STUDIES ON THE BIOLOGY OF ANTS ASSOCIATED WITH CITRUS TREES.

BY

N.J. MYERS, B.Sc. (Hons.),

Department of Zoology and Entomology,
Rhodes University, Grahamstown, 1957.

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RESUME.

Several ant species may be associated with the same honeydew producing insect in citrus orchards. Recently antagonism and competition between two such ants were reported from Letaba.

This report stimulated the present study, the purpose of which is to ascertain which ant species are most numerous in citrus orchards in the Eastern Cape Province; the reasons for these ants being able to occupy orchards; and, finally, their relationships.

A survey of the Sundays River Valley and the Fish River Valley revealed that three species - *Anoplolepis custodiens* Smith, *Anoplolepis steingroeveri* Forel, and *Pheidole megacephala* Fabricius - were commonly found in citrus orchards in association with Soft Brown Scale insects. The territorial relationships of these ants were determined by plotting their distribution at intervals for over a year.

It was found that their distribution could be correlated with seasonal climatic conditions, the effects of farming practices, brood rearing requirements and behavioural differences between the three species.

The ant, *A. steingroeveri*, had not been previously studied, and since foraging is an integral part of territorial behaviour, some aspects of its biology, and more especially its foraging activity, were investigated to compare it with the known biology of the other two species.

Observations on the foraging activity of *A. steingroeveri* were made at monthly intervals for almost a year, and correlated with climatic conditions prevailing at the time.

Some seasonal and daily variations in foraging behaviour could not be readily explained in terms of the effects of temperature and humidity on the ants. Other factors, including trophallactic stimulation and overcast skies, were found to influence ant activity.

Owing to the apparent lack of information in the literature the possibility of periodic honeydew production by Soft Brown Scale insects controlling ant activity was investigated in the laboratory.

The results of this study showed that it was not likely that honeydew excretion restricted the activity of the ants. Several investigators have also found that many interrelated climatic factors may be correlated with ant foraging behaviour, but have expressed dissatisfaction at not being able to reach the crux of the matter.

To clarify the issue a constant temperature chamber was constructed in which a colony of Crematogaster ants was housed, and the ants were subjected to a series of temperatures at different humidities, all other factors were eliminated or kept constant. The effects of these two factors on the thermokinetics and foraging activity of the ants were registered.

This thesis contains several sections, and at the end of each the results are discussed in the light of the available literature and comparisons are drawn between the species under investigation. The main results are given in the summary.

After the summary two appendices are included. One is an attempt to compare the effect on ant size of the honeydew diet of orchard colonies with the proteinaceous diet of veld ants. The other appendix is an experiment to control citrus ants with an insecticide.

INTRODUCTION.

This dissertation embodies the results of an investigation into the biology of ants associated with citrus orchards in the Eastern Cape Province of the Union of South Africa.

Citrus farming is practised there in river valleys on alluvial deposits. Variegated alluvial soils drain easily which make them pre-eminently suitable for citriculture.

The chief citrus producing areas are the Gamtoos, Sundays River Valley (S.R.V.), and the Fish River Valley (F.R.V.), together with its tributaries, the Kat and Koenap rivers. Citrus is produced in other river valleys to a lesser extent. In this investigation only the S.R.V. and F.R.V. were considered.

The industry is concentrated in river valleys since successful farming is dependent on irrigation. The surrounding country, as a result of low rainfall, has a sparse vegetation which Dyer (1937) and Acocks (1953) term 'Karroid'. Where overgrazing has occurred it approached typical Karroo in character. In both the areas in question the annual rainfall is about 15 inches.

Irrigation has turned these valleys into virtual oases in a semi-desert. This is particularly true in the S.R.V. Plant growth is stimulated both in and around orchards, thus encouraging the spread of indigenous and less hardy plants which would not survive without irrigation. The insect fauna has reacted in a similar manner. Many insects formerly living in the surrounding scrub have moved to this attractive environment. (Smithers, 1953). Many non-indigenous insects, especially citrus pests, have been introduced or have invaded the area, and attempts at biological control of these pests have resulted in the introduction of predatory and parasitic species.

Among the introduced insect pests of citrus are honeydew secreting Homoptera, especially the Soft Brown Scale (*Coccus hesperidum* Linn.), the Citrus Mealy Bug (*Pseudococcus citri* Risso), the Australia Bug (Icerya purchasi Mask˘l.), and the Citrus Aphis (Toxoptera aurantii Fonsc.), together with a few other Homoptera of lesser importance. Many insects, especially ants and Diptera, are attracted to the honeydew on which they feed. The insects associated either with the secretion or the consumption of honeydew, together with their enemies, may be spoken of as the "Honeydew Complex".

