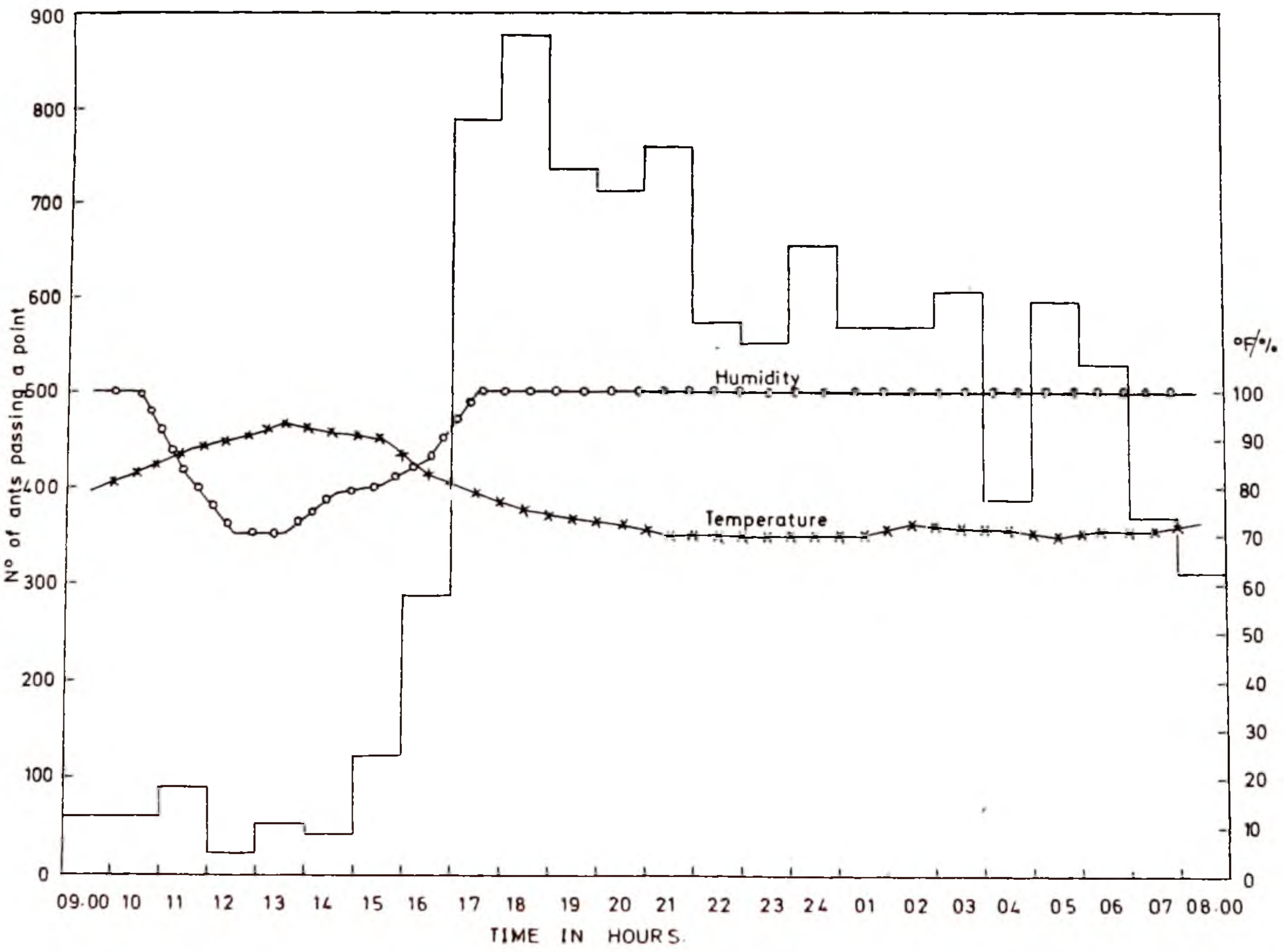


Fig.5.2: Macromischoides activity counts in plot H10b$_3$, Tafo, 14th December 1970

Right hand scale (0,10 - 100): temperature in °F, R.H percent.

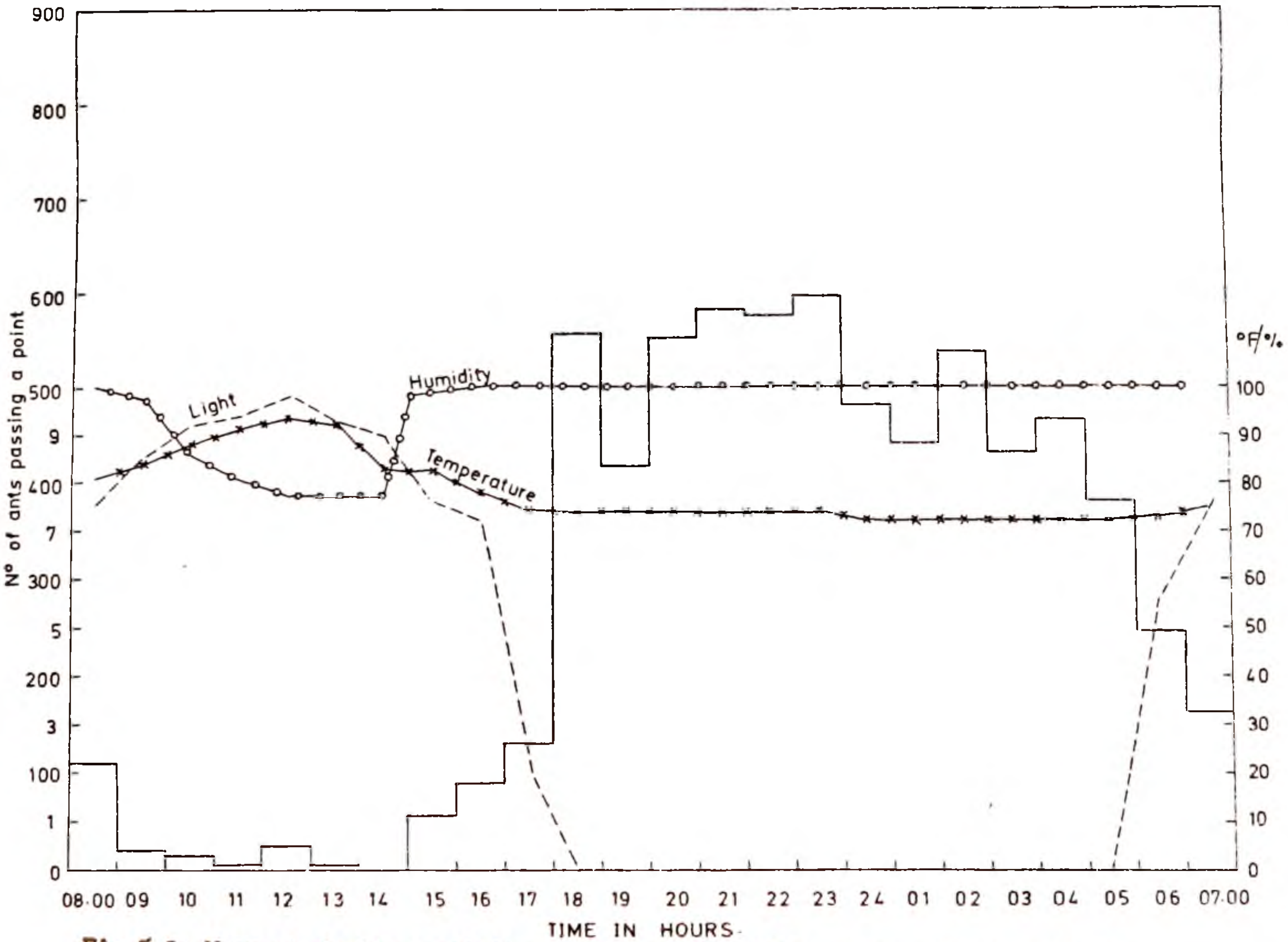


Fig.5.3: Macromischoides activity counts in plot H10b$_1$, Tafo, 20th April 1971.
Left hand scale (1,3 - 9): light in units (Weston Master V exposure meter)
Right hand scale (0,10 - 100) temperature in°F; R.H. percent.

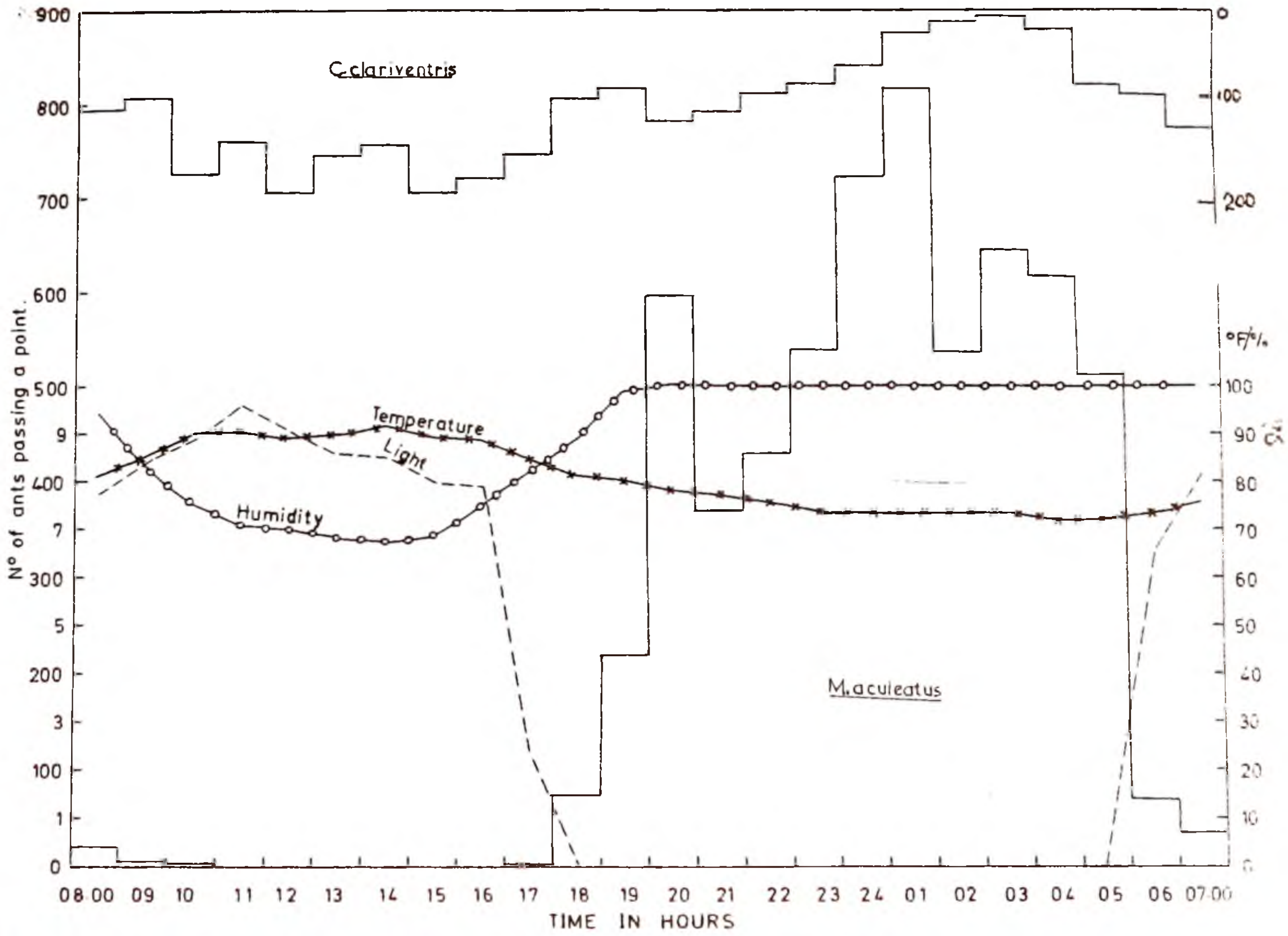


Fig.5.4: M. aculeatus and C. clariventris activity counts in plot D14, Tafo 23rd April 1971
Left hand scale (1,3 -9): light in units (Weston Master V exposure meter)
Right hand scale (0,10 - 100): temperature in oF; R.H. percent.

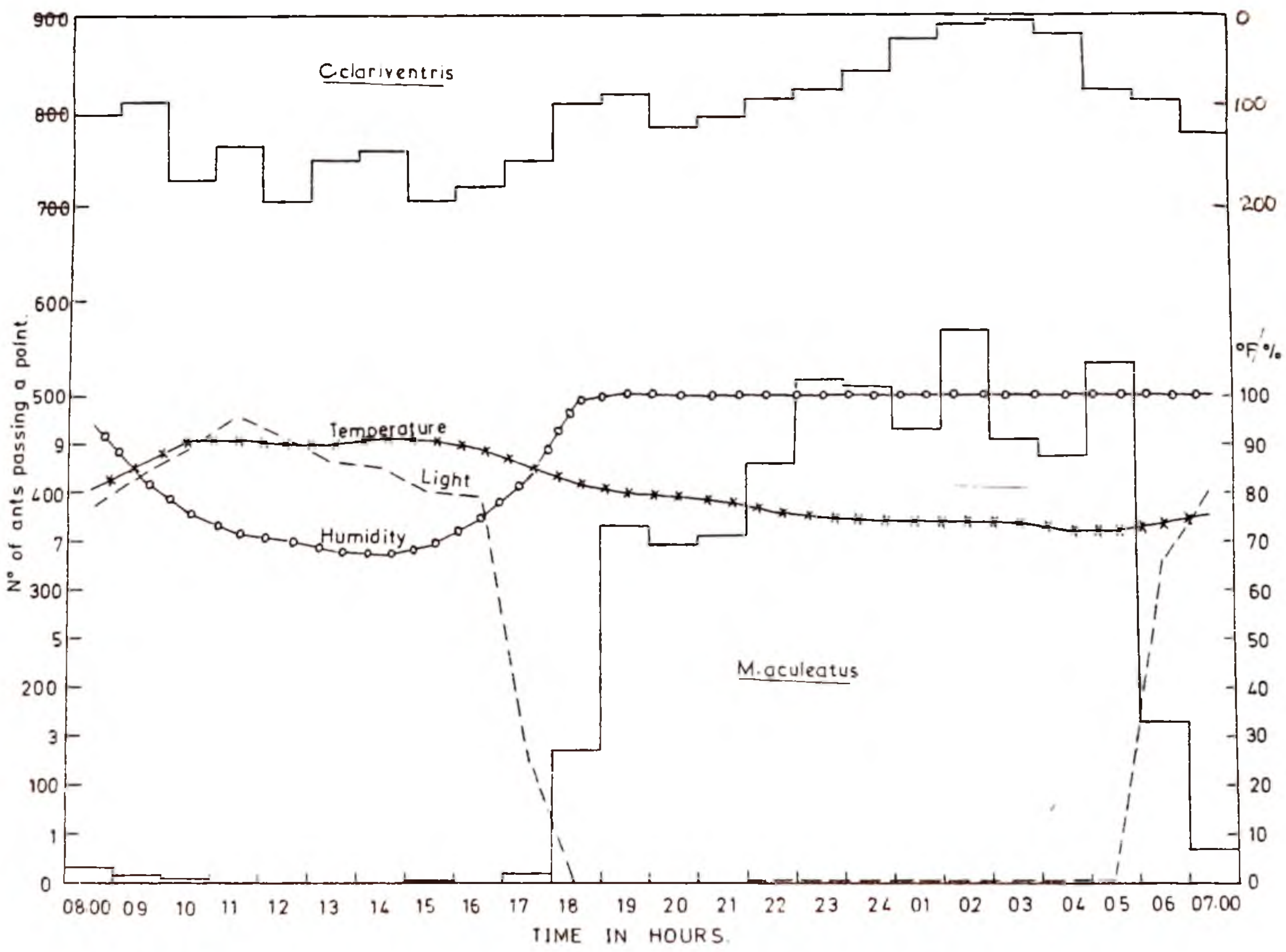


Fig.5.5: M. aculeatus and C. clariventris activity counts in plot D14, Tafo, 23rd April 1971. Left hand scale (1,3 - 9): light in units (Weston Master V exposure meter) Right hand scale (0,10 - 100): temperature in °F; R.H. percent.

there was virtually no activity during the day and start ~~t~~of activity was delayed till about 18.00 hours. *Macromischoides* activity increased as that of *clariventris* declined (Figs.5.4 & 5.5). Peak activity was found between 24.00 hours and 02.00 hours. The presence of a predator such as *Oecophylla longinoda* is another factor which effects a change in the pattern. Once *Oecophylla* lays siege to the nest entrance, *Macromischoides* will not come out until the former retreats. Thus the day activity pattern is modified. No quantitative work was done on this.

Rather surprisingly, there was a sharp increase in activity at 05.00 hours on one occasion. Following some ants it was found that large numbers of them were drinking water (condensed dew). This has since been found on several occasions as shown in Figs. 5.1 - 5.3 and 5.5. The drop in temperature and light intensity that precedes rainfall does not seem to affect activity. During a rain storm however the ants were seen to stop still, brought the legs close to the body and gripped the substratum firmly. When it started raining they hurriedly retreated into the nest but came out in large numbers as soon as the rain stopped. But since it rained for less than 30 minutes during the period of observation, the average count for the hour was not much affected.