The richness of the insect population of orchards is shown in the work of Smithers (1953) in the S.R.V. He counted the dead insects which fell onto plastic collecting sheets during fumigation at night. He estimated that his catch represented only a quarter of the total insect population normally present in citrus trees during the day. The number of insects he recorded per tree varied from 33 to 269, with an average of 126. The following is a list of the orders into which the insects and other arthropoda fell in order of decreasing abundance:-

Coleoptera; Araneida; Diptera; Hymenoptera;
Homoptera; Lepidoptera; Neuroptera; Hemiptera;
Orthoptera.

The environment is subject to frequent change. Farming operations such as harrowing, and spraying of citrus pests with insecticides, disturb the floral and faunal populations. In this way the orchard insect fauna is, both directly and indirectly, affected detrimentally and is always in a state of flux.

Ants have been recorded in citrus orchards in many parts of the world, and their success in fostering infestations of Homoptera and hindering predators and parasites of citrus pest insects, make them economically important. Similarly, ants are also to be found fostering Homoptera on such crops as coffee, cocoa and various others, which are grown in plantations.

The ants which are concerned in the bionomics of the orchards in the S.R.V. and F.R.V. are:-

(1) Anoplolepis custodiens Smith,
(2) Anoplolepis steingroeveri Forel,
and (3) Pheidole megacephala Fabricius.

Formerly Iridomyrmex humilis Mayr was reported in the S.R.V., but it is apparently no longer present.

Ants, like most animals, are frequently restricted in their distribution by climatic factors. Skaife (1955b) has shown that the Argentine ant, Iridomyrmex humilis Mayr, is limited in its distribution to low-lying regions with a mild, equable, mediterranean type of climate in both hemispheres. In South Africa this ant is most successful in the area around Cape Town in the Western Cape Province, elsewhere it finds the climate too severe; this, together with competition from other ants, hampers its spread.

The Cosmopolitan Brown House ant, Pheidole megacephala, on the other hand, in addition to being found in both hemispheres, has a wider distribution than the Argentine ant and is not restricted to such narrow geographical regions as the latter species. This shows that the Brown House ant is adapted to tolerate a much wider range of climatic conditions. This ant is well known and is widely distributed in South Africa and has been recorded both in low-lying coastal areas (Carnegie, 1955) and the high veld (Broekhuysen, 1948). The Pugnacious ant, A. custodiens, has a similar distribution in South Africa to that of the Brown House ant, and both species are known to occur in orchards (Smit, 1934; Steyn, 1954a, 1954b; Stofberg, 1954).

Competition between different species of ant is well known, and the size and behaviour of two competing species often differ considerably. Where two species are competing for the same food source and for a common habitat, that species which is best adapted to prevailing conditions will tend to dominate the other species. Thus climate may offer one or other species more suitable conditions at different seasons, while farming operations may create deleterious or beneficial conditions for one or other of the two species.

This may be put in another way: citrus orchards are subject to the general climate of their area, but the environment is altered by the various operations called for in citriculture. An ant species most likely to succeed under such conditions is one which thrives in the particular climate of the area and is least affected by farming operations. That such an ant will tend to become the dominant species has been shown by Way (1953) in the cocoanut groves around Zanzibar where _Oecophylla longinoda_ Latr. has been replaced by _Anoplolepis longipes_ Jerd. Subsequently _A. longipes_ has been driven out of certain portions of the island by _A. custodiens_.

Steyn (1954a) records that _P. megacephala_ and _A. custodiens_ are antagonists, or competitors, in citrus orchards at Letaba. These two ants are associated not only with Soft Brown Scale from which they obtain honeydew, but also with Red Scale (_Aonidiella aurantii_ Mask.), although what benefit, if any, the ants derive from the latter relationship is not known. He also notes that there is a seasonal change in the behaviour of these two ants towards each other. In winter _P. megacephala_ becomes more active and makes attacks on _A. custodiens_ at night, but the latter species usually recoups its lost territory during the day. This is an instance of climate favouring one species. Steyn also mentions that farming operations influence _A. custodiens_ in its selection of nesting sites.

These observations stimulated the undertaking of a more detailed study with a view to finding out:

1. which are the dominant ant species in the S.R.V. and the F.R.V.;
2. what are the relationships (a) between dominant species and (b) between them and subordinate ant species occurring in orchards;
3. in what ways the climate and farming operations favour or handicap the different species;
4. to what extent, if any, the selective forces operating on ants in the orchards have modified the behaviour of these ants.

Fully to answer these questions a study of the territorial relationships and the activity rhythms of the different ant species under consideration is necessary. Thus the investigation resolves itself into two main aspects:-

1. The territorial and general relationships of the ant species under consideration;
2. The activity rhythms of these ant species which would enable us to assess when the ants are most active, and how climatic factors affect their foraging potential.

From the results of these studies the relative economic importance of the different ant species could be ascertained.