Food and foraging habits

1. Observations on wild colonies

A. Searching patterns

a. Movement: Paths followed by ants in and out of a nest depend on the position of the nest on a leaf. Three main movement patterns were identified as follows:

Nests near petiole: Movement is from the entrance (usually on the petiolar end) along the midrib, the petiole and directly on to the branch. The ants then move along the upper surface of horizontal or slanting branches. Downward movement usually stops at the main fork of the tree, but occasionally continues right down to the ground. Upward movement ends at the terminal buds and leaves where ants usually attend coccids and wingless aphids or prey on winged ones.

Nests at leaf apex: Movement is not necessarily along the midrib; once out of the nest the ants move freely on any part of the leaf blade before converging on the petiole. Ants from a nest can get on to contiguous leaves but eventually converge on the main branch and follow the trail.

Sandwiched nests: The pattern of movement in sandwiched nests is not easy to determine. The ants usually move in and out of the nest along one petiole, and at times a hole made in the leaf blade is used as an entrance.

b. Search for food: Ants commonly move out of the trail on to stalks and pods, entering all crevices and forks. A worker stops to investigate any strange object it comes across. If it is dead but big prey, it may bite a piece off the prey and carry this to the nest or it may just return to the nest, presumably to recruit more workers.

c. Prey-killing and transport: *Macromischoides* both bites and stings. In stinging the ant first secures hold of the object with its strong mandibles, doubles itself up, and then stings. The result is very painful but no swelling occurs (Wheeler, 1922). Both the mandibles and the sting are employed in killing prey. Prey can be killed by several workers at the same time or by a single worker depending upon its size. If several ants join in killing prey or overpowering an enemy, one or two of them confront it squarely, bite and hold on. The other workers usually adopt a 'hit-and-run' method. Or several workers will grab the legs, antennae or other parts of the prey and pull in different directions at the same time. Prey or an enemy can be dismembered by this means. The sting is not often used in this communal killing. When however a worker engages in a solo-fight with either prey or an enemy it usually makes use of the sting. It grabs with the mandibles and stings as is described below.

One worker was found killing prey, *Pheidole* sp. (Formicidae) in the field. The prey was grabbed with the strong mandibles, the body raised off ground, the legs held wide apart, and the gaster bent forward through the parted legs to reach the target which was stung several times. A short while after, the prey gave up struggling, but did not release its hold on the predator's leg. The worker bit off the gaster and thorax, but the head of the prey remained stuck to its leg. A similar method of killing was observed during a raid on small wood termites. Whatever means are used in killing a prey, it must be carried into the nest either whole or in bits. Very often large prey is dismembered and the broken-pieces carried either individually or in teams into the nest. The ants adopt a 'push-and-pull' method for transporting large pieces of food. Small prey however such as Collembola and aphids are conveyed into the nest by single workers. The question of how the worker finds its way back into the nest is discussed below.

d. <u>Trails</u>: Various experiments were performed in the field to determine whether the ants lay and follow trails. In one experiment a bare finger was rubbed over the surface of a branch on which the ants were moving along a particular path. Without exception, all ants, whether moving nestwards or away from it, stopped abruptly at either edge of the rubbed section. They became confused and disorganised. However, after a short time, a diversion was found along the unrubbed part. (Fig.5.6). This experiment was repeated using a handkerchief and a clean piece of cloth held with a pair of forceps to rub the 'trail', and similar results were obtained. It is concluded that the ants follow a trail.

In another experiment a dead grasshopper was placed outside the trail of a group of ants. Straying ants (scouts?) coming across it, quickly hurried away. This continued for some time until finally

INTERRUPTION EXPERIMENT

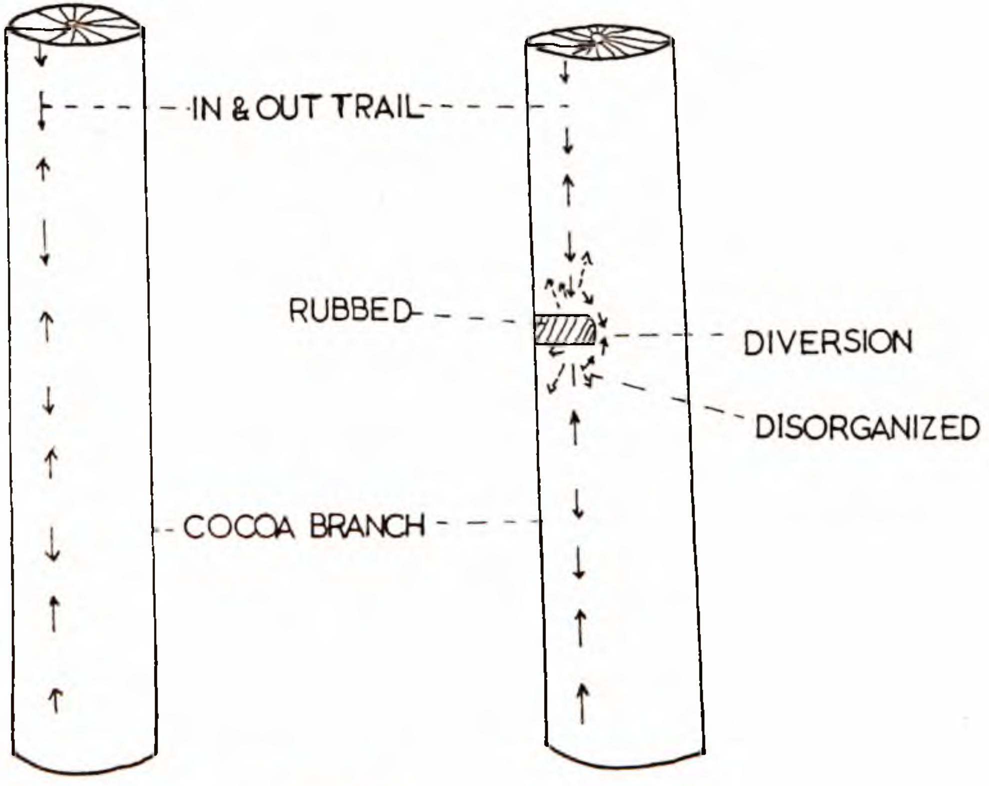
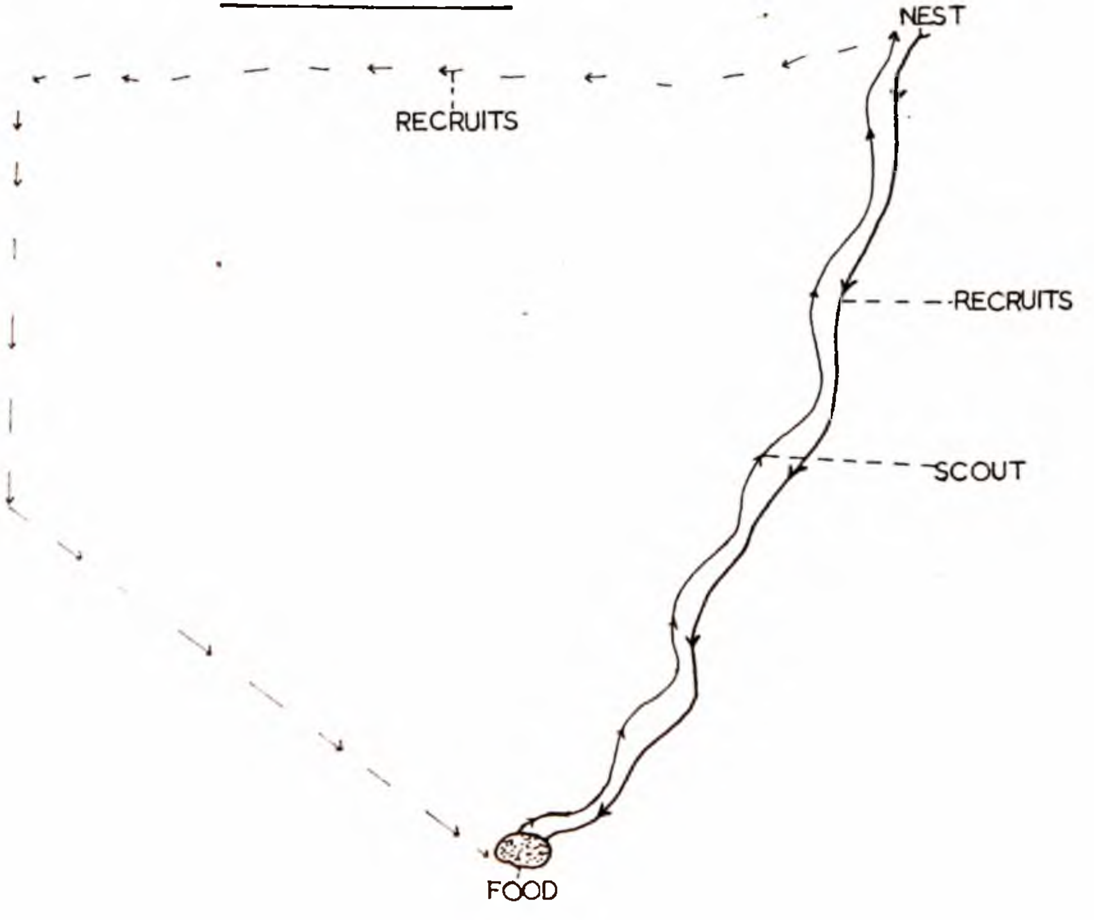


Fig 5.6

two ants stopped at it. A third one joined them. One of the three left and moved up the tree towards the nest. In less than 30 seconds all traffic was directed to the body of the grasshopper. Rubbing part of the trail caused confusion and disorganisation.

A second hopper was placed about six inches from the first one. The first ant that came across it attempted to lift it, but failed. It then worked its way round the entire body of the prey as if assessing its size. Meanwhile three more workers had joined it. The first, however, left and went straight into the nest without stopping to engage in antennal greetings. Several workers then came out from the nest and moved straight to the prey. Ants from all the nests on the tree (some started earlier than others) as well as those from four other nests on a nearby tree connected to the first one by fallen branches of a shade tree, fed on the same grasshopper. This shows that all the nests on the two trees belong to the same colony. Rubbing the trails at various points elicited the same reaction as before.

A third grasshopper was placed at one corner of a plain white sheet of paper and its position marked. One edge of the paper was placed against the stem of a cocoa tree (with nests on) with the hopper at the farthest end. Three ants moving undirectedly discovered it. One left later and moved zigzagly away with the body very close to the paper and the antennae virtually brushing the paper. Just as it pulled out, the path it had followed was marked in pencil (Fig.5.7).



TRAIL LAYING

Fig 5.7

Soon many ants descended from the nests and followed the marked path. A few, however, followed another path along the edge of the paper, but abandoned it later to join the main traffic. The paper was then turned so that the prey was now nearest the stem. Ants leaving the prey still followed the old trail which no longer led into the nest. This confused state continued for some time before a short cut was discovered.

2. Observations on laboratory colonies

Caged ants: A large number of caged ants escaped from the cage and constructed a nest under the table on which the cage was sitting. The ants moved in and out of the cage along a definite path. A dead grasshopper was placed in the cage. Some few ants wandering in the cage found it. Two left and went back into the nest. Within a matter of seconds a large number of workers forming a thick column was seen coming out of the nest and heading towards the cage. After a few had passed into the cage, a piece of brown paper measuring 3 x 1 in was placed on the path, making sure the ants were not disturbed. When ants moving from and to the nest reached the edges of the brown paper; they stopped confused. Some returned either to the nest or the feeding site, whilst others moved confusedly about. A diversion was made but this was also blocked. Since they had no other place to pass, they managed to reconstruct their original trail. A second piece of brown paper with equal measurement as the first was carefully laid upon the first. The ants became disorganised once more.

But with the removal of this second sheet of paper they quickly retraced their trail along the first brown paper almost immediately.

3. Food items

Several workers were intercepted and robbed of their food. Food remains were also collected from several nests (91) opened in the field and also from the nests used for the population counts. Since the ants commonly chip bits off their prey and carry them into their nests, not many recognisable animal food remains were obtained. But with the help of Mr D. Leston quite a large number were identified to family, generic and specific levels. The list of the various identified food has been compiled and is presented in tabular form (Table 5.6). The ants were found once feeding on wet bird dropping on a leaf.

4. Association with some Coccoidea, Aphidoidea, Pentatomidae (Hemiptera) and Lycaenidae (Lepidoptera)

The ants were found on several occasions attending some coccids, pseudococcids, lecaniids, aphids and lycaenid caterpillars.

Coccidae: The ants attend the scale insects on leaves, stems and branches, terminal buds, pods and pod stalks. Several *Steatococcus* spp. were found being attended by the ants, mostly on leaves. On two occasions the ants were found attending nymphal coccids, *Phenococcus* spp., under felt nests they had built over the scale insects (Plates 5.1 - 5.3).

Stictococcidae: *Stictococcus multispinosa* are mainly stem dwellers, and are usually attended by many *M. aculeatus*.

Table 5.6

Analysis of food remains and food obtained by interception

Order	Breakdown
Coleoptera	Chrysomelidae, Scarabaeidae, Carabidae, Curculionidae
Hemiptera	Pentatomid larva Reduviidae (Harpactorinae and Saicinae (*Polytoxus* sp.) Lygaeid (Rhyparochrominae) Cydnidae *Distantiella* larva Membracidae, Coccidae *Sahlbergella* exuviae
Dictyoptera	Blattidae
Isoptera	-
Lepidoptera	Noctuid larva (*Chracomastictigrapta*) Big caterpillar remains (horny)
Hymenoptera	Formicoidea: *Camponotus* large *Odontomachus* Doryline workers *Crematogaster clariventris* Ponerine sp. *Oecophylla* females *Cataulacus* sp. ant parts Thynnidae Ichneumonoidea: *Pimoitica*
Psocoptera	Psocidae
Collembola	-
Orthoptera	Tettigonid, Cricket
Diptera	Muscidae, Drosophilidae
Myriapoda	Millipids
Mollusca	
Arachinidae	Salticidae
Vertebrates: Amphibia?	Radius

Plate 5.1: Nest construct~~ion~~ed on a cocoa twig over coccids.

Plate 5.2: Part of 'nest' removed to show the coccids.

Lecaniidae: Several scale-insects belonging to the Lecaniidae were seen on the nest floor of a large number of nests. All developmental stages of the bug could be found in a nest, i.e. motile ones as well as the sedentary ones. The ants carress the bug with their antennae, stopping now and then to apply the mouth to the body of the scale-insect.

Pseudococcidae: Some mealybugs were collected from the nest. These have not yet been identified.

Since several ants were found attending the coccids it was decided to find out whether any differences existed between the ordinary foragers and the coccid attendants. This was done by collecting 10 workers from each group and taking measurements of their head width and length, since the differences between workers are most marked in the head and jaws (Wilson, 1953). The cephalic index is then obtained by dividing the mean headwidth by the mean head-length and multiplying by 100. (Table 5.7). The indices obtained showed that there was no significant difference between the two groups.

Aphidae: The ants were found attending wingless aphids on cocoa flowers and terminal buds. The alate aphids usually moved freely among the ants. But surprisingly the ants were found on several occasions carrying dead alate aphids into their nests.

Lycaenidae: On three different occasions lycaenid caterpillars were found pupating inside the nests of the ants. One successfully developed into an adult. The other two died. The one which emerged was identified as Thecla esmeralda. Field observations showed that

Table 5.7

Cephalic Index

	COCCID ATTENDANTS		ORDINARY FORAGERS	
	Head length	Head width	Head length	Head width
1.	28	23	32	26
2.	28	23	30	24
3.	28	24	31	26
4.	34	27	27	23
5.	26	22	27	24
6.	30	25	30	24
7.	29	25	29	25
8.	28	24	31	25
9.	30	25	28	24
10.	28	24	30	25
Total	289	242	295	246
Mean	28.9	24.2	29.5	24.6

COCCID ATTENDANTS	ORDINARY FORAGERS
Mean Cephalic index $\frac{24.2}{28.9} \times 100 = 83.73$	Mean Cephalic index $\frac{24.6}{29.5} \times 100 = 83.38$

the ants attend the caterpillars by carressing the posterior, somewhat flattened extremity of the caterpillar with their antennae, and licking some droplet of a colourless, perhaps sugary liquid (Wheeler, 1913). Several trees were visited, recording the number of the caterpillars on the cocoa flush and the number of ants attending them. The results are shown in Table 5.8.

Pentatomidae: Some pentatomid eggs were occasionally found in the nest. The ants were once found congregated on a batch of *Bathycoelia thalassina* eggs. The eggs were collected, and three days later several adult hymenopterous parasites hatched out of the eggs.

Discussion

The results of the activity counts show that the ants are normally very active during the night, but not in the day time. But several field observations have shown that this pattern can be modified by certain factors. Notable among them is the presence of an available food. Thus the ants come out to forage, even in the intense sun, if they discover some food item nearby. This observation agrees with Wheeler's (1910) assertion that hunger influences activity of ants. Wallis (1962) also found that the 'hunger' of a colony of *Formica rufa* affected the activity of the workers. The presence of brood has been found to stimulate nest building in *M. aculeatus* (Section 8), and may probably promote foraging activity as well . (~~Wallis, 1962~~). Predators are also likely to hinder activity as has been found in *Oecophylla longinoda*.

Table 5.8

Association of *Macromischoides* with lycaenid caterpillars

Plot	Tree	No. of larvae	No. of ants	No. of larvae without ants
H10b1	1	1	11	-
"	2	1	1	-
H10b2	3	1	9	-
"	"	1	6	-
"	"	1	2	-
"	"	1	8	-
"	"	1	5	-
"	4	1	1	-
"	5	1	1	-
Total	5	9	44	-

Perhaps by being nocturnal the ants escape high predation, since most of their predators, such as, Oecophylla longinoda, some Reduviinae (e.g. Acanthaspis bilineolata), many skinks (e.g. Mabuya sp.) are day feeders, but most geckos are nocturnal and arboreal. Perhaps their nocturnal activity pattern is a device to synchronise their foraging period with availability of their prey. But a look at the list of prey (Table 5.6) does not seem to suggest this. Perhaps the most important advantage is an escape from desiccation. Macromischoides constantly move brood from one nest into another during their active period. If this were done during the day when the evaporation rate is high due to high temperatures and low relative humidities, the larvae might die of desiccation or at least be adversely affected. A relative humidity of about 80 percent and a temperature of 23.8°C to 26.6°C seem to be suitable for activity build-up. Their inactivity during the day may also be determined by a negative response to light, since the ants always moved from any bright light shone on them during the night.

But light may be playing a more important role than this. It is very likely that light rather than temperature and humidity is the main trigger that sets normal activity in motion and brings it to a stop. A careful scrutiny of figs.5.3 - 5.5 seems to support this, for on all the three occasions when light intensity was measured, increase activity started just after a sharp drop in light intensity at about 17.30 hours, and continued throughout the night only to decline at 06.00 hours the following morning after a sharp rise in light intensity. Suitable temperature and humidity perhaps help to maintain the activity after it has been triggered by light. But in the day time, under normal field conditions, light intensity is positively correlated with temperature and hence with humidity, thus making it difficult to determine which is responsible for the low activity level although all three may be jointly responsible (Ayre, 1958).

Unlike the situation in the clariventries free area, where there was some slight activity during the day, the ants remained totally inactive during the day in areas where clariventris is present. Thus the presence of clariventris is responsible for the complete absence of activity. When the activity of clariventris declines that of aculeatus increases. The two ants are therefore able to coexist because they are segregated in time. However the same meteorological factors that influence activity in the clariventris free areas are in operation where it occurs as well.

Perhaps the habit of Macromischoides of searching all crevices and other dark areas such as forks, angles between pod and stem, and branch apices is what makes it effective predator of capsids. Youdeiwei (1968) has shown that capsids usually aggregate in the dark places between the pod and the stem, where the females oviposit. Thus by frequenting these spots oviposition will be disturbed and the tender first instar nymphs predated.

All the trail interruption experiments outlined really show only that the ants will not cross clean ground. They do not show what was on the ground or how the ants use it (Sudd, 1967). The only evidence of trail laying was the ant that moved with the body low mentioned earlier. Perhaps it uses its sting with secretion from Dufour's gland to lay the trail, as this is a common feature of the subfamily Myrmicinae. The ants do follow trails since the recruited workers moved on the marked path of the scout. Trail laying and following are big assets to nocturnal insects like Macromischoides, since they can go out to forage and return to the nest without difficulty. Their food is highly varied as the list shows. Though there were few capsid remains, this does not mean the ants are ineffective against the cocoa capsids. Thus Collingwood (1971) has categorically stated that Macromischoides is "consistently negatively associated with Distantiella theobroma". This may imply that the capsid nymphs being so soft-bodied are preferred to other hard-bodied insects like the ants. The scarcity of capsid remains found may also be due to their being soft-bodied. Macromischoides obtains its protein supply by feeding on other animals. But carbohydrates are very essential in ant diet. These it obtains by attending coccids, aphids and lycaenid caterpillars which produce honey-dew and other saccharine liquids. Another source of carbohydrates may be from the soft juicy coating of the seeds of Solanum verbascifolium which are commonly found incorporated in the nest in areas where the trees occur. Leston (personal communication) finds that Macromischoides utilises the sugars of extrafloral nectaries of at least three common cocoa farm shrubs. Minerals and essential salts they obtain perhaps from bird or reptile droppings they feed on. Ofer (1970) has reported a similar finding in Polyrachis simplex in Israel.

The scale-insects and mealybugs which these ants attend are not vectors of the swollen shoot virus disease (Strickland, 1951); The aphids are not serious pests in the cocoa farms, while the lycaenids are relatively unimportant defoliators. Lodos (1968) claims that the ants attend the eggs of B. thalassina and drive away parasites but do not carry the eggs away. Contrary to this observation some eggs were found in the nests and those found being attended were all parasitized. These observations are not in conflict. If the ants found the eggs only after they were parasitized, they might not know the difference. What does seem likely is that if they attend the eggs, they later predate the first instar nymphs.

The rate of spread of the radioactive sugar through the various colonies within such short periods (Section 3) denotes a high rate of inter-nest movement. It is very likely that the rate was aided by food-sharing, a common behaviour of ants. Chauvin et al, (1961) found that radioisotope given to Formica polyctena was transmitted to F. rufa by oral exchange. However, M. aculeatus has never been seen indulging in food sharing outside the nest. Perhaps this takes place inside the nest.

Section 6. Interrelationships of *M. aculeatus* with other ants

6. INTERRELATIONSHIPS OF M. ACULEATUS WITH OTHER ANTS

Introduction

One of the few available comments on the interrelationships of *M. aculeatus* and other ants such as *Oecophylla longinoda* and *Crematogaster* species in its environment was by Collingwood and King (1970). These authors, using direct field scoring methods, claimed that *M. aculeatus* was significantly negatively associated with *Oecophylla longinoda* and *Crematogaster* spp. They also stated that this negative association was not absolute for *O. longinoda* and *M. aculeatus* occasionally occurred together whilst *M. aculeatus* and *Crematogaster* extremely rarely coincided. The species of *Crematogaster* worked on were not however mentioned. Leston (personal communication) however suggested a positive relationship between *M. aculeatus* and *C. clariventris* from the results of the analysis of his field data. Room (personal communication) has demonstrated this relationship with fuller data and a better sampling technique.

The present work was undertaken to attempt to establish in more visual, and thus more concrete form, the interrelationships between *M. aculeatus* and its neighbour ants such as *O. longinoda*, *C. stadelmanni*, *C. clariventris* and other minor ants.

Materials and methods

When mapping the distribution of *M. aculeatus* with respect to the different shade regimes, dominant ants, such as *O. longinoda* and *C. stadelmanni* occurring in the area were also mapped. Two more areas were later mapped to show the distribution of M. aculeatus and C. clariventris.

The degree of coexistence was determined by calculating the Coexistence Index (Ed) and the coefficient of coexistence (Ec) for each mapped area using Hayashida's (1960) method. A number of other indices, using the same parameters, are available. (Southwood, 1966).

Ed measures the degree of coexistence of one species (A) to another (B) in a whole area. It is simply calculated by the formula:

$$Ed = 100.\frac{h}{a}$$

h and a are respectively the number of samples in which both A and B or A only was discovered. For our purpose Macromischoides was taken as (A) and any other ant occurring with it as (B).

Coexistence in each habitat, Ec, which for our purpose are the different shade regimes, was obtained by the formula:

$$Ec = \frac{hn}{ab}$$

a, b, h are respectively the number of samples in which either species A or B occurred or in which both species were discovered together and n is the number of samples in each habitat. The coexistence positively or negatively deviates from the chance score, of which statistical significance is given by X^2 test with Yate's correction. However a change was made in the formula as given by Hayashida to suit the present purpose. In the first place Ec was not calculated for each habitat, such as each shade regime; rather each mapped area was taken as being a habitat. Thus in fact both Ed and Ec measure the same thing, such as the degree of coexistence. Secondly chi-square was not used to check the significance because some cell values were too small, some even had zero.

Ant predators: Field observations were made to find out the predators, and Oecophylla longinoda and Polyrachis laboriosa in the radioisotope experimental area were monitored for radioactivity.

Results and observations

Figs.3.4 - 3.6 and 6.1 - 6.2 show the distribution of M. aculeatus in relation to O. longinoda, C. stadelmanni and C. clariventris respectively. Table 6.1 shows the interaction of the ant species.

Macromischoides, Oecophylla interaction: Oecophylla longinoda is a day feeder that nests on shade and cocoa trees usually in more open areas. It generally forages on Macromischoides nest-trees but occasionally the two nest on the same tree. The two are antagonistic and fierce fighting ensues if they meet. Oecophylla even besieges, attacks and predates Macromischoides. They were found to be radioactive when monitored, and a worker was found carrying a radioactive Macromischoides larva. Moreover three out of five Oecophylla nests in the area were radioactive. Some Oecophylla remains were however found among food collections in Macromischoides nests. The test for the degree of coexistence gave 20 per cent as the greatest value in all the three mapped areas (Table 6.1).

Macromischoides, C. stadelmanni interaction: Unlike Oecophylla longinoda C. stadelmanni nests only on shade trees with its carton nests high up

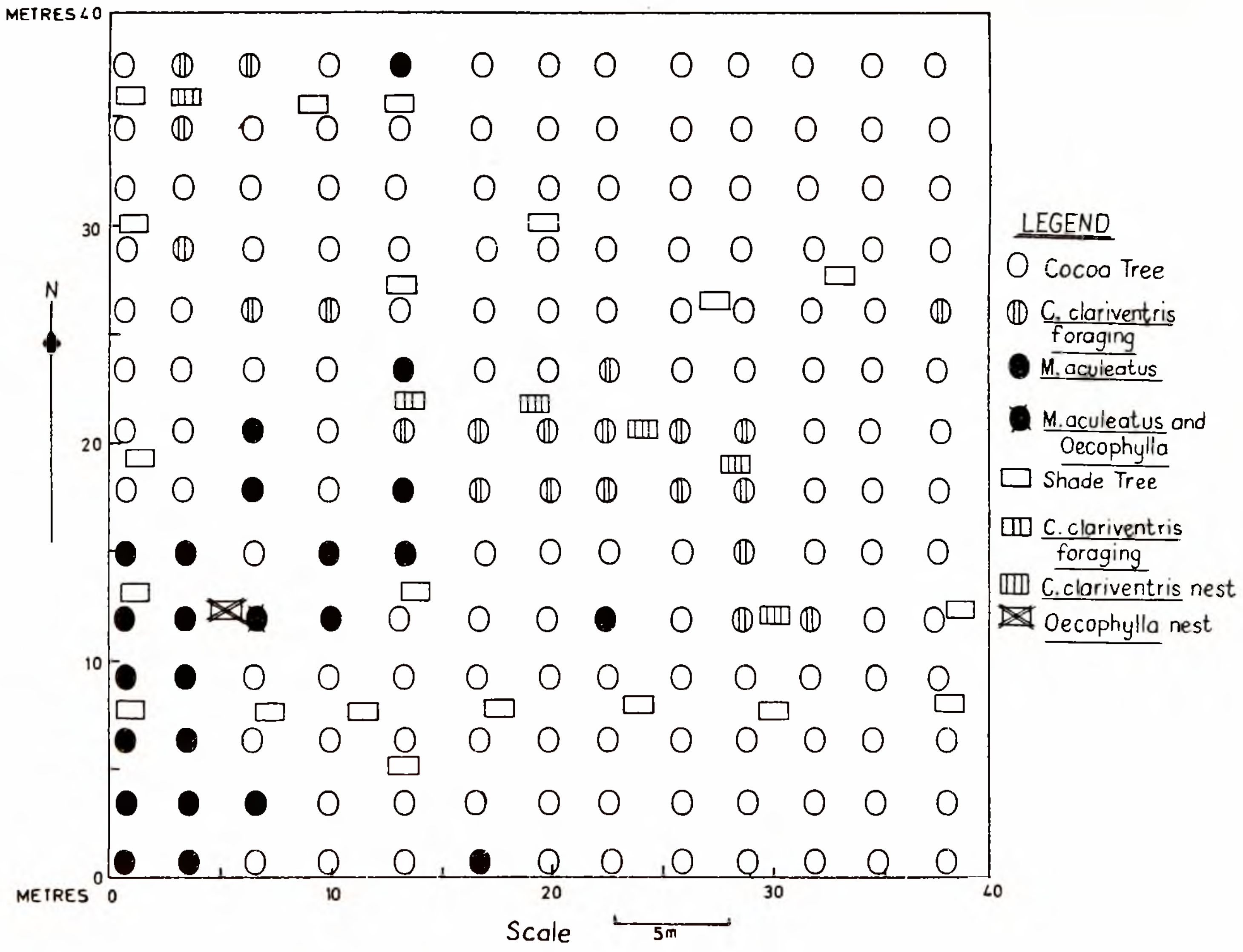


Fig.6.11: The distribution of M. aculeatus in relation to other dominant ants in plot C4
9th March 1971.

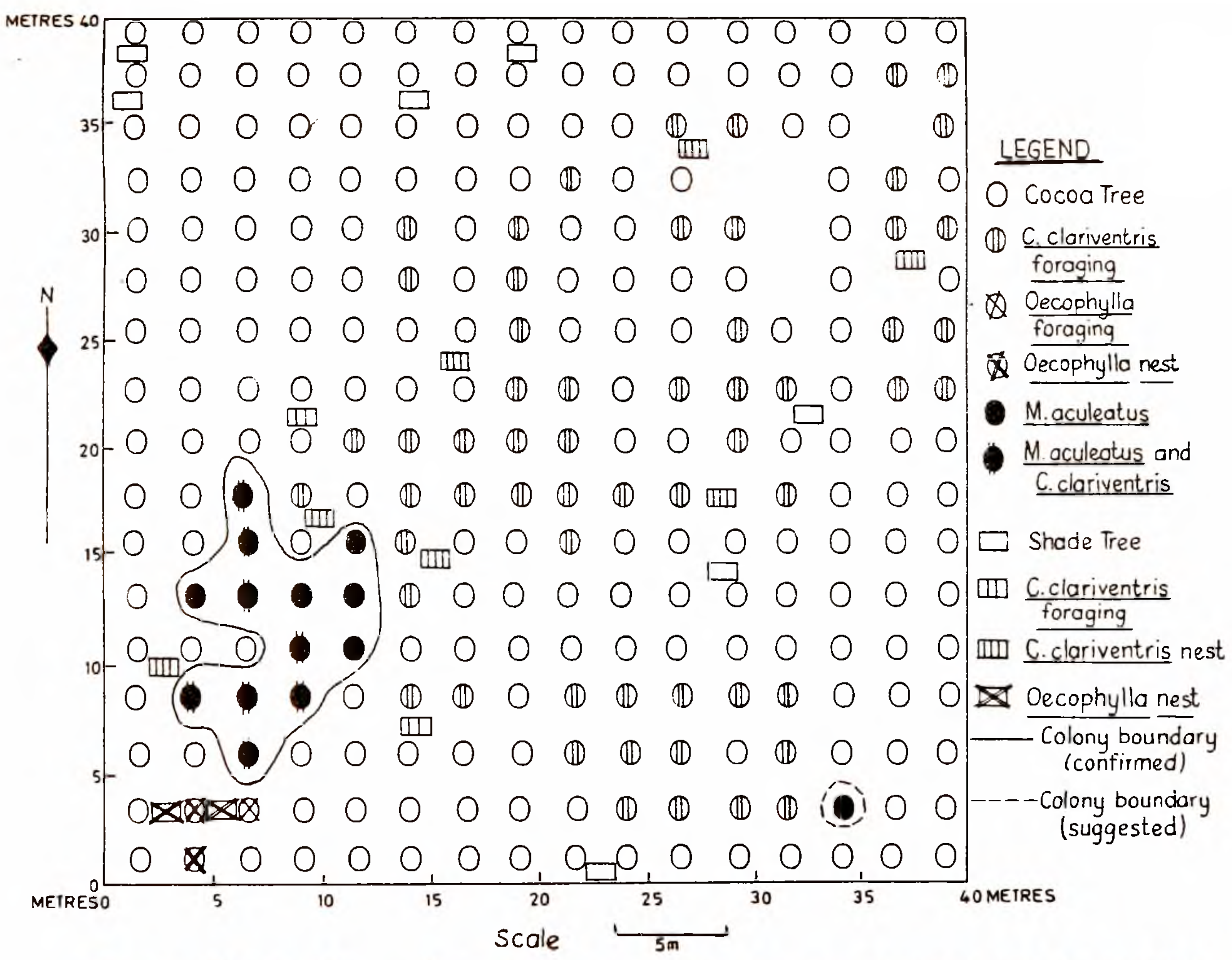


Fig.6.2: Distribution of *M. aculeatus* in relation to other dominant ants in plot D14 16th March 1971.