A. ANT TERRITORY.

I. METHODS.

The investigation, it was decided, could best be made on the following lines:-

(a) Extensive quantitative surveys of the farms in the S.R.V. and F.R.V. to establish which ants were the most widespread and the dominant species.

(b) From these surveys it was hoped that suitable orchards would be found where at least two different species of ants would be competing in the same orchard. The territory each species occupied, in terms of the number of trees it foraged, would be recorded on maps. Such distribution records were to cover a period of between one year and eighteen months, and individual maps were to be made at intervals of about three months.

(c) During these regular visits to orchards, observations of the behaviour of different ant species towards each other would be made, and thus their relationship might be established.

Two critera were employed to determine the territory held by the ants:-

1. Foraging territory, in which citrus trees were visited by ants from nests outside the tree 'islands', or uncultivated soil beneath the trees. A tree was considered as being the territory of a particular species if one or more individuals were found on that tree. Tapping of the tree trunk with the fist had the effect, in cases of doubt, of bringing ants down the tree.

2. Settled territory, in which the tree 'island' contained one or more colonies of ants of the same species. The tree of such a territory need not necessarily be foraged. This applies especially to A.custodiens which has a partial hibernation during winter.

Where an obvious ant nest entrance was seen, but no ants appeared, stamping on the ground or blowing tobacco smoke into the nest brought out the ants if they were present. Digging up the upper portions of nests confirmed the results derived by stamping and tobacco smoke. Frequently there was no response, and ants were recorded as being absent from that area or island. This happened in winter, because in the polydomous nesting system of A.custodiens, 'outpost' nests are vacated and the ants temporarily withdraw to base nests.

P. megacephala, because of its burrowing habits, presented a similar problem. When no individuals were seen on the trunk, the surface soil around the base of the trunk was dug up. If ants were found by this means the area was considered to be P. megacephala territory.

All territory observations were made during times when the ants were most active, and the results were recorded on maps. In these maps foraging and settled territory were not differentiated, and were simply recorded as being the territory of the ants in question. There is one exception which will be discussed later.

No attempt was made to estimate the density of Soft Brown Scale per tree, and only its presence or absence was recorded. It was felt that the categories laid down by Steyn (1954b) were not practical and hence they were not used. Similarly Aphids and Fulgorids (Hilda patruelis Stål) were also recorded as being present or absent.

II. PRELIMINARY SURVEYS OF ANT DISTRIBUTION.

(a) *Sundays River Valley*. A survey of this valley was made during March, 1955. Where possible, farms with known heavy infestations of ants were visited, but in fact the survey extended along the entire length of the valley. In all, twenty farms were visited and *A.custodiens* was found to be the dominant ant on all these farms.

The following ants occurred with *A.custodiens* in the same orchards:-

(i) *Pheidole megacephala* on two farms;

(ii) *Crematogaster gerstaeckeri* D.T. var. *infaceta* Sant. on two farms;

(iii) *Anoplolepis steingroeveri For.* on three farms.

A.steingroeveri, although not in any way so important or so widely distributed as *A.custodiens*, was the only ant which seemed capable of competing with it. In one orchard in particular *A.steingroeveri* was sufficiently numerous to make worth while a more detailed study of the relationships of these two species. At several places the two species foraged adjacent trees, and it was felt that the relationships of these ants called for closer study since their similarity in most respects made them well-matched competitors.

Other species of ant were found in orchards but did not appear to be associated with scale insects. These subordinate species are listed below:-

Monomorium distinctum Arn.(var.*leviceps* var. nov., M.S.)
Tetramorium quadrispinosum Em var. *eudoxia* For.
Tetramorium akermani Arn. (var. *myersi* var. nov., M.S.)
Technomyrmex albiceps Smith race *foreli* Em.
Dorylus affinis Shuck.
Monomorium delagoensi For. var. *belli* For.

(b) *Fish River Valley*. Four farms in the F.R.V. in the vicinity of Fort Brown and Piggott's Bridge were surveyed. Citrus cultivation in this district is discontinuous, contrasting with the continuous cultivation in the S.R.V. Individual farms are separated by farms which do not cultivate citrus, and individual orchards even on the same farms may be several miles apart.

The orchards are surrounded by overgrazed scrub. First impressions of the survey made in April, 1955, suggested that on any one farm either *A.custodiens* or *A.steingroeveri* was to be found, but not together. Thus the distribution of these two ants was different from that in the S.R.V.

Other species of ant were found in the orchards occupied by the two *Anoplolepis* species. These subordinate species were in most cases in small isolated colonies and did not have any really significant bearing on the problems under consideration. However, on the farm 'Dunbar', where *A.steingroeveri* was the dominant *Anoplolepis* ant, colonies of *Pheidole megacephala* race *punctulata* Mayr were equally numerous, if not more abundant.

This latter situation ideally suited the conditions under which it was hoped that the problems outlined above could be investigated.

On the same farm several other species of ant were found living close to, and frequently within, the territory of either *A.steingroeveri* or *P.megacephala*. Two of them are predominantly grain-eating, and as such did not compete for honeydew in the orchard. The presence of grain-eating species reflects the aridity of the area since these ants usually inhabit deserts. Also the numerous species found on a single farm indicate that this environment was invaded by ants from the scrub bordering the orchards. Most species found in the veld also occurred in the orchards.

The overall impression gained from these surveys was that on '*custodiens*'farms only a few other ant species were tolerated, and these occupied rather poor sections of the orchards in which it is thought *A.custodiens* had no real interest. These subordinate ants, with the exception of *Crematogaster* spp., do not occupy any special niche within the orchards. Where there is a dense population of *A.custodiens* colonies these ants are not found.

'*steingroeveri*' farms presented a different picture. Here several species of ant appeared free to roam through the territories of both *A. steingroeveri* and *Pheidole*. This relationship will be explained later in terms of food requirements, and the habits of the ants concerned.

Crematogaster was found in this area and the S.R.V. on citrus trees in poor condition and in a state of neglect. Once a tree has been neglected, and not farmed in any way, it must be considered as no longer being part of the citrus orchard environment. Thus these ants did not form any part of the 'honeydew complex'.

In 1948 Whitehead made a brief study of *A. custodiens* and *Crematogaster liengmei* For. race *waetzaeckeri* E. in the S.R.V. and he records:-

> ".....these two species of ant are seldom found on the same trees. When a high percentage of the population is made up of *A. custodiens* there is invariably a complete absence of *C. liengmei* and vice versa. The occurrence of *C. liengmei* was too isolated ......".

The 'isolated' occurrence of *C. liengmei* corresponds with my observations.

The subordinate ants occurring in the F.R.V. orchards are listed below:-

1. "*custodiens*" farms:-
    - *Monomorium distinctum* Arn. (var. *leviceps*; var.nov. M.S.)
    - *Crematogaster peringueyi* Em.
2. "*steingroeveri*" farms:-
    - *Messor barbarus* L. race *capensis* Mayr, var. *decipiens* Fo
    - *Tetramorium setuliferum* Em. var. *cluna* For.
    - *Monomorium albopilosum* Em. race *thales* For.
    - *Camponotus rufoglaucus* Jerdon, race *vestita* Smith.
    - *Camponotus rufoglaucus* Jerdon, race *cinctella* Gerst
    - *Camponotus maculatus* Fab.

(c) Summary.

1. *A. custodiens* is undoubtedly the dominant and most widespread ant in the S.R.V., but several subordinate species were also found.

2. In the F.R.V. in the area about Fort Brown a peculiar situation exists where in some cases entire orchards are dominated either by *A. steingroeveri* or *A. custodiens*. In other orchards mixed populations of mainly *A. steingroeveri* and *P. megacephala*, together with other ants of no economic importance, were found.

III. CONDITIONS IN THE SUNDAYS RIVER VALLEY AND THE FISH RIVER VALLEY.

The behaviour of the ants under consideration must to some extent be dependent on climate. It is, therefore, desirable to have on record the general conditions under which the ants in these two valleys exist. In recent years greater consideration has been given to climatic factors within highly localised micro-habitats since the conditions obtaining in these niches are frequently more important to the species concerned than the regional climate. Micro-climates, however, must be considered as offshoots derived from macro-climates.

Macro-climatic conditions are usually expressed in terms of air temperatures, air humidity and rainfall. These conditions are markedly affected by the topography of the region, but within a given area small features such as vegetation, soil type, and slope of the land, give rise to a series of micro-environments. (Edney, 1954; Gosswald, 1941; Wheeler, 1932).

These micro-environments intergrade, but within certain limits they have considerable value for different species of Isopods (Edney, 1954). Gosswald (1941) has shown that the distribution of ants of different species within forests, grass-lands and other habitats, is largely limited by the specific heat requirements necessary for the successful development of the brood of each species. Some ant species have overcome the short-falls of the climate by constructing mounds of earth and twigs to obtain greater insolation and run-off of rain (Andrews, 1927).

It has been mentioned that Pheidole and Anoplolepis are widely distributed throughout South Africa, and that species of these two genera respond in different ways to seasonal changes in climate at Letaba in the Transvaal. In the Eastern Cape Province citrus is farmed in low-lying river valleys, and the climates of the two valleys under consideration will be contrasted with each other and with that of Letaba. These climatic data are useful in explaining population fluctuations of insects and how orchard environments may be derived from a macro-climate.

General conditions in the S.R.V. and F.R.V. will be described and then summarised in a table, together with detailed records of climatic conditions. The latter will be contrasted with those of Letaba.

(a) General conditions.