Table 6.1

Ant interaction in Plots H10b$_3$ and b$_4$, C4 and D14

Site			**O. longinoda**				**C. stadelmanni**		Site
H10b$_4$ (i)	**M. aculeatus**	**Present**	**Absent**	**Total**	**M. aculeatus**	**Present**	**Absent**	**Total**	H10b$_3$
	Present	1	5	6	Present	0	10	10	
	Absent	3	29	32	Absent	22	13	35	
	Total	4	34	38	Total	22	23	45	
	Ed = 20.0%, Ec = 0.6				Ed = 0.0%, Ec = 0.0				
			O. longinoda				**C. clariventris**		
H10b$_3$ (ii)	**M. aculeatus**	**Present**	**Absent**	**Total**	**M. aculeatus**	**Present**	**Absent**	**Total**	D14
	Present	1	9	10	Present	8	57	65	
	Absent	5	30	35	Absent	6	197	203	
	Total	6	39	45	Total	14	254	268	
	Ed = 11.1%, Ec = 0.8				Ed = 133.3%, Ec = 1.6				
			O. longinoda				**C. clariventris**		
C4 (iii)	**M. aculeatus**	**Present**	**Absent**	**Total**	**M. aculeatus**	**Present**	**Absent**	**Total**	C4
	Present	0	6	6	Present	0	22	22	
	Absent	4	12	16	Absent	24	136	160	
	Total	4	18	22	Total	24	158	182	
	Ed = 0.0%, Ec = 0.0				Ed = 0.0%, Ec = 0.0				
			O. longinoda				**C. clariventris**		
(i-iii) combined	**M. aculeatus**	**Present**	**Absent**	**Total**	**O. longinoda**	**Present**	**Absent**	**Total**	D14
	Present	2	20	22	Present	0	3	3	
	Absent	12	71	83	Absent	65	200	265	
	Total	14	91	105	Total	65	203	268	
	Ed = 10.0%, Ec = 0.4				Ed = 0.0%, Ec = 0.0				

the tree. It forages however on cocoa trees and even on the ground. The two ants usually fight when in contact. Fig.3.6 shows that there is no overlapping whatsoever between them. Some deserted *Macromischoides* nests were however found on trees now occupied by *stadelmanni*. Ed value for the two is zero per cent.

Macromischoides, *C. clariventris* interaction: *C. clariventris* nests on tall shade trees and like *C. stadelmanni* forages and nests on cocoa and other trees and shrubs. It seems that there is little hostility between the two species as they seldom fought when in contact. On few occasions moreover, *clariventris* workers were even found resting in deserted *aculeatus* nests. The two ants coexist fairly well as Fig.6.2 indicates. There seems however to be a superficial negative association between them in plot C4 as Fig.6.1 shows. The association tests were therefore positive in plot D14, but negative in C4.

Macromischoides versus other ants:

Polyrachis laboriasa coexists with *M. aculeatus* as both very often nest on same trees. Moreover the former moves freely among the latter. They became radioactive during the radioisotope tagging experiment. *P. rivoili* does not construct nests of its own. It nests rather in preformed cavities in dry cocoa pods and trees. They were found on several occasions occupying deserted *M. aculeatus* nests. *P. rivoili* were vanquished by *M. aculeatus* when a straight encounter was organised between them.

Camponotus acvapimensis does not seem to be hostile to M. aculeatus. C. acvapimensis moves freely but rapidly among Macromischoides. Another ant found occupying same trees with aculeatus is Cataulachus sp. Pheidole megacephala was found occupying trees in Macromischoides areas. In C5a Pheidole sp. attacked and destroyed an incipient colony. In the laboratory they always attacked and annihilated cultures.

Discussion

The results obtained show that O. longinoda and M. aculeatus are mutually exclusive. This observation agrees with Collingwood and King's (1970) finding. There is however an occasional overlapping, which is more transitory than permanent, since Oecophylla nests were found on trees previously occupied by Macromischoides. It is very likely therefore that O. longinoda pushes M. aculeatus out if they both occur on same tree, especially so since both nest on leaves. This suggestion is further substantiated by the earlier observations that Oecophylla actively besieges and predates Macromischoides. The fact that Oecophylla nests became radioactive and a worker was found with radioactive Macromischoides larva proves beyond doubt that Oecophylla exerts predatory pressure on Macromischoides. Gibbs (1969) asserts however, that Oecophylla succeeds in reducing the Macromischoides population only in areas where it is already low. There seems to be mutual predation between the two species as some Oecophylla remains were found among Macromischoides food store. M. aculeatus may not attack Oecophylla but may kill Oecophylla in self- or nest-defence, or they may still obtain Oecophylla corpses.

Gibbs (1969) claims further that *Crematogaster* is largely excluded by *Oecophylla*. This was confirmed by Collingwood and King (1970) and the present results indicate a very strong negative association between the two ants. The straight fight between *Oecophylla longinoda* and *Crematogaster clariventris* in plot D14 is evidence of the hostility between them.

The same degree of hostility exists between *Macromischoides* and some *Crematogaster* species, especially *C. stadelmanni*. The two ants are antagonistic and fight when in contact. The same cannot however be said of *C. clariventris*. This ant coexists fairly well with *Macromischoides*. In fact the two are mutually tolerant and rarely fight when in contact under normal circumstances. This does not exclude the possibility of fighting if the two ants are suddenly brought together. How *clariventris* comes to occupy *aculeatus* nest is not certain. But it may not be an active process, such as fighting. It is very likely that the occupied nests had been previously deserted by *aculeatus*. The interdigitation of the two ants in Plot C4, (Fig.6.1) may be an initial stage of coexistence. Perhaps they are able to coexist since, though they occur on same tree, they occupy different parts of it. *Macromischoides* nests on leaves, and being largely nocturnal does not usually make use of the branches and stems where *C. clariventris* rests and forages in the day time. When *clariventris* activity declines in the evening, the branches and stems become free for *Macromischoides* to use. Thus differences in nesting and resting sites as well as seggregation in time play an important part in making their coexistence possible. Collingwood and

King's (1970) claim of the rarity of coincidence of *Macromischoides* and all *Crematogaster* ants is thus not true.

Among the minor ants *P. laboriosa* is closely associated with *M. aculeatus*. *Cataulachus* sp. and *Camponotus acvaprimensis* also seem to be neutral but to what extent is not known. *P. rivoili* may occupy deserted *M. aculeatus* nests. *Pheidole* ants are very hostile and responsible for the destruction of many incipient colonies.

Section 7. Interrelationships of *M. aculeatus* with other animals (excluding ants).

7. INTERRELATIONSHIPS OF M. ACULEATUS WITH OTHER ANIMALS (EXCLUDING ANTS)

Introduction

A vast number of arthropods are associated with ants in one way or another and for various reasons. These insects or other arthropods that inhabit ant-nests either throughout life or during one or more of their developmental stages are collectively known as myrmecophiles or ant-guests in a broad sense. Wheeler (1910) subdivided the myrmecophiles into four major groups: Those which live as scavengers or predators and which the ants treat with hostility; those which attract less attention due to their smallness or sluggishness and are thus indifferently treated; the true-guests which are thus amicably treated and even attended; and the parasites both external and internal ones.

Other arthropods or invertebrates in general and some vertebrates predate ants and are called myrmecophags.

A vast literature exists on all aspects of the above subject. Notable and relevant ones for our present purpose are the works of Wasmann, Janet, Wheeler, Imms and Leidy.

Not much attention was given to this subject as a whole. However the little information obtained on some aspects of the subject is given in the following paragraphs.

Materials and methods

Nests brought to the laboratory for population counts were examined for inquilines, parasites and predators. Those found were placed in 70% alcohol and labelled. In the field several ants infested with ectoparasitic mites were collected on leaves far away from their nests. The number of mites and their positions on the body were recorded. Ant workers with distended gasters were dissected and the nematode worms were removed and placed in 70% alcohol. Gut analysis was made on a skink suspected of predating the ants.

Results

The main inquilines found were the psocids which live in the nest wall. These are very small and fast moving. Their number in the nests was very variable, but as many as 48 were counted in one nest. Since they quickly vanished out of sight when a nest was opened they were never observed feeding. Several Collembola were found living with the ants in a laboratory culture. These were scavengers living on the food remains especially the decomposed or dried ones. The Collembola, though not living inside the ant nests, moved freely among them.

Louis (personal communication) has found out that the nymphal instars of some Reduviinae, e.g. Acanthaspis bilineolata predate the ant and deposit the corpses on their backs.

Several Macromischoides ants were found in the gut contents of the skink, Mabuya sp in the laboratory.

The ectoparasites found were some red and brown mites. The red mites attach to the legs, especially the femora, and there might be as many as four on one ant. The infested ants looked very sluggish and usually remained motionless on leaves as if resting. The brown mites are much bigger and attach to the body rather than the legs.

Long white nematode worms were collected from the gaster of many workers. The worms, usually coiled several times over, occupy the visceral cavity and may measure up to 30mm.

Discussion

The psocids (Psocoptera) are synechtrans that feed on the organic waste of the colony. Ofer (1970) reported that they had been seen to attack and harm the cocoons of pupae which had been separated from a colony of Polyrachis simplex. In his list of British synoeketes, Imms (1925) included the Collembola of the genus Cyphodemus. There is however no report in the available literature of their being harmful to their hosts. Possibly since they multiply fast, much faster than their hosts, they might interfere in one way or another with the day to day activity. But in the field M. aculeatus preys on Collembola. Skinks are common in the cocoa farms. They are day feeders that move mainly on the ground but occasionally climb cocoa trees. Though they were never seen predating the ants in the field, it is not unlikely that they do so since the ants forage both on trees and on the ground. The laboratory finding seems to confirm this.

It is very interesting that several ants infested with the parasitic gamasid mites were collected outside the nests and few were found in the nest populations. The reason for this is not clear. Such infested ants will not survive since, as has also been shown by Ofer (1970) working with Polyrachis simplex, they are unable to feed themselves. The nematode worms may also add to the mortality rate.

Leidy (1851) described a similar worm in a grasshopper and claimed that the worm could extend from the abdomen into the head. This may not be possible in the ant which has a constriction between thorax and gaster and may explain the extensive coiling of the worm in the gaster.

Perhaps the worst enemy of *M. aculeatus* is rain storm. Storm damage has recently been found by Leston (personal communication) to cause mass deaths in *M. aculeatus* and *O. longinoda*. The storm forces sandwiched nests apart and dislodge both exposed and sandwiched ones.

Section 8. Nests and nesting habits.

8. NESTS AND NESTING HABITS

Introduction

There is very little information in the vast ant literature on the nest and nesting habits of Macromischoides aculeatus. The earliest mention of it was by Santschi in 1909 (quoted by Wheeler, 1922) who described the structure of the nest as consisting of the "leaf of a tree or shrub rolled up and lined with a felt-work of very fine vegetable debris and of a mycelium bearing fructifications". In 1916 Forel (quoted by Wheeler, 1922) commenting on the variety rubroflava remarked that it was found in nests woven of silk and fixed to leaves. Wheeler (1922) took both authors to task for their "miscomprehension" in regard to the structure of the nest. He correctly described the nests as consisting of particles of the most diverse vegetable substances, bits of bark, dead leaves, trichomes etc. loosely felted together and invaded by a fungus mycelium bearing no fructifications. Nicol and others working at the then W.A.C.R.I. (now C.R.I.G.) described the nest as "carton" and built on the underside of leaves of trees and shrubs (reported by Voelcker, 1947). Ledoux (1958) describing the nest erred by including soil particles in the building materials. Ledoux's illustrations are inaccurate.

The present work aims at correcting some of the errors of the earlier authors and at providing more information on the description, materials, construction, architecture, and type of nests, as well as the light and height preferences of the nesting sites, not leaving out information on the causes of nest abandonment and the stimulus for nest building.

Materials and methods

Nest building - Several workers from three nests together with brood and one queen were released into a glass cage containing three cocoa seedlings as well as leaves, pods and twigs of cocoa, fresh and dry leaves and also fruits of Solanum verbascifolium, a shrubby weed common in cocoa farms, in addition to litter from the cocoa farm and soil in petri dishes. The aim was to simulate the cocoa farm environment as much as possible. The legs of the table on which the cage sat were stood in cans containing gas oil to keep out other insects. Water was provided in petri dishes and the ants were fed on insects obtained by sweeping. The contents of the sweeping net were squashed to weaken the insects and then the entire contents were emptied on the board or cage for the ants to select their prey. Several replicates were set up, but big open boards were substituted for glass cages. One such arrangement is shown in Plate 8.1. The effect of light was determined by performing a similar experiment in a dark room. Field observations were also made on the method and materials of nest building. Many ants carrying building materials were intercepted and robbed of their load.

Stimulus of nest building: Experimental arrangements similar to the above were used to investigate the stimulus for nest building. Workers from the same or different nests but belonging to the same colony were divided into two groups. One group was given brood only or brood and reproductive male and female alates. The second group was either left without any brood whatsoever or in some cases with reproductives or brood

Plate 8.1: Laboratory arrangement for rearing
<u>*M. aculeatus*</u>.

introduced at a later period. In the field the workers that came out to attack when a nest was disturbed were made to move on to a twig and carried far away from their nest tree to be treated as 'without brood'. Those remaining with the brood inside the nest were forced out together with the brood on to the ground. The two groups were then observed for nest building.

Nest architecture: To investigate the internal structure of and arrangement of brood and castes in nests several nests were removed from the trees with a pair of secateurs and immediately dropped into a large polythene bag containing a large amount of either chloroform or ethyl acetate. The ants became unconscious and movements ceased almost instantly, thus much of the internal arrangement of brood and castes was preserved. Back in the laboratory each nest was sectioned with a pair of scissors into strips of about 5cm wide from petiolar to apical ends. The contents of each strip were examined and recorded.

Description of a cocoa tree: A typical cocoa tree has a short main stem (usually straight) which forks into 3-5 almost horizontal branches (the so-called 'fans' or jourquette') about 1-2 metres above ground to form the first storey or tier. Suckers grow from the fans into straight vertical stems (chupons) which give rise to more fans thus constituting a second storey. Trees may be found with three to five storeys depending on plantation practice. The maximum height is however about 10 metres (Urquhart, 1955) although at Tafo the average height is about 5 metres.

The trees usually have a bushy appearance as the branches touch the ground. This is especially so in coppiced cocoa which have several chupons growing from the cut stem.

Nesting habits: Height preference: A long stick marked in metres was held vertically against each tree containing *M. aculeatus* nests and number of nests found within the various height bands were scored.

Nest abandonment: To find out the rate and causes of nest abandonment several nests were labelled. These were observed 28 days later and a record made of the abandoned nests and visible causes of their abandonment, such as ageing leaves, mechanical i.e. nests forced apart by wind, and presence of enemies. Record was also made of new nests built during the period.

Results

The caged ants first took shelter temporarily on the moist soil surface. The following morning about ten workers were noted beneath a silk matrix spun on the under surface of a leaf, stretching from one edge of the leaf blade to the midrib. A depression roofed over by the silk matrix was therefore created. Several workers started carrying building materials composed of pieces of fine rootlets, chips of dry cocoa leaves, twigs,pods, vegetable debris, and pieces of deserted spider webs to the building site. These were disposed randomly on the matrix. Each worker normally worked its own piece of building material into the matrix by the help of the mandibles and the first pair of legs. Several workers would however co-operate in the incorporation of large pieces. Work was at first concentrated on the firmer edges, i.e. areas bordering the midrib and the leaf edge, of the matrix. After these areas were nearly covered, attention was turned to the opening near the petiole. Meanwhile some workers had started carpeting the floor (leaf surface) with very fine vegetable debris glued to the leaf surface. At this stage evacuation of brood from the soil surface into the nest started. Thus building and brood transportation went on side by side.