1. Sundays River Valley.

A stretch of some twenty miles along this valley from Addo to Kirkwood is under irrigation, which is regulated from Lake Mentz. Monthly irrigations are made throughout the year except in May, June and July. This gives an average of eight or nine irrigations per year. This number may be increased or decreased depending on the rainfall and the amount of water available in Lake Mentz.

Irrigations are made from a canal running from Lake Mentz to Addo. This canal is tapped at intervals and the water is led along furrows to individual farms. The 'Basin System' of irrigation is widely practised. A basin is made by banking up the soil along a row of trees, each tree being isolated by shorter banks running across the main banks. Individual basins vary in size according to the size of the trees. Frequently there is an area between the main basin banks which is not irrigated, and is known as the 'lane'. The lanes are not irrigated but receive seepage on which weeds and grass thrive. The soil basin banks are not permanent and are destroyed during harrowing, which makes bank rebuilding necessary before the next irrigation. (Fig.I)

Cultivations (mainly harrowing) are made after every second irrigation. 'Clean', or more assiduous cultivations, are made in December, January and February. Moderate weed growth is tolerated in autumn and winter to assist in retaining moisture during the 'drought' months.

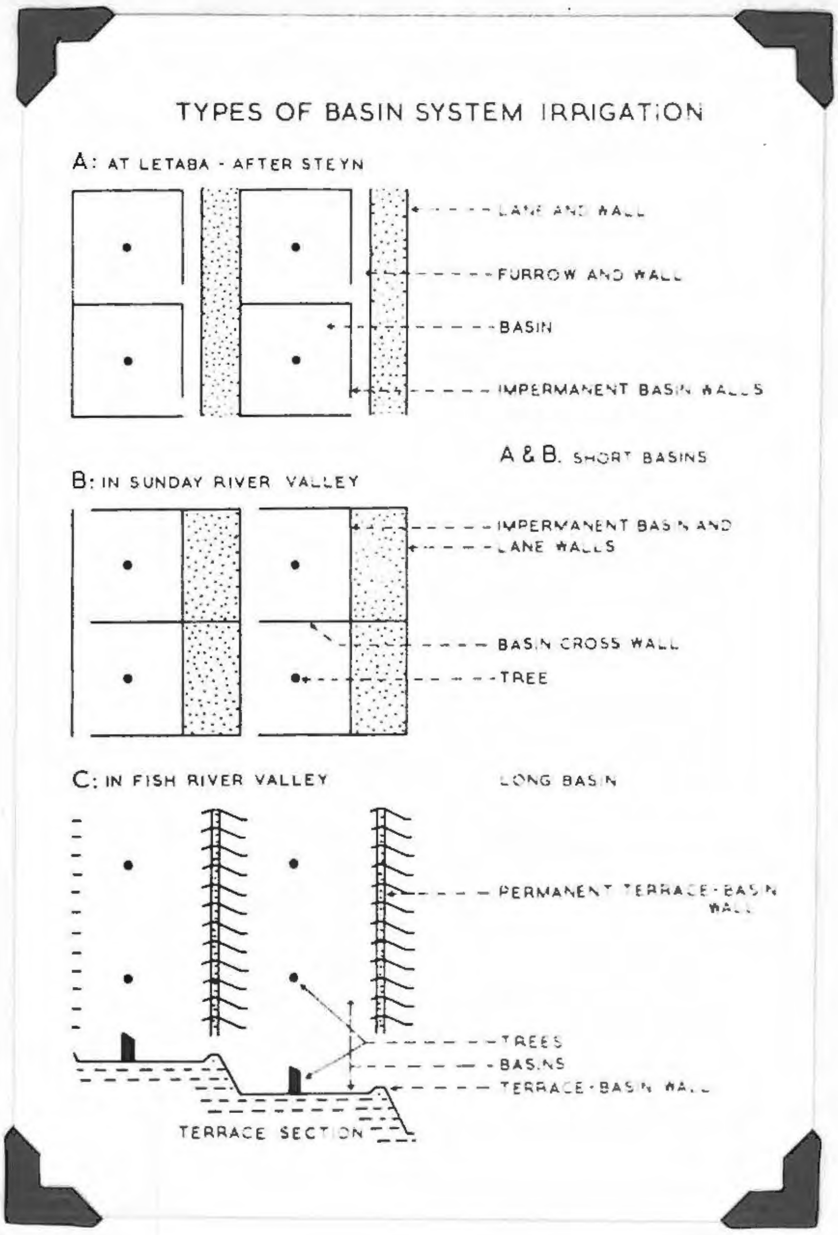
TYPES OF BASIN SYSTEM IRRIGATION
A: AT LETABA - AFTER STEYN
LANE AND WALL
FURROW AND WALL
BASIN
IMPERMANENT BASIN WALLS
A & B. SHORT BASINS
B: IN SUNDAY RIVER VALLEY
IMPERMANENT BASIN AND LANE WALLS
BASIN CROSS WALL
TREE
C: IN FISH RIVER VALLEY
LONG BASIN
PERMANENT TERRACE-BASIN WALL
TREES
BASINS
TERRACE-BASIN WALL
TERRACE SECTION

FIGURE 1.

2. Fish River Valley.

There are considerably fewer citrus farms here than in the Sundays River Valley, since citrus farming is a harsher proposition in this area. There is no dam from which stored water may be drawn for irrigation. Water is pumped directly from the river to orchards. Small weirs hold back some of the water, but for the main part irrigation in this area is a function of the water level in the river. Droughts are not infrequent. The valley is deeply incised and the alluvial deposits are restricted to a narrow bank along the river banks.

Terracing is imperative, since the orchards are set close to the river. Virtually every row of trees is on a terrace. Terracing is combined with the basin system of irrigation and therefore the raised terrace banks are retained as permanent structures and not destroyed during cultivation.

The 'long basin system' is used in conjunction with the terrace banks. Rows, or groups, of trees are irrigated in the same basin, not individual trees as is the practice in the S.R.V. (Figs. 1 and 7).

Cultivations are not so regular as in the S.R.V., and each farmer uses his own discretion as to when he harrows and weeds. Harvester termites are more numerous in this area than in the S.R.V., and their cropping of grass and weeds has an effect somewhat similar to that of cultivation in that the soil cover is removed, but the soil surface is not disturbed.

(b) Climatic conditions.

In the S.R.V. records of rainfall and temperature have been kept since 1934 and 1936 respectively, at Hermitage, by the Citrus Research Officer. There is no meteorological station at Fort Brown in the F.R.V., and rainfall records made by farmers are the only climatic data available.

During the course of another section of the investigation at Fort Brown, both air and soil temperatures were recorded for one day in each month for the period June, 1955 to May, 1956.

Readings of the soil and air temperatures were taken at hourly intervals during the day on which the observations were made. Some of the records are incomplete. Nevertheless, these records have some usefulness for purposes of comparison with those of the S.R.V. They cannot, however, be considered as being a true reflection of the average monthly air temperature.

The mean average monthly air temperature records are derived on the basis of $\frac{\text{mean Max.} \quad \text{mean Min.}}{2}$

Similarly, mean day temperatures were calculated from the formula $\frac{\text{Max.} \quad \text{Min.}}{2}$

(c) <u>Comparison of the climates.</u>

(1) <u>Temperature</u>: The figures in Table 1 reflect the similarity of the air temperatures of the two valleys, but the data for the F.R.V. are too incomplete to make more accurate comparison.

The figures do, however, show that both these areas experience high temperatures.

(2) <u>Rainfall</u>: Table 1 also gives the rainfall figures for the period covered by this investigation. Both valleys received almost identical amounts of rain during 1955, of less than 15 ins., which are below the average amounts usually received by these areas.

These figures indicate the relative aridity of the surrounding scrub.

Both air temperatures and rainfall are higher at Letaba than those recorded in the S.R.V. and F.R.V.

TABLE 1. Comparison of climatic conditions in the Sundays River Valley, Fish River Valley, and at Letaba.

Air temperature: °C.

Month.		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	Av. total.
S.R.V.	1936-1954	22.6	23.2	21.9	19.1	16.2	13.9	13.3	14.6	16.3	18.0	19.6	21.2	18.3
	1955	22.1	21.3	21.9	17.6	17.4	14.0	13.8	12.9	15.2	16.6	18.9	20.4	17.7
	1956	24.1	22.6	22.7	18.1	14.0	-	-	-	-	-	-	-	
F.R.V.	1955						14.0	-	10.4	16.9	17.6	-	16.8	
	1956	25.5	19.8	17.4	13.5	13.4	-	-	-	-	-	-	-	
Letaba	1943-1955	23.9	24.3	23.3	21.2	17.7	15.4	15.1	17.2	19.4	22.2	23.3	23.9	20.58
	Rainfall.													
S.R.V.	1910-1954	-	-	-	-	-	-	-	-	-	-	-	-	15.16
	1955	0.81	3.44	1.40	0.20	0.29	1.04	0.40	1.15	0.57	0.35	2.14	1.78	13.57
	1956	1.51	0.87	1.26	0.28	1.78	-	-	-	-	-	-	-	
F.R.V.	1910-1929	-	-	-	-	-	-	-	-	-	-	-	-	13.49
	1955	1.35	1.84	2.17	0.39	0.14	1.75	0.10	0.42	1.02	1.11	1.75	0.24	12.35
	1956	0.00	0.62	1.95	0.20	0.58	0.00	0.23	-	-	-	-	-	
Letaba	1925-1955	-	-	-	-	-	-	-	-	-	-	-	-	29.21
	1955	8.46	10.26	6.45	2.22	1.10	0.32	0.29	0.01	0.20	2.50	6.30	9.67	47.78
	1956	0.63	20.29	6.29	0.44	1.11	0.15	-	-	-	-	-	-	-

(d) Soil temperatures and brood rearing.