The large opening at the petiolar end was partitioned. This was done by building a broad-based pillar on the leaf surface and extended to touch the roof. Thus the single opening was divided into two. Later one opening was sealed leaving only one small opening which served as the main entrance. The opening at the apical end was similarly divided into two by a pillar, but both were later sealed. Another pillar was seen under construction inside the nest, but it became difficult to find out what was happening inside the nest since it was nearly covered over. By the third day extension work had began on the other half of the leaf blade. Materials brought in were glued to the main lateral veins as shown in Fig.8.1. These served as foundations upon which walls were built. The ants successfully roofed over the space between two adjacent veins. It was noticed at this stage that the number of workers on the job had started decreasing and work was almost coming to a stop. Further investigation revealed a large nest that the ants had built underneath the table. This became their permanent nest. Several nests were constructed in the laboratory in corners of stools; indeed the ants nearly always ignored the seedlings provided them. In all, four nests were successfully built on leaves of cocoa seedlings but a silk matrix was used in only one. Some of the nests built in the corners of

NEST CONSTRUCTION

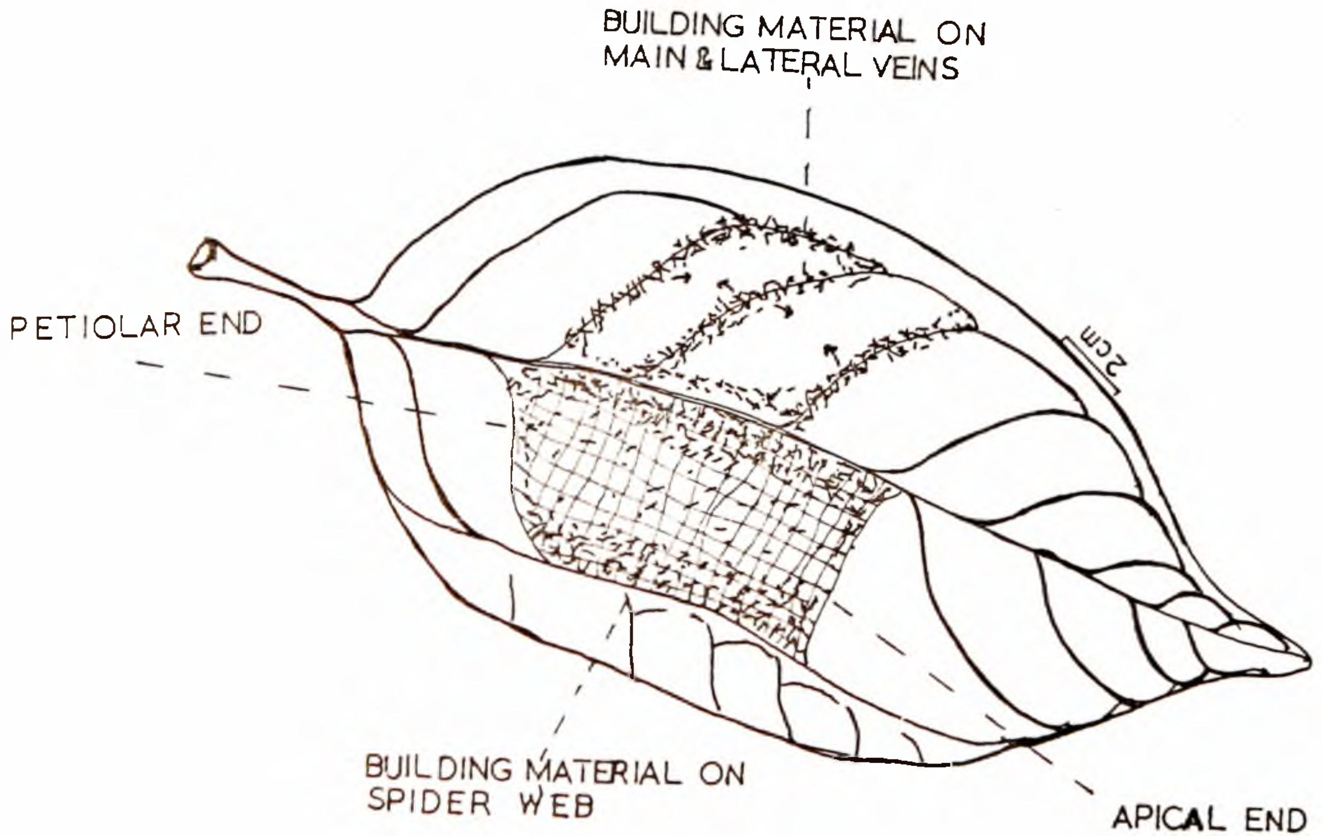


Fig 81

stools and other obscure places are shown in Plates 8.2 - 8.6. The ants kept in the dark built a nest on top of a metal plate that fastened the tap in the room to the wall.

Under normal conditions in the field the ants usually chewed the pieces of building material into a pulp, thus making it very difficult to recognise them. On almost all occasions building started right on the leaf surface along the main veins. On one occasion in plot C5a that some 'displaced' ants were found depositing building materials on a deserted spider web, while others took shelter in a crevice in the stem. This nest was however never finished.

Building can go on during the day but more usually it coincided with foraging in the night. Thus both food and building materials were transported simultaneously during the activity period.

Nests could be built either of homogenous or heterogenous materials, but always of vegetable origin. Plate 8.5 shows a long tubular nest built in a corner between a board and a stool. This nest was built with cotton wool fibres only. However, some paper material scrapped from an empty sugar packet shown in Plate 8.1 was incorporated later. Paper used in the field to label the nests was chipped off, reduced to pulp and used in nest building. The white part of the nest shown in Plate 8.7 is an example of this. Several nests found in the field were built solely with chewed leaves and fruits of Solanum verbascifolium. During the harmattan when kapok or silk cotton, the fibres surrounding the seeds of Ceiba pentandra (Bombacaceae), was very common extensions were made to many existing nests using only this material. More commonly,

Plate 8.2: Nest constructed on the underside of a laboratory stool.

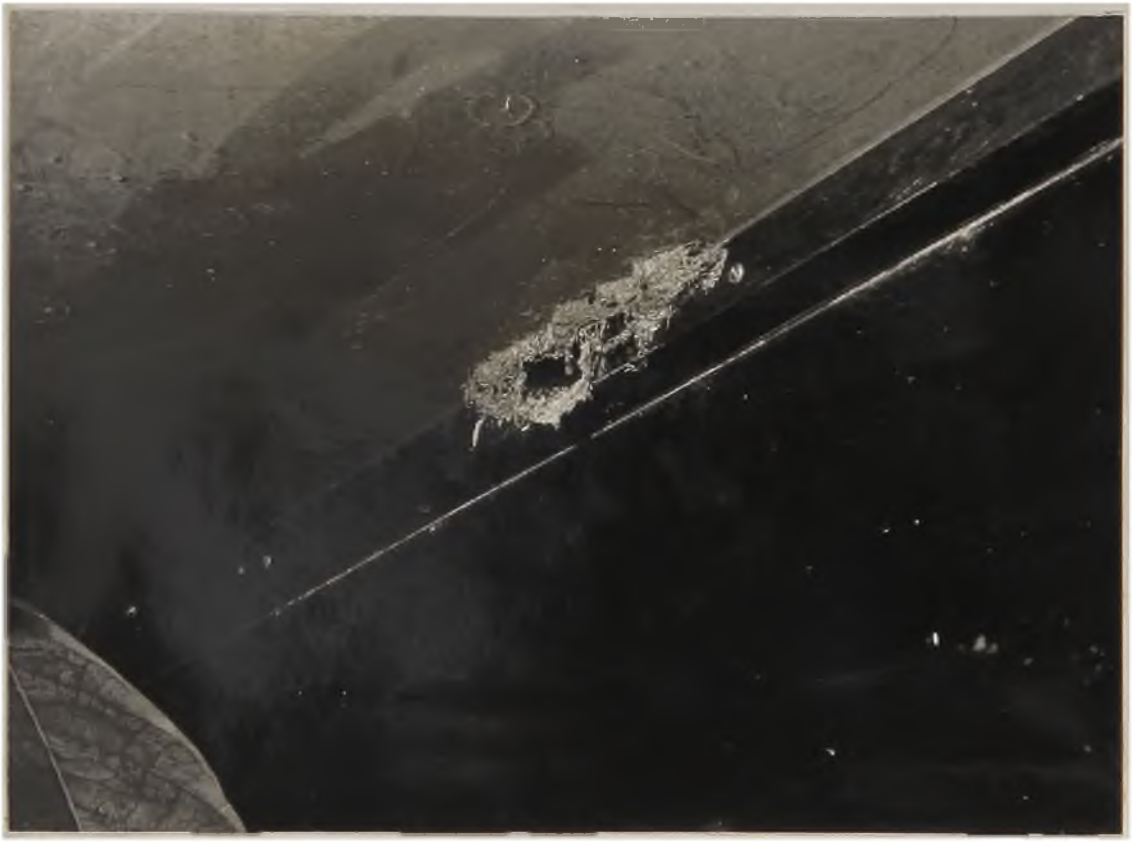


Plate 8.3: Nest constructed on a top corner of a glass cage.

Plate 8.4: Two out of four nests constructed under a laboratory stool.

Plate 8.5: Long tubular nest constructed mainly with cotton wool fibres in a corner between a board and a stool.

Plate 8.6: An unfinished nest on the side of a stool.

Plate 8.7: An exposed nest with the white part constructed from paper and the black portion from the usual building materials.

however, nests are constructed of heterogenous vegetable materials as already described above.

On the floor and walls of many nests were ramifications of fungal mycelium. The walls of some few nests seemed to have a moss covering. Usually the floor of the nest has a wet shiny appearance, as if polished with a wax-like substance.

Nest architecture: The various sections cut showed that a nest has two main architectural plans. It may either be single tier or several tiers. Single tiers were very common in sandwiched nests where growth in depth was hampered by the leaves that form the floor and the roof. These nets were longer and broader than they were deep. Exposed nests usually tended to be more compact and contained two or even several tiers of intercommunicating compartments. It was also evident from the sections that no special cells were given to a particular caste or instar. Thus eggs, larvae, pupae, and workers could be found in all the compartments though there might be a predominance of a particular developmental stage, say, larvae, in a particular chamber. No special queen cell was also found.

Types of nests: As has already been outlined above there are two main types of nests: exposed and sandwiched nests. The former are usually single compact nests constructed on the adaxial parts of a leaf or leaves. In this type the leaf surface forms the floor whilst a definite roof is constructed. These nests are usually more complicated, and contain more cells or compartments than the sandwiched ones. The sandwiched ones may be built between leaves either on the same branch or different branches on the same tree or from different trees. Here the abaxial side of one leaf forms the floor, whilst the roof is formed by the adaxial surface of another leaf. Types of nests are shown in Plates 8.8a & b.

Nesting habits: The results of the investigation to determine the preferred height for siting nests are shown in Table 8.1 and Figs.8.2 and 8.3. It was found that the preferred height lies between one and two metres from the ground as shown in Fig.8.2. Few nests are found above three metres from the ground and none above four. When the ants were displaced they took shelter in cavities, crevices and forks of trees in the field. Some workers from a laboratory culture broke off from the mother colony and occupied a hole in the soil in which a seedling was grown. This is shown in Plate 8.9.

Stimulus for nest building: Workers with either brood only or brood plus reproductives always built nests and very fast too. They initially found temporary shelter for the brood under stones, leaves and other shaded and moist places before nest building started. In all the four laboratory and three field trials, nests were built in each case. In one out of the seven trials, workers with alate reproductives built only an unfinished nest in the laboratory. Workers without brood, however, always failed to build nest, but if the brood was added later they then constructed a nest. The results are shown in Table 8.2.

Nest abandonment: Analysis of the data obtained show that 62% of nests found deserted were on normal green leaves, 28% were on either dead or dying leaves and 10% on both normal and ageing leaves (Table 8.4). Also, in a period of 28 days, 50 nests or 18% of the total number of

Table 8.1

Height of nests above ground

Tree	1m	2m	3m	4m	Total
10b$_1$					
1	7	2	0	0	9
2	0	6	2	0	8
3	0	5	2	0	7
4	0	1	0	1	2
5	0	2	0	0	2
6	0	3	0	0	3
7	0	4	2	0	6
8	8	9	3	0	20
9	3	1	2	0	6
0	0	13	4	0	17
1	0	9	8	1	18
2	0	4	1	0	5
3	0	2	0	0	2
4	0	2	0	0	2
5	0	1	0	0	1
10b$_2$					
6	0	5	0	0	5
7	0	2	0	0	2
8	0	2	1	0	3
9	0	12	1	0	13
20	0	0	1	0	1
10b$_3$					
21	0	6	0	0	6
22	0	2	0	0	2
23	0	1	0	0	1
24	0	0	1	0	1
4					
25	1	0	1	0	2
26	1	4	0	0	5
27	0	2	0	0	2
28	0	1	0	0	1
29	0	6	0	0	6
30	3	4	2	0	9
31	1	1	0	0	2
32	1	2	1	0	4
33	0	1	0	0	1
34	0	0	1	0	1
35	3	2	0	0	5
36	2	0	1	0	3
37	0	1	0	0	1
38	0	5	0	0	5
39	0	7	1	0	8
40	0	1	3	0	4
41	2	3	0	0	5
42	0	1	0	0	1
43	0	9	0	0	9
44	0	2	3	0	5
45	0	4	1	0	5
46	1	2	0	0	3
47	0	3	0	0	3
48	0	9	0	0	9
49	2	4	0	0	6
50	0	9	1	0	10
51	2	6	0	0	8
52	2	3	1	0	6
53	0	1	2	0	3
C5a					
54	3	1	0	0	4
55	3	1	1	0	5
56	0	1	0	0	1
57	1	4	2	0	7
58	0	3	1	0	4
59	0	2	0	0	2
60	0	1	0	0	1
61	0	6	0	0	6
62	0	1	0	1	2
63	6	7	0	0	13
64	0	1	0	0	1
65	1	1	1	0	3
66	0	1	0	0	1
67	0	2	0	0	2
68	0	1	0	0	1
69	0	1	0	0	1
Total	53	221	51	3	328

PREFERRED HEIGHT FOR SITING NESTS

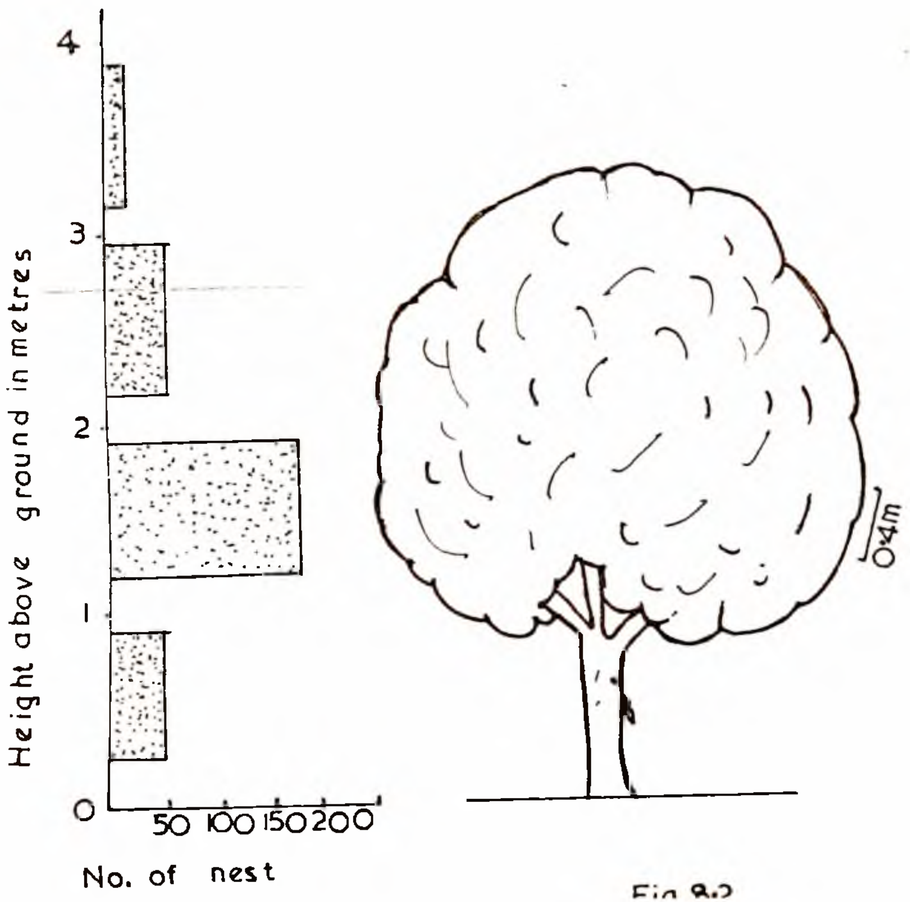


Fig 8.2

Table 8.2

Stimulus for nest building

Treatment	Results
Workers only	No nests
Workers plus alates	No nest
Workers plus brood (from start)	Nest built
Workers plus brood (later)	Nest built
Workers plus eggs plus queen	Nest built

Table 8.1

Height of nests above ground

Tree	1m	2m	3m	4m	Total
$\mathrm{H10b}_1$					
1	7	2	0	0	9
2	0	6	2	0	8
3	0	5	2	0	7
4	0	1	0	1	2
5	0	2	0	0	2
6	0	3	0	0	3
7	0	4	2	0	6
8	8	9	3	0	20
9	3	1	2	0	6
10	0	13	4	0	17
11	0	9	8	1	18
12	0	4	1	0	5
13	0	2	0	0	2
14	0	2	0	0	2
15	0	1	0	0	1
$\mathrm{H10b}_2$					
16	0	5	0	0	5
17	0	2	0	0	2
18	0	2	1	0	3
19	0	12	1	0	13
20	0	0	1	0	1
$\mathrm{H10b}_3$					
21	0	6	0	0	6
22	0	2	0	0	2
23	0	1	0	0	1
24	0	0	1	0	1
25 D14					
25	1	0	1	0	2
26	1	4	0	0	5
27	0	2	0	0	2
28	0	1	0	0	1
29	0	6	0	0	6
30	3	4	2	0	9
31	1	1	0	0	2
32	1	2	1	0	4
33	0	1	0	0	1
34	0	0	1	0	1
35	3	2	0	0	5
36	2	0	1	0	3
37	0	1	0	0	1
38	0	5	0	0	5
39	0	7	1	0	8
40	0	1	3	0	4
41	2	3	0	0	5
42	0	1	0	0	1
43	0	9	0	0	9
44	0	2	3	0	5
45	0	4	1	0	5
46	1	2	0	0	3
47	0	3	0	0	3
48	0	9	0	0	9
49	2	4	0	0	6
50	0	9	1	0	10
51	2	6	0	0	8
52	2	3	1	0	6
53	0	1	2	0	3
C5a					
54	3	1	0	0	4
55	3	1	1	0	5
56	0	1	0	0	1
57	1	4	2	0	7
58	0	3	1	0	4
59	0	2	0	0	2
60	0	1	0	0	1
61	0	6	0	0	6
62	0	1	0	1	2
63	6	7	0	0	13
64	0	1	0	0	1
65	1	1	1	0	3
66	0	1	0	0	1
67	0	2	0	0	2
68	0	1	0	0	1
69	0	1	0	0	1
Total	53	221	51	3	328

PREFERRED HEIGHT FOR SITING NESTS

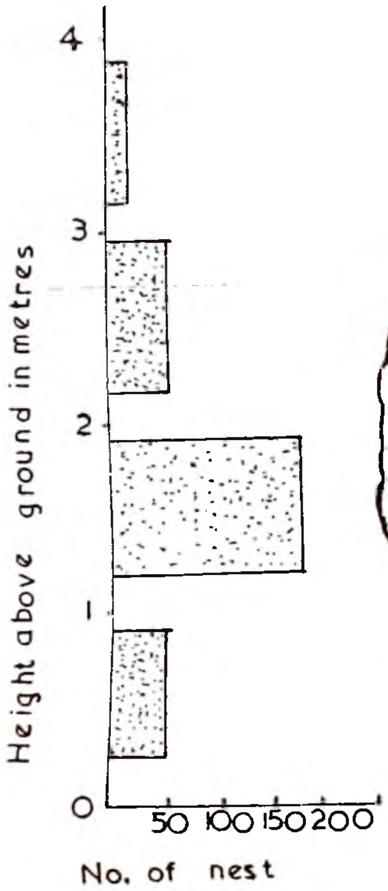


Fig.8.3.