Soil temperature records at Fort Brown were made by inserting thermometers into the ground at surface level (0.25 ins. (0.5 cm.)) and to a depth of 12 ins. (30.5 cm.). Temperatures of exposed bare soil were taken together with those of the 'umbrella', or shaded area, directly beneath citrus trees.

1. Technique.

A hole was bored in the ground to the required depth with an awl of the same diameter as the thermometer. A close fit betwen the sides of the hole and the thermometer is necessary to prevent the air temperature affecting the thermometer. Care was also taken not to remove the thermometer completely from the soil and only to draw it out sufficiently for the reading to be taken. Nonetheless each reading must be taken quickly and accurately when extreme temperatures are prevailing since the soil thermometer is affected by both the air temperature and the soil temperature gradient.

Soil surface temperatures (0.25 ins.) were obtained by standing a thermometer upright with the mercury bulb buried in the sand. The remaining exposed portion of the thermometer was sheltered from the sun by placing a cylindrical cardboard cover over it. The thermometer was tilted to the South to prevent its shadow being cast over the soil at the base. The bulb was left undisturbed while readings were taken and only the cardboard cover was lifted slightly to make the reading. In this way it is hoped that a true reflection of the soil surface temperatures was realised.

2. Microenvironments.

There are three distinct environments within orchards which are available to ants. These are the shaded area beneath the trees, the exposed portion between the trees, and finally, the basin banks. Where the areas between the trees or terrace basin banks are permanent, they have definite survival value for the ants.

The figures in Table 1 allowed a comparison to be made between soil temperatures at depths of 0.25 ins. and 12 ins. in exposed areas and those at similar depths beneath the umbrella. It will be seen that the temperatures in the former area, as is to be expected, are considerably higher throughout the year. The exposed soil temperatures also show a marked seasonal variation, while those beneath the umbrella are less variable. Similarly, the soil temperature variation is more marked in the exposed soil than beneath the umbrella where the variation is slight (Fig. 2). Temperatures taken at depths of 0.25 ins. and 12 ins. below the umbrella approximate closely, and at times the deeper soil is hotter than the soil surface, while the reverse applies in the case of exposed soils.

The higher temperature of the deeper umbrella soil is explained in terms of accumulation of heat over a series of days. At a depth of 12 ins. there is excellent insulation; it requires several days for the soil to warm up, but once having reached a certain temperature it takes equally long to cool down. Low-hanging branches buffer the effects of wind and air temperature which ultimately affect the soil temperatures at lower levels. Surface layers are particularly susceptible to temperature changes by loss of heat, and by moisture evaporation from the soil which is accelerated by the wind.

It has been pointed out that ants require a temperature above a certain threshold for brood development, and the ability of the ants to select and transport developing brood to those portions of the nest best suited for maturation of each stage in their development is well known (Wheeler, 1910).

3. <u>Results</u>.

Table 2 shows the difference, over the brood rearing months, between soil temperatures at 0.25 ins. and at 12 ins. in exposed and shaded areas in an orchard at Fort Brown. These temperatures are correlated with the data produced by Steyn (1954a) for the rate of brood development in its different stages at different temperatures.

It appears that A.custodiens brood could complete its maturation in exposed areas at a depth of 12 ins., but would be able to produce only a limited number of broods. However, Steyn's data, which apparently correspond with the time taken for the development of brood in veld nests, were obtained from brood reared in Janet nests kept in insectaries where, it is assumed, the nests were not subjected to direct sunlight. Hence they did not receive temperatures higher than 30.6°C., which is considerably lower than those prevailing at soil level in exposed places during the day. The absence of these high temperatures may account for Steyn's inability to rear many pupae.

Later it is suggested from the distribution of A.steingroeveri that it prefers hotter and drier localities than A.custodiens, and may require higher temperatures for brood maturation.

Obviously, the temperatures at both soil depths beneath the trees are quite unsuitable for the rearing of A.custodiens brood, and almost certainly for A.steingroeveri as well. A.steingroeveri colonies proved extremely difficult to maintain in artificial nests which prevented life history studies being made on this species.

P.megacephala, however, would be able to produce brood under the umbrella as Broekhuysen's (1948) data suggest, but the exact position of their brood chambers in relation to the stem and umbrella were not determined. The galleries of P.megacephala extend from the base of the tree stem to the periphery of the umbrella. Should the temperatures beneath the umbrella prove unsatisfactory, the brood could undergo their development just outside the umbrella in the insolated soil.