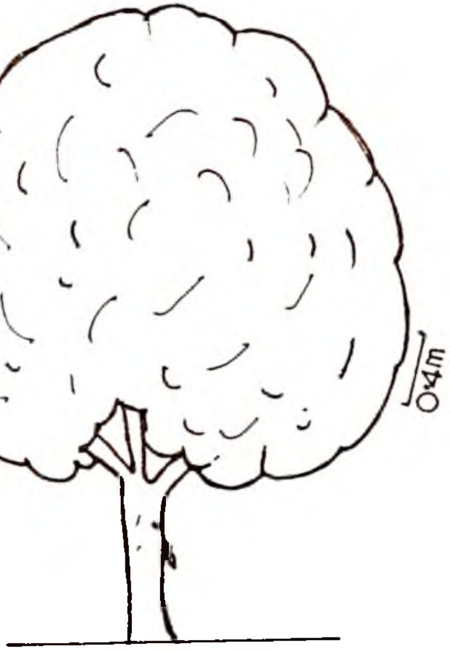


Fig 8.2

Table 8.2

Stimulus for nest building

Treatment	Results
Workers only	No nests
Workers plus alates	No nest
Workers plus brood (from start)	Nest built
Workers plus brood (later)	Nest built
Workers plus eggs plus queen	Nest built

Table 8.3

Causes of nest abandonment

Plot	Nol of nests	Nest No.	Condition of leaf		Remarks
			Fresh	Ageing	
H10	1	55	-	+	A new nest nearby
	2	36	+	-	-
	3	37	+	-	New nest nearby
	4	38	+	+	Increase population in 39
	5	30	+	-	Increase population in 29
	6	10	+	-	-
	7	27	-	+	-
	8	24	+	-	New nest nearby
	9	6	+	-	-
	10	28	+	-	Leaves forced apart
	11	5	+	-	-
	12	71	+	+	New nest being built
	13	73	-	+	Only nest area brown
	14	82	+	+	-
	15	84	+	-	Nest washed off by rain
	16	86	+	-	Nest washed off by rain
	17	89	+	-	New best nearby
	18	91	-	+	Only nest area brown
	19	95	-	+	Only nest area brown
	20	120	-	+	-
	21	121	-	+	Nest dropped. New nest nearby
	22	115	+	-	Oecophylla around area
	23	112	+	+	-

Table 8.3 (continued)

Plot	No. of nests	Nest No.	Condition of leaf		Remarks
			Fresh	Ageing	
C5b	24	31	+	+	-
	25	1	-	+	Nest dropped
	26	35	+	-	Few workers present
	27	11	+	-	New nest nearby-
	28	36	+	-	Dropped
	29	44	+	-	New nest nearby
	30	8	+	-	-
	31	47	+	-	-
	32	7	-	-	Missing
	33	68	-	+	Dropped
	34	6	+	-	-
	35	19	+	-	-
	36	12	+	-	-
	37	14	+	-	-
	38	15	-	+	New nest nearby
	39	16	+	-	-
	40	17	+	-	-
	41	21	+	-	-
M4	42	32	-	+	-
	43	35	-	+	Nest area only brown increase population in 36
	44	31	-	+	Nest area only brown
	45	16	+	-	Leaves forced apart

Table 8.3 (continued)

Plot	No. of nests	Nest No.	Condition of leaf		Remarks
			Fresh	Ageing	
	46	28	+	-	-
	47	33	+	-	New nest nearby
	48	48	+	-	Increase population in 49
	49	13	+	-	-
	50	6	-	+	Nest area only brown

Table 8.4

Breakdown of deserted nests

	Fresh leaves (A)	Ageing leaves (B)	Both A and B
No. of nests	31	14	5
Percentage	62	28	10

Table 8.5

Further analysis of Table 8.3.

	Nests labelled	Deserted nests	New nests
Total No.	277	50	9
Percentage	-	18.0	3.2

Plate 8.8a. Exposed nest of M. aculeatus found in the field.

Plate 8.8b. Types of sandwiched nests of M. aculeatus found in the field.

Plate 8.9: *M. aculeatus* nesting in a hole in soil.

nests (277) were deserted, and within the same period 9 new nests forming 3.2% of total number of nests were constructed as shown in Table 8.5. Table 8.3 gives the raw data.

Discussion

The occurrence of silk in *M. aculeatus* nest does not seem to be normal. In fact silk was found in only two nests out of the thousands of nests examined both in the field and the laboratory. On each of the two occasions the ants were disturbed. They were therefore forced by circumstances to seek shelter. Since *Macromischoides* will, if disturbed, build nests anywhere using any available vegetable materials provided brood is present it is not surprising that in these two cases they incorporated a deserted spider web into the nest. Similar occurrences might have misled Santschi (1909) and Forel (1916) to include silk in their description of the nest, ignorant of the fact that adult ants do not produce silk and Myrmecine ant larvae have no silk glands (Wheeler, 1922). Usually building materials are deposited directly on the leaf surface and glued to it, as described by Ledoux (1958). From observations made it appears the glue comes from the mouth, as the gaster was never involved in the building process. Maschwitz *et al* (1970) claimed that *Lasius fuliginosus* workers use honey-dew and sugar solution as glue and not secretions from the mandibular glands. But since *M. aculeatus* is able to build nests in the laboratory where there was no honey-dew or sugar solution suggests that some natural secretion was being used. Moreover there was no discernible difference in the consistency of the nests built in thefield and laboratory. The secretion is possibly derived from the mandibular glands. No soil particles or for that matter any earthen materials were ever found among the building materials, contrary to the findings of Ledoux (1958). Moreover the fact that no solid particles remained after burning the nest proves the absence of any soil particles. Ledoux (1958) also claims that elongated pieces of leaf and moss are used in building nests. Leaves are certainly used but they could seldom be recognised as the ants usually chew them and reduce them to pulp. Moss occurred very infrequently in nests; when it did occur it was growing mainly in the outer wall and not incorporated in the nest as Ledoux has claimed. The part played by the fungus mycelium found in the nests is not well understood. The claim by some authors, for example Elliott (1915) dealing with Lasius, that the fungal hyphae give stability to the nest wall by binding the building particles together is not applicable to the case of Macromischoides since not all nests collected from the field and none constructed in the laboratory had fungal ramifications; yet their walls were as firm as those which contain mycelium. Wheeler's (1922) suggestion that the high moisture content of the environment encourages fungal growth seems reasonable. Moreover the carpeting substance, as well as honey-dew from the coccids found in nest floor, are very likely to form a very good substratum for fungal growth.

In the field, nests were nearly always found constructed on leaves although on two occasions nests were found built on a stem over a group of young coccids (Plates 5.1 - 5.3). Thus the habit of constructing nests under stools in the laboratory rather than on leaves may be due to a negative response to light. The building of a nest on top of a metal plate in a dark room lends support to this suggestion. Thus light may play an important part in the selection of nesting sites on a tree. Perhaps the preference of the 1-2 metre-level is due, among other things to the low level of light intensity. Similarly the habit of taking shelter in crevices and holes can be explained in terms of light avoidance. Although there is no quantitative evidence, field observations show that sandwiched nests are found more commonly in open areas than in heavily shaded areas within a colony. It is also interesting that three out of the four nests built in the laboratory on cocoa seedlings in the glass cage were sandwiched. Thus light seems to influence both the siting of nests and their type.

Brood, it has been claimed, encourages foraging activity. The present work has established that brood not only encourages foraging activity but nest building as well. Thus, perhaps, the faster the queen lays eggs and more larvae and pupae are produced, the more the workers are stimulated to build nests to enlarge the colony.

It is very difficult to determine the causes of nest abandonment. It may possibly be due to absence of brood, workers vacating their own nests to join others which have brood. This is supported by the fact that after the mating flight, a 'regrouping' of workers takes place; a few nests become highly populated while large numbers are deserted. The populated nests almost invariably contain brood. Thus it appears that after the nup~~t~~ial flight, the few brood left in various nests are concentrated into a few nests followed by their nurses. Similar movements during the pre-flight period may account for the abandonment of nests. The observation that 18% of nests were deserted while only 3.3% new ones were constructed over the same period, probably, indicates that several of the inmates of the deserted nests moved into other already existing nests.

Section 9. Flight activity, colony founding and colony expansion.

9. FLIGHT ACTIVITY, COLONY FOUNDING AND COLONY EXPANSION

Introduction

For a better understanding of the ecological and geographical distribution of ant species, a knowledge of mating flights and of the behaviour of fertilized females in founding colonies is essential. This is so because the mating flights constitute the only dispersal phase in the life of ant colonies and the behaviour of the mated females in selecting nesting sites will determine the distribution of colonies.

Much work has been done on both aspects. Investigators on flight activities include Talbot (1943, 1948, 1956, 1957) and Talbot and Kennedy (1940). Wheeler (1933) has also laid the foundation for the study of colony founding behaviour of fertilized females.

Much work has been done on colony founding behaviour of the temperate species of the primitive subfamilies, Myrmecinae and Ponerinae. Notable among these are works of Wheeler (1933) and Haskins and Haskins (1950) on <u>Myrmicia</u> and <u>Odontomachus</u>. These primitive ants have an independent method of colony founding, by which the female forms a brood chamber which has an external opening permitting her to forage for food while her eggs develop. They therefore form a link between the true social hymenoptera and the solitary members of the Order.

Colony founding behaviour of the Myrmicinae has however been relatively neglected. It is intended to study the nuptial flight, colony founding and its expansion in <u>M. aculeatus</u> a tropical member of the subfamily in this work.

Materials and methods

Mating flight: No light trap was ran personally. However data obtained by J. Majer from one he ran at Kade from February 1971 to May 1971, thus coinciding with the period of this work, have been used with his permission.

Incipient colonies: (i) Field: Several trees were examined for incipient colonies (single small nests). Each incipient colony found was carefully lifted up with a pair of forceps and queen gently driven out. The contents of the nest were examined and record made of number of eggs, larvae, pupae and adults (callows). A few incipient colonies were examined from time to time to investigate the frequency of egg laying.

(ii) Laboratory: Six mated females (dealates) collected from around light in a house at Tafo were put into match boxes and petri dishes and provided with food (insects and sugar solution) and water. One half of the petri dish was covered. They were supplied with cotton wool. Some alate males and females were also placed together in two petri dishes to observe mating behaviour. In the laboratory ten alate females, seven alate males and eight workers were placed in a glass breeding cage (Fig.10.1) and provided with food and water.

Results and observations

Flight activity: The results shown in Fig.9.1 are based on light trap catches and indicate that flight activity started in February and with but few fluctuations remained low until April, when there was a sudden rise during the third week, reaching a peak the following week. This was then followed by a sharp drop in the first week of May.

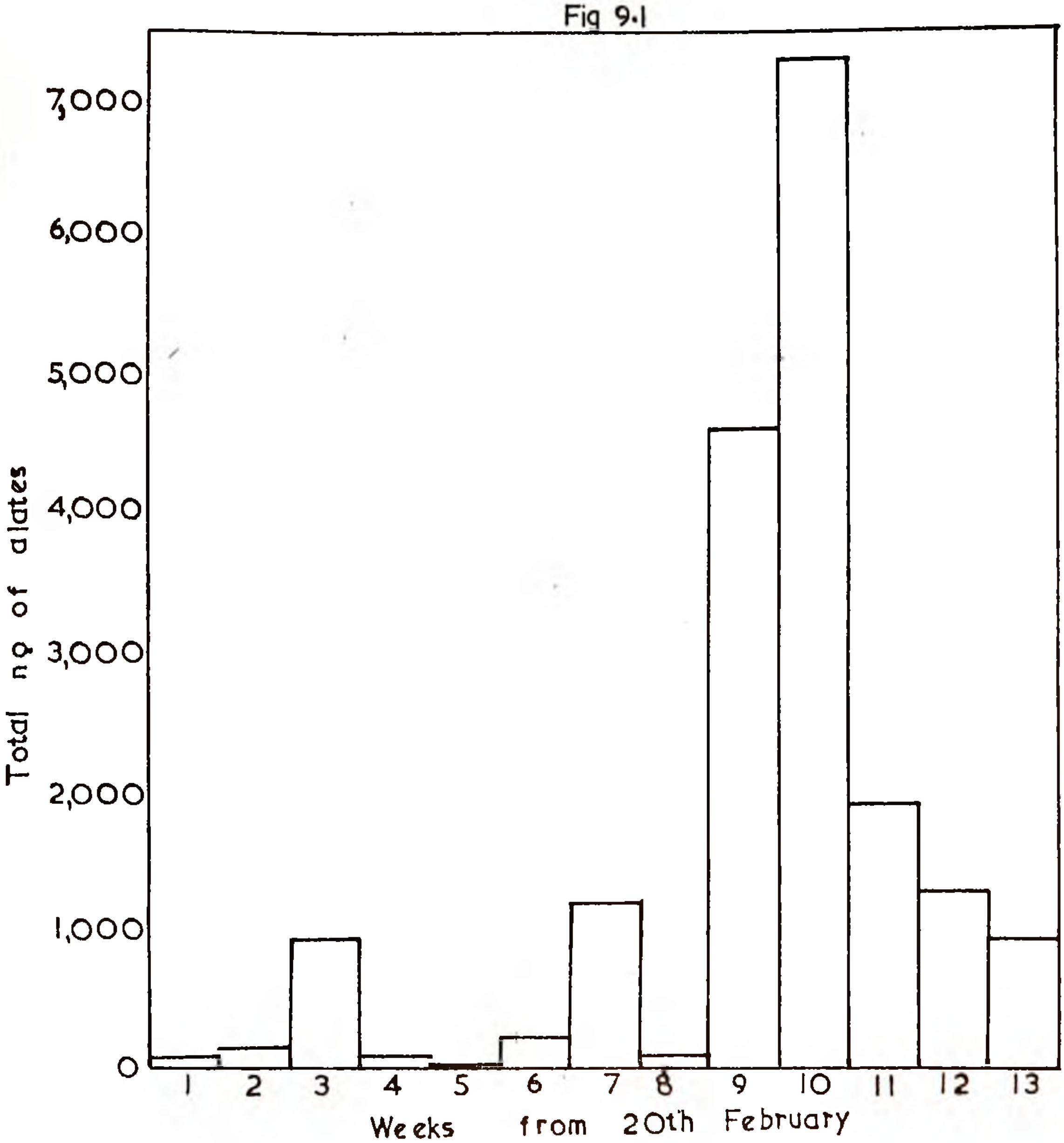


Fig.9.1: Flight activity of <u>*M. aculeatus*</u> alates. Kade. U.V. trap.

Incipient colonies: Table 9.1 summarises the results of the analysis of the nest contents of the 24 incipient colonies examined. The results indicate that more than one mated female may alight and found a colony on one tree. Four were found on one tree, three on another and three again on a third. It is evident that the initial batch of eggs is very small, varying from two to six. This is inferred from the number of larvae (both advanced and young) obtained from each colony. Even the next batch of eggs seems to be quite small and not more than 24. Field observations tend to show that the queen starts laying as soon as the foundation of the nest has been laid; and that egg laying and nest construction proceed simultaneously. The evidence for this is the mated female in nest 18, Table 9.1. This female was found when she was putting building materials on a leaf to start a nest and on examination one egg was found in thenest. On one occasion an incomplete nest was found with four eggs in it. At the end of a week the number of eggs had increased to thirteen, and the nest was nearly completed.

None of the mated females put into match boxes and petri dishes lived long enough to lay eggs. They all died within four days without attempting to construct nests.

Behaviour of alates: The alate pairs in petri dishes did not mate. The females were found to be more active than the males. Usually a female may prod a male with her antennae, and at times climb on top of the male. At times several females might crowd over a male. No mating took place, as none of the females shed her wings. Similar observations were made in the laboratory breeding cages. Six out of the seven males were found

Table 9.1

Colony founding

Incipient colonies (C5a - 25th April 1971)

Tree	Nest	♀♀	No. of Eggs	No. of Larvae	No. of Pupae	No. of Callows	Remarks
1	1	1	21	-	-	-	
1	2	-	-	-	-	-	
2	3	1	9	-	-	-	
2	4	-	-	-	-	-	
3	5	-	-	-	-	-	
4	6	1	9	6 4 big 2 small	-	-	
5	7	1	6	4 3 big 1 small	-	-	
6	8	1	12	31	14	22	On same tree with fairly old incipient colony (1 nest).
7	9	1	15	2	-	-	
8	10	1	20	2	-	-	
9	11	1	2	-	-	-	Nest quite old.
9	12	1	17	6 4 big 2 small	-	-	
9	13	1	17	2	-	-	
9	14	Not found	10	3	-	-	
10	15	1	20	4	-	-	
11	16	1	16	4	-	-	
11	17	1	6	6 4 big 2 small	4	4	
11	18	1	1	-	-	-	Nest under construction.
12	19	1	22	4	-	-	
12	20	-	-	-	-	-	
12	21	1	3	-	-	-	
13	22	1	13	-	-	-	
14	23	1	8	-	-	-	
15	24	1	24	3	-	-	
15	24	20	251	77	18	26	

dead with part of their gaster eaten; a similar occurrence has been found in nests. The ten females were always found surrounding the remaining male. They were kept for sixty-five days, but they did not mate, the females retaining their wings throughout. One, probably mated female, from another laboratory culture in a glass cage, was however found on a cocoa seedling trying to drop her wings. This she did by vigorous flexing of the thorax and constantly brushing the wings with the hind legs. Unfortunately she did not succeed in dropping her wings before she fell into a dish of water. She was rescued from drowning but did not continue the operation.

Discussion

Flight activity starts in February at the end of the dry, sunny season and continues to rise steadily to reach a peak in April-May just before the heavy rains begin in June. This finding is in complete agreement with that of Billes (1946) and also with my earlier results on seasonal patterns in section 4. The period of swarming and thus of colony founding coincides mainly with the first wet, sunny, and partly with the first wet-dull seasons of Gibbs and Leston's classification. These periods are characterized by low temperatures, moderately low light intensities and high humidities. These weather conditions may perhaps be ideal for swarming. This sort of weather is possibly essential for the first batch of eggs, if they are going to escape desiccation, since they are deposited in unfinished nests and thus exposed to the atmosphere for as long as the nests remain unfinished.

What environmental factor or factors serve as a releaser for nest building is not known, but it is likely that the presence of the first batch of eggs may serve as a stimulus for its completion, since the presence of eggs (queen was present) has been shown to stimulate workers to build a nest (Section 8).

The life of a cocoa leaf has been shown by McKelvie (1962) to be about eight or nine months. Thus nests constructed on the new leaves formed after the leaf fall in the dry season are likely to be retained for that long. This then may make the colony more stable than if the leaves had a short retention period. The large area of leaves during the rains and after, may also help the alighting of females and establishment of nests (Billes, 1946).

<u>Incipient colonies:</u> It is unfortunate that the ants were not seen mating. Marikovsky (1961) has reported that females of <u>Formica rufa</u> bit off the abdomen of males mating with them; thus perhaps the males found dead with their gaster bitten off may have attempted to mate with females.

The finding that several mated females can establish incipient colonies on one tree, and several incipient colonies can be found on several contiguous trees is interesting. It has been established earlier that a colony of several nests normally has only one queen. Thus some elimination of incipient colonies must take place. Presumably one colony might take over the workers of another, while killing one of the queens, or kill both workers and queen. Perhaps the fecundity of one queen, as well as the numerical strength coupled with the ferocity of the early workers might be contributory to success, while doubtless many young nests fall victims to predation by other insects or are last as a result of the dropping of leaves.

It will be useful at this stage to construct a continuous story of colony founding from the information available.

There is a mass flight of males and females from the nests, mostly at night. It is not yet known whether swarming occurs from all nests of a colony at the same time or whether the alates in different nests of a colony may swarm at different times or even whether all alates in a nest leave on the same night. Females are fertilized, after which they shed their wings by brushing them with the feet and flexing the thorax. Each dealate female constructs a small, dome-shaped, open nest on the underside of a leaf as shown in Plate 9.1. Several females may nest on one tree or on contiguous trees. Egg laying starts as soon as the female starts putting down material for a nest and may continue until the nest is finished. Initially a small number of eggs is laid, usually four. These are tended and hatched and the young fed by the female. The female is very active during this period.

By the time the first batch of workers emerge, more eggs may have hatched and they, together with the queen, nurse the young larvae. From field observations it seems as if the queen remains active for a long time, foraging and nursing brood, but eventually with an increasing worker population the queen assumes the role of egg-laying only.

As the number of workers increases and more brood are produced, the original incipient colony is expanded and new nests are built away from

Plate 9.1: A young nest built by a queen.

the mother nest. Eggs, larvae and pupae are continually removed from the queen's nest into the satellite ones.

The story as outlined here agrees in essential details with Wheeler's (cited by Haskins & Haskins, 1950) hypothesis concerning the 'normal' method of colony found in the higher ants, as well as in *Myrmecia* and the ponerines including *Odontomachus*.

Section 10. Some aspects of the life history

10. SOME ASPECTS OF THE LIFE HISTORY

Introduction

It appears from the general accounts of the life history of ants given by Wheeler (1910), Forel (1928) and Imms (1925) that ants exhibit the usual holometabolous development of egg-larva-pupa-adult. But usually interposed between the larval and pupal stages is a semi- or prepupa. The simplest description of this will be "pupa in larval skin". Few accounts, however, exist on the life history of specific ants. The most recent one by Ofer (1970) on Polyrachis simplex shows that the egg, larval, and pupal stages lasted 15, 24 and 21 days respectively.

The life history of Macromischoides aculeatus has not been worked out. Wheeler (1922) has described the adult worker, male and female as have the larvae by Wheeler and Wheeler (1955). The eggs and pupae have not been described.

An account of the few observations made on life history as well as adult and brood behaviour are given below.

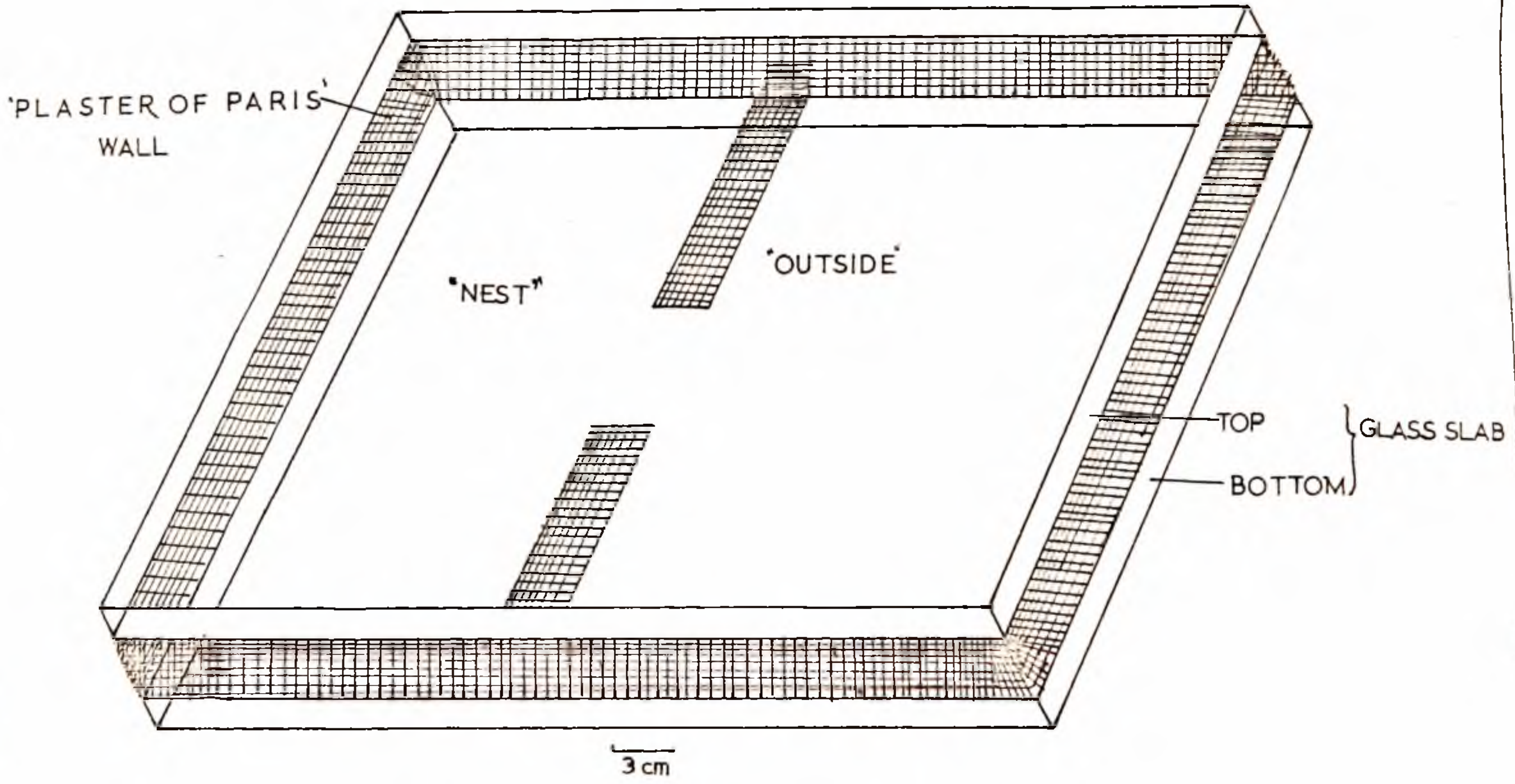
Materials and methods

Breeding cages: The Fielde model was used with slight modifications. Walls of about 5mm height and with a basal width of about 15mm but tapering upwards were raised round the four edges of a glass slab, using either plasticine or Plaster of Paris. The former material was later rejected due to its strong smell. A partition wall was built to divide the cage into two unequal, intercommunicating chambers. The smaller chamber was to be used as the 'nest', while the bigger one represented the 'outside world' where the ants could forage or dump refuse. A piece of cotton wool soaked with water was placed inside the nest to raise the humidity. Loose pieces of cotton wool were also added to serve as building material for the ants. Food in the form of insects and sugar solution, as well as water were provided in the bigger chamber in small plastic cups and petri dishes. A second glass slab was then placed on top, making sure that all escape routes were blocked with cotton wool. A thick book placed on top of the nest-side served to darken the smaller chamber (Fig.10.1).

Transfer of ants into cage: Initially the ants were immobilized by placing them briefly in a chloroform or ethyl acetate chamber. This method was abandoned later as it was not producing the desired result due to timing difficulties connected with the use of the anaesthesia. Carbon dioxide was also used for sometime. The method most frequently used was simply to open the nest without immobilizing the ants in any way. The contents were quickly shaken into the nest and covered. The remaining ones were trapped in cotton wool fibres and placed into the cage. This was done by dabbing a piece of cotton on the ants. Carbon dioxide was however used whenever the nest contents needed sorting.

Observation chambers: Either eggs, larvae or pupae were put into a small petri dish together with workers to attend them. Wet or dry blotting paper or cotton wool was placed on the floor of the dish depending on the type of brood. Eggs and larvae received the wet treatment, whilst pupae were given dry blotting paper or cotton wool. The petri dish was

Fig 10.1 BREEDING CAGE



placed under the dissecting microscope and observation could be carried out for long periods of time, especially when the ants were behaving normally after the initial period of agitation.

Results and observations

When emptied into the breeding cages the workers quickly collected the brood into the nest. Eggs, larvae and pupae were all mixed up. Eggs and larvae were however more numerous in the wettest part of the nest near the cotton wool, with pupae more in the periphery. The queen was also crowded over by workers who gradually led her into the nest.

The queen: The queen was never seen coming out to forage. She sits in one place with numerous workers round her, constantly grooming her especially the gaster. Presumably she was also fed but this was not observed. Of all the queens kept only one laid some few eggs.

Eggs

The eggs are elongate, elliptical and transparent white measuring about 0.2mm in length (Fig.10.2a). They are very sticky and usually several eggs adhere together forming big egg-masses. The eggs laid in the laboratory did not hatch before they disappeared from the nest. It was therefore impossible to determine how long it took theeggs to hatch. Very small larvae were found among theegg-masses collected from the field. These were taken to be first instar larvae. The eggs were also licked by the workers.

Fig 10·2

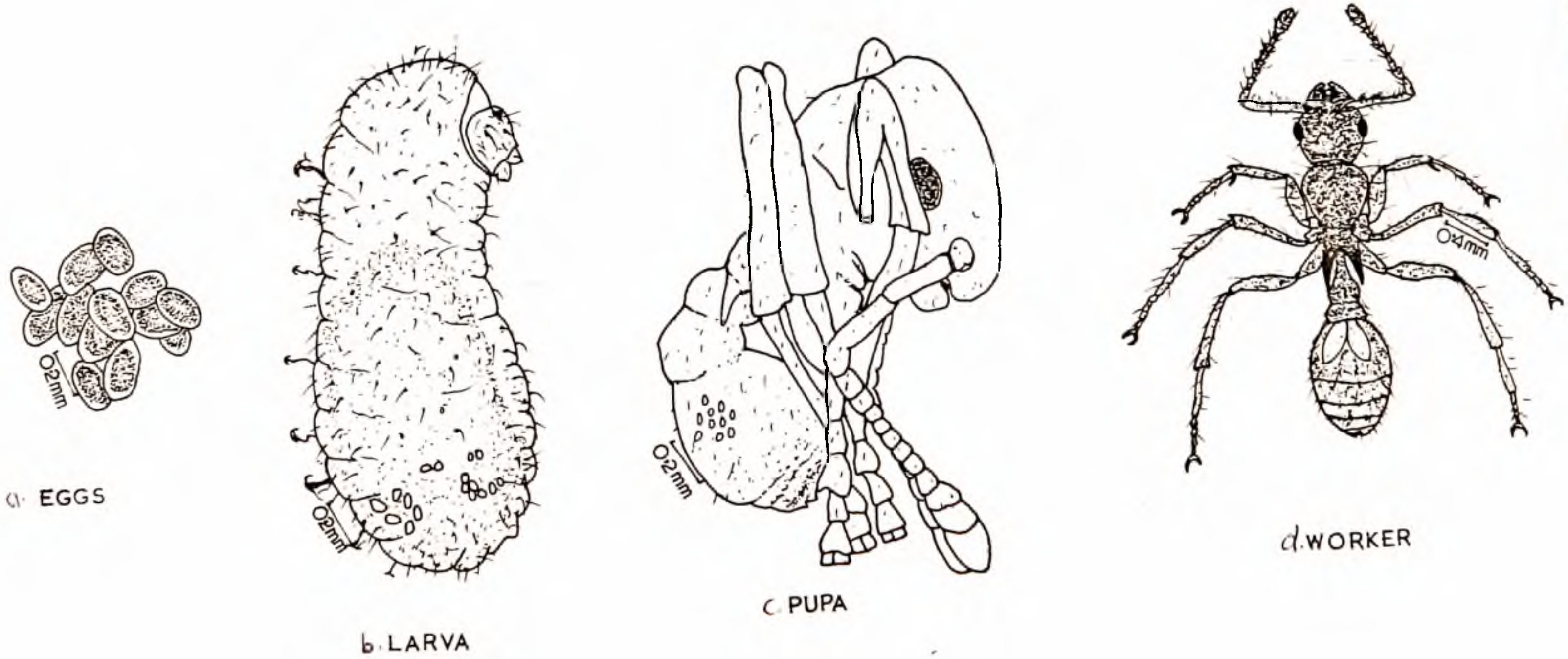


Fig.10.2: Stages of *M. aculeatus*.

Larvae

Morphology: The first instars are extremely small only slightly longer than theeggs, having an average length of about 0.4 millimeters. They also are very sticky and attach to any object with which they come into contact. Since they are not immediately separated out on hatching, they are usually found intermingled with the eggs. They can however be distinguished from the eggs by their slightly more elongated and segmented body as well as the dark-brown or brown midgut (meconium) which is conspicuous in the abdominal region and discernible through the transparent cuticle. Wheeler and Wheeler (1955) have adequately described the larvae and provided diagrams. Fig.10.2b is a drawing of a larva.

Care: The larvae are constantly licked and moved from one place to another. In transporting a Larva under normal circumstances, a worker stands astride it with the head of the larva pointing posteriorly. The worker then seizes the mid-section of the larva with her mandibles and carries it away. The head-end of the larva is thus protected under the worker's body. In an emergency the larva is however, just grabbed and carried away without any special orientation .

Feeding: When feeding, a larva is usually placed on its back with the mouth pointing up. A worker then comes and places its mouth against that of the larva. What follows is a vigorous 'swallowing' movement which is indicated by the bending of the larval head ventrally. The worker then moves away and another one comes to repeat the process. Feeding is periodic, as workers retire now and then especially outside foraging hours to carry out self and mutual grooming. Whenever a larva is disturbed, such as by touching it, it gives out a big drop of clear liquid from the anus.

The larva passes through thedifferent stages of development, which are not easily distinguishable, into a pupa. The prepupal stage can however be distinguished. The borders of the somites, become inconspicuous due to the distension of the body. The posterior end becomes transluscent, perhaps marking off the gaster. As development proceeds, the legs, and head appendages can be easily seen, though folded and closely applied to the body. The body shrinks at the end of this stage. Moulting takes place. Two prepupae were observed moulting into pupae. The workers consumed the exuviae.

Pupae

Morphology: The newly emerged pupa which already looks exactly like the adult ant in form is completely unpigmented. Even the mouth parts are not tanned. Sometimes the gaster appears yellowish. The legs and antennae are folded and applied closely to the body as shown in Fig.10.2c.

Pupal changes: The eyes intially colourless start developing colour 24-hours later. Small reddish spots appear dotted on the compound eyes; these spots spread out and intensify to deep red, brown and finally black. The claws of the legs are unexpanded at the initial stages, and the tarsus, though demarcated is not well defined. The antennae look very much like legs. The spines of the thorax are present right from eclosion, though not tanned. Meanwhile colour has started forming on the rest of the body, which passes through shades of brown to black. The pupal instar takes about 23 days at 27°C, for two larvae which pupated between 29th and 30th November emerged on the 21st and 22nd December respectively.

Care: Pupae are frequently groomed. They are also shifted about like the larvae.

Adults

The newly emerged adults are usually paler than the older ones and are referred to as callows. The workers of incipient colonies are smaller than those of matured colonies and are thus called nanics. In *Macromischoides aculeatus* nanics have an average body length of 2.7mm and headwidth of 0.6mm whilst adult workers from matured colonies generally measure 3.8mm long and have headwidth of 0.8mm.

Morphology: The adult has been described by Wheeler (1922). He described workers as well as males and females. Fig.10.2d shows a drawing of the adult worker.

Behaviour: The workers stop work, now and then, and engage in mutual grooming. One stands still while the other one licks it, anteriorly from the abdomen to the mouth parts. At times the one being licked leans sideways to ensure proper grooming. One worker may lick or nibble one or two of its nest mates, while itself being similarly treated by another.

Self-grooming takes place more frequently than mutual grooming. In self-grooming a worker mainly cleans the legs and antennae, and at times bends the gaster forward through the legs to reauh the mouth.

The workers also carry their nestmates.

Discussion

It is most probable that the concentration of eggs and larvae in the moist area is to prevent desiccation and ease larval ecdysis. Pupae on the other hand are more resistant to desiccation, and as Sudd (1967) states, they are usually separated out into a warm dry part of the nest. This type of domestic arrangement ~~was~~ however, not observed in the nests collected from the field. Perhaps it existed but was destroyed through mishandling of the nest or maybe the humidity in the natural nest is more uniform than in the artificial nests.

Queens are usually nursed, fed and in certain cases even 'delivered' (Sudd, 1967). It was not surprising therefore that the workers were seen crowding the queen and tending her, and since the queen was never seen coming out to forage, it is most probable that she is fed. Her failure to lay eggs in the laboratory may be due to mechanical disturbance in handling or to the chemicals used to immobilize the ants.

As reported the only eggs laid in the laboratory disappeared; presumably they were eaten by the workers and or the queen since no larvae were found. This is not uncommon in ants. Thus according to Freeland (1958) Myrmecia forceps queens never eat anything but eggs! Brian (1953) reasonably points out that queens would be unable to survive on their own eggs only, and that in this circumstance the egg pile must be augmented by large quantities of sterile workers' eggs. No workers' eggs (usually smaller than queen's eggs) were noticed among M. aculeatus egg masses. This does not however rule out the possibility of workers laying eggs. Workers seen with distended gasters had nematode worms in them, not eggs.

As the workers lick the eggs continuously, they leave a salivary coating on them which makes them sticky and possibly reduces water loss as well. Neglect of the eggs by the workers results in the loss of the coating; when this dries out, the eggs no longer adhere loss of coherence and consequently the egg-piles collapse. The licking is also said to protect both eggs and larvae against fungal attack (Sudd, 1967).

Wheeler and Wheeler's description of the larvae agrees well with my own observations. The first instar larvae are not segregated from the egg pile. They feed on the eggs, as reported by Brian (1953) for Myrmica rubra and Weir (1959) for Myrmica rubra microgyna. They are only removed after their first moult and are then fed by the workers. The subsequent larval instars are fed by the workers. It was not possible to determine on what the larvae were fed, whether malaxated insect meat or regurgitated food. Perhaps the sclerotized mouth-parts of larvae enable them to feed on solid or hard food.

The hairs on the body of the larvae serve various functions. Ofer (1970) described five types in Polyrachis simplex but could not assign functions to each. Wheeler and Wheeler (1955) found three types of hairs in Macromischoides aculeatus, which they described as (1) few, simple, minute, (0.001-0.027mm), (2) with denticulate tip, 0.027-0.072mm long, the most abundant type; (3) anchor tipped, about 0.22mm long. The anchor-tipped type may help the attachment of one larva to another, thus keeping them in larval piles. This aggregation of larvae into piles is possibly advantageous because when danger threatens a large number of larvae would be carried all at once to safety. The denticulate-tipped hairs, being the most numerous may perhaps form a protective covering on the body of the larva. The few, simple minute type - could be sensory in function, since ants are known to possess hair sensillae. (Sudd, 1967).

The constant removal of brood from one part of the nest to another may serve to place each larva in the most suitable conditions obtaining in the nest; this also may be the reason why brood is moved from one nest into another in the wild.

The 23 days duration obtained for the pupa is not vastly different from that reported by Ofer (1970) for P. simplex. The absence of pigmentation in the pupa is a common occurrence in ants, as reported by Wheeler (1910), Forel (1928) as well as other modern authors such as Sudd (1967). Full colour is developed some days after emerging into adult.

Perhaps callows perform intranidal duties such as nursing the larvae and licking the eggs. They start foraging only when they are fully pigmented. This suggestion is lent weight by Freeland's (1958) report that nanitic workers of Myrmecia forceps were normally seen near the brood and refrained from foraging while there were larger workers which could do so.

The mutual and self grooming noted in the adults may prevent fungal attack and also help dislodge mite parasites.

Section 11. General Discussion

11. GENERAL DISCUSSION

Macromischoides aculeatus is widely distributed in southern Ghana as Fig.3.1 indicates. The ant has become closely associated with cocoa farms. It also nests on a wide variety of wild trees including *Culcasia scandens* (Araceae), *Ficus exasperatus*, *Ficus asperifolia* (Moraceae) *Milletia* sp. (Papilionaceae) *Phialodiscus unijugatus*, *Rauwolfia vomitaria* and *Solanum verbascifolium* (Solanaceae). It is attracted to cocoa, perhaps due to its broad leaves which are retained for a fairly long time. Moreover the typical structure of a cocoa farm with top canopy or upper storey and cocoa canopy make the place dark and humid and this may offer special attraction to the ant which is largely photophobic. These conditions are not obtainable in many other crop farms and this may account for the absence of the ant in those places. Their sparse occurrence in cocoa farms in the Akwapim areas may be due to the dearth of shade trees in these farms.

The ant is largely crepuscular and nocturnal. Since normally temperatures are low and relative humidities high in the night the ant, especially the eggs and larvae, will escape desiccation as brood circulation takes place in the night. It may be safe, to some extent, from predation by its diurnal predators, *Oecophylla longinoda* and *Mabuya* spp. Furthermore, its habit of nesting on the under side of or between leaves may increase its chances of escaping predation by a predator like *Mabuya* that hunts by sight, since the nests are difficult to detect. The nests are also thus sheltered from rain and perhaps to some extent from light. Sandwiched nests are, however, not so safe since either strong wind or a rainstorm can easily tear them open. Since however, the habit of constructing such nests persists, they must have some other advantage over the simpler pattern.

Fungal mycelia found in M. aculeatus nests do not seem to play any part in holding the nest materials together, as nests with or without the mycelia have the same consistency and stability. It is more likely that a secretion from the mandibular glands serves as glue for holding the building materials together. The claim by early authors of silk in the nest is not completely wrong, as the ants are capable of incorporating a deserted spider's web into nests. Since however, the larvae are incapable of producing silk, any silk that appears in the nest is of foreign source.

The nests are unequally and sparsely distributed on the trees; thus a colony of seventy-four nests was found to occupy as many as seventeen trees. It will be interesting to investigate what factors determine the number of nests to be constructed on a tree. This colony pattern is an advantage to cocoa cultivation since several trees may be protected by a single colony against capsid attack and perhaps indirectly against swollen shoot, M. aculeatus being antagonistic to the SSV - vector attendants, except Crematogaster clariventris. An overall average of 363 workers per nest was obtained over the period of sampling. Thus a colony of 140 nests may contain as many as 50,000 workers, and even a colony of two nests may comprise more than seven hundred workers. If really the ants are active predators, a tree carrying only two or three nests will be kept free from capsid attack. The dispersal of cocoa capsids takes place during the maximum population peak between November and December; this coincides with the maximum population peak of Macromischoides workers. It is very likely that those capsids which settle on trees containing Macromischoides will not survive either to cause damage or to reproduce. Moreover, since during this period large sexual larvae are present and the presence of brood stimulates high activity in the workers, the predation rate will be high. By this means M. aculeatus may conserve the health of good cocoa.

Unfortunately not much can be learnt from the results of the seasonal population counts, since samplings had to be made in different colonies, and these may or may not be in phase. The results however, substantiate the earlier observation of Billes (1946) on the emergence of sexuals between March and May, and also agree with the results obtained with the light trap. Since Kade where the light trap was run is about 45 miles from Tafo the production of sexuals is probably in phase over a wide area.

The method of colony founding after the flight period by individual queens is worth considering. The earlier account on this subject in section nine showed that several females could start colonies on one tree. Eventually however, only one colony containing usually one queen remains in the area. What happens to the other incipient colonies is not known. The results of the radioisotope experiment showed however, that a small colony of a few nests might be almost surrounded by a different and usually large colony. In C5b and H10, a few nests never became radioactive. The inmates of these nests were attacked by those from the big colony when the two were brought together. This showed that those nests were alien to the larger colony. From these observations it can be concluded that a certain form of elimination was going on.

Knowledge that each mated female is capable of founding a colony independently can be advantageously utilized to establish the ants over a wide area in a biological control scheme. If several incipient colonies are found on one tree, or on several contiguous trees, all but one or two, can be removed and re-established on other trees situated wide apart. By this means many more trees might be made to harbour the ants, thus conserving their health. This can, however, be done only after removing other species of dominant ants from the area either mechanically or chemically.

Macromischoides aculeatus colonies are not completely monogynous, since in a few nests more than one queen has been found, although generally not exceeding two or three. This is in accord with Wilson's (1959) observation that monogyny was the normal pattern in the ant species he studied in the tropical rain forests in New Guinea, but that, in exceptional cases where there were multiple queens, their number did not exceed two or three.

The early batches of workers, or nanics as they are often called on account of their smallness, take over the duty of nursing, foraging, building and defence from the foundress queen, who concentrates her energies on egg production. The seasonal population studies have shown that production of sexuals is seasonal, starting from December to about June. There are two main hypotheses to explain sexual production. The oogenic hypothesis claims that sexuals are produced from special eggs; whilst the trophogenic hypothesis holds that different types of food fed to the same kind of larvae may cause them to develop into workers or sexuals.

As the number of workers increases the queen is stimulated to lay more eggs (Brian & Brian, 1951). The workers are in turn stimulated by the increasing number of eggs, larvae, and pupae to build new nests, and expand existing ones. The incipient colony nest, the one built by a queen usually measures 1.5cms across and 1.0cms high, whilst some nests built by workers are very big measuring about 17.5 x 11.0 x 1.5cm in sandwiched nests, and 19.4 x 7.6 x 2.5cm in exposed nests.

The fact that a cocoa leaf has a life of about eight to nine months indicates that a nest could last for that long. It does not, however, mean that the colony collapses with the fall of the leaves. New nests are continually built while old ones are deserted. The reason for nest abandonment is not yet known. One possibility arises from the fact that a cork layer forms at the junction of the leaf petiole and the stem, and this, long before visible signs of leaf fall appear, may cut out water supply to the leaf. As a result transpiration is reduced and the humidity in or around nest may fall. Another possible result is that the lecaniids inside the nest may not be able to obtain enough water to produce honey-dew. Such factors could be signals for nest desertion and may explain why large number of nests on apparently fresh leaves are deserted. Depletion of food resources is not likely to be responsible since the new nest is usually built very near the abandonned one.

Macromischoides aculeatus has been found to be both an active predator and a carrion feeder. It has been explained elsewhere that the fact that few capsid remains were found in their nests did not imply that they were poor predators of capsids. They may feed on the early instars of the cocoa capsids without leaving any residue, since these are soft-bodied. The observations of Nicol *et al* (1947), Marchart and Leston's (1968) radioisotope tagging experiment, Collingwood's (1971) statement, and my own recent observations, all establish the fact that *M. aculeatus* is a predator of cocoa capsids. The degree of predation has, however, not been assessed. Finnegan's (1969) mechanical devise for assessing predation by ants on insects might be used to determine the effectiveness of *M. aculeatus* as a predator of cocoa capsids.

To supplement their protein diet with carbohydrates the ants attend coccids, aphids and lycaenid caterpillars for honey dew, and visit extra floral nectaries. Fortunately the coccids attended are not vectors of swollen shoot viruses and it is generally believed that aphids are not harmful to cocoa. There is a form of mutualism between the ants and the lycaenid caterpillars. The latter are protected while the former get some sugar substance in return for the protection. The caterpillars are classified as a minor pest of cocoa in Ghana.

It seems strange that the ants should obtain their mineral salts from bird or reptile droppings whilst they can, as well, get them from their prey. The ants are known to be general feeders, thus may feed on anything that they come across. Since the bird dropping was wet, it contains water and presumably things like skatol which might be attractive, being normally associated with potential carrion.

The positive association of M. aculeatus with Crematogaster clariventris raises problems. While C. clariventris has been shown to be an active predator of cocoa capsids by Marchart and Leston (1968) using radioisotope tagging and the joint-predation of cocoa capsids by the two ants might help reduce the incidence of capsid damage considerably, nevertheless this mutual tolerance is detrimental to cocoa, since C. clariventris is an important attendant of Planococcoides njalensis, the vector of the swollen shoot virus. Thus, though, trees on which the two ants occur may be free from capsid attack, they may suffer from swollen shoot. C. stadelmanni is, however, negatively associated with M. aculeatus. It also attends P. njalensis and it is not known as a capsid-predator. Trees on which it occurs may therefore suffer capsid damage and from swollen shoot diseases.

Section 12. Summary and conclusions.

12. SUMMARY AND CONCLUSIONS

Macromischoides aculeatus has been shown to be widely distributed in Southern Ghana, occurring mainly in the forest areas, where its distribution seems to overlap that of cocoa. It has become closely associated with cocoa farms but occurs on a large number of wild and cultivated trees as well. It does not exhibit any nest-plant specificity although it seems to prefer trees with large and long-retained leaves to those with small and short-lived leaves.

The ant prefers areas with dense shade, such as those with both top shade and good cocoa canopy, to more open ones. The nest is constructed with vegetable matter on under side of or sandwiched between leaves. Colonies are polydomous and largely monogynous and of variable sizes. Colonies do not overlap. Production of sexuals is periodic; and individual queens found colonies independently. Pupal life is about 23 days.

Diurnal activity studies have shown that M. aculeatus is largely crepuscular and nocturnal. High activity starts usually at about 17.00h and 18.00h, continues through the night, and falls again the following morning. Factors such as presence of food, brood and predators can modify the pattern.

The ant is a general feeder, actively predating other insects including cocoa-capsids, and collecting insect carcasses. To supplement its food with carbohydrates, it attends coccids, aphids and lycaenid caterpillars.

Its association with *Oecophylla longinoda* and *Crematogaster* species has been shown to be negative. It is, however positively associated with *C. clariventris*.

Gamasid mites and nematode worms parasitize it.

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Appendix

Weather data for Tafo from January 1970 - June 1971

1970

Month	Total rain in ins.	Temperature of	Rel. Hum. 0.900	Hum. 15.00	Sunshine hours
January	1.92	80.0	87.4	64.0	7.4
February	0.63	83.1	83.2	51.8	7.2
March	5.12	81.0	81.1	60.8	7.1
April	2.60	78.5	77.6	60.2	5.9
May	5.31	79.9	82.0	69.5	6.0
June	6.06	79.2	83.0	69.7	5.8
July	4.10	77.1	84.9	73.4	3.9
August	0.75	76.9	84.9	69.8	3.4
September	9.56	78.2	83.6	69.0	4.0
October	8.92	79.5	81.2	66.6	6.4
November	1.57	79.0	80.6	64.3	7.4
December	0.03	78.6	82.5	52.2	7.3
		1971			
January	2.09	78.0	86.9	55.1	7.2
February	7.29	79.8	83.1	56.7	6.6
March	3.28	80.0	81.5	61.1	7.1
April	5.15	80.6	78.6	58.7	6.9
May	9.38	79.7	78.4	61.1	8.1
June	9.24	77.9	84.7	77.6	5.1

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