(e) Wind and soil temperatures.

The effect of wind is clearly shown in Table 3 and Fig. 2.

These data were obtained in Spring, 1955, on two days (23rd and 25th October) close to each other. On the first day

TABLE 2.

	EXPOSED SOIL					UMBRELLA SOIL				
Month	T1	Time (hours)	T2	T3	T1-T2	T1	Time (hours)	T2	T3	T1-T2
1955										
IX	25.9	9	18.5	19.0	7.4	18.1	7	16.5	-	1.6
X	42.1	10	20.1	20.9	22.0	18.2	10	15.6	15.6	2.6
XI	-	-	-	-	-	-	-	-	-	-
XII	41.9	11	22.5	21.4	18.4	18.9	9	16.4	16.4	2.5
1956										
I	47.3	12	24.9	24.6	22.4	-	-	-	-	-
II	30.9	8	26.0	26.1	4.9	(20.2)	-	(21.4)	21.4	-
III	22.4	7	19.0	18.8	3.4	(15.6)	-	(18.8)	18.8	-
IV	31.3	9	18.0	18.8	13.3	19.2	7	17.2	17.4	1.8

A.custodiens.

Brood developmental times: temperature (After Steyn, 1954a)

Stage	Highest Av mean temp. °C.	Time (days)	Lowest Av. mean temp. °C.	Time (days)
Egg	22.8 ± 7.2	10-11	20.6 ± 6.7	17-18
Larvae (Minor)	23.9 ± 6.1	16-17	22.8 ± 7.2	22-23
Pupae (Minor)	22.8 ± 7.2	33-34	22.8 ± 6.7	39-40
Pupae (Media)	22.8 ± 6.1	37-38	19.4 ± 6.7	50-51

T1 is the mean soil surface temperature for that period in hours when it is greater than at 12 ins. depth.

T2 is the mean temperature at 12 ins. depth, over the same period as T1.

T3 is the mean temperature at 12 ins. depth for the total number of observations during the day.

T1-T2 is the difference between the mean temperatures at 0.25 ins. and 12 ins., respectively.

The figures in brackets represent overcast days when the soil surface temperatures of the umbrella did not exceed those at 12 ins.

it was windy; calm on the second day.

The exposed soil surface is rapidly cooled, while that of the umbrella is not affected to such a marked degree. This is caused directly by the wind reducing the temperature of the soil surface, and increasing the evaporation rate.

In exposed soils at 12 ins. depth there is not much difference between calm and windy days.

It is clearly noticeable how little daily variation there is at 12 ins. depth in both exposed and shaded areas.

TABLE 3.

The effects of wind on soil temperature (in degrees Celsius) in exposed and shaded (umbrella) places.

Time	EXPOSED				UMBRELLA			
Depth	0.25 ins.		12 ins.		0.25 ins.		12 ins.	
	Windy.	Calm.	Windy.	Calm.	Windy.	Calm.	Windy.	Calm.
5 a.m.	10.0	-	20.4	-	12.1	-	16.0	-
6 "	10.9	12.5	19.8	19.5	12.5	12.2	16.0	15.2
7 "	18.5	16.0	19.8	19.5	14.0	13.0	15.8	15.5
8 "	19.3	26.5	19.5	18.5	15.8	15.0	15.8	15.5
9 "	38.4	38.0	19.5	18.5	17.0	15.7	15.8	15.5
10 "	39.0	46.1	19.5	18.5	18.8	16.5	16.0	15.5
11 "	43.2	50.8	19.5	18.5	20.5	17.2	16.0	15.5
12 "	44.6	53.0	20.0	18.5	21.3	18.3	16.0	15.5
1 p.m.	43.5	52.5	20.2	21.5	22.1	19.1	16.0	15.5
2 "	39.8	47.0	20.5	21.0	22.6	19.8	16.0	15.5
3 "	37.2	42.3	21.0	22.0	20.0	20.2	16.0	15.5
4 "	31.2	32.8	21.0	22.0	19.0	19.6	16.1	15.6
5 "	25.0	32.2	21.5	22.0	17.4	18.7	16.1	15.8
6 "	18.1	21.5	21.5	22.0	15.5	17.2	16.1	15.8
7 "	12.0	17.2	21.5	22.0	13.8	15.7	16.1	16.0
8 "	11.5	14.5	22.0	22.5	12.8	14.7	16.5	16.0
9 "	10.6	13.2	21.8	22.5	12.5	14.2	16.3	16.0
10 "	10.3	11.5	21.0	22.5	12.0	13.5	16.1	16.0
11 "	9.2	10.8	20.0	22.5	11.5	13.2	16.0	16.0
12 "	9.1	10.2	20.0	22.5	11.0	12.5	16.0	15.8

23:X:55 - Windy day
25:X:55 - Calm day.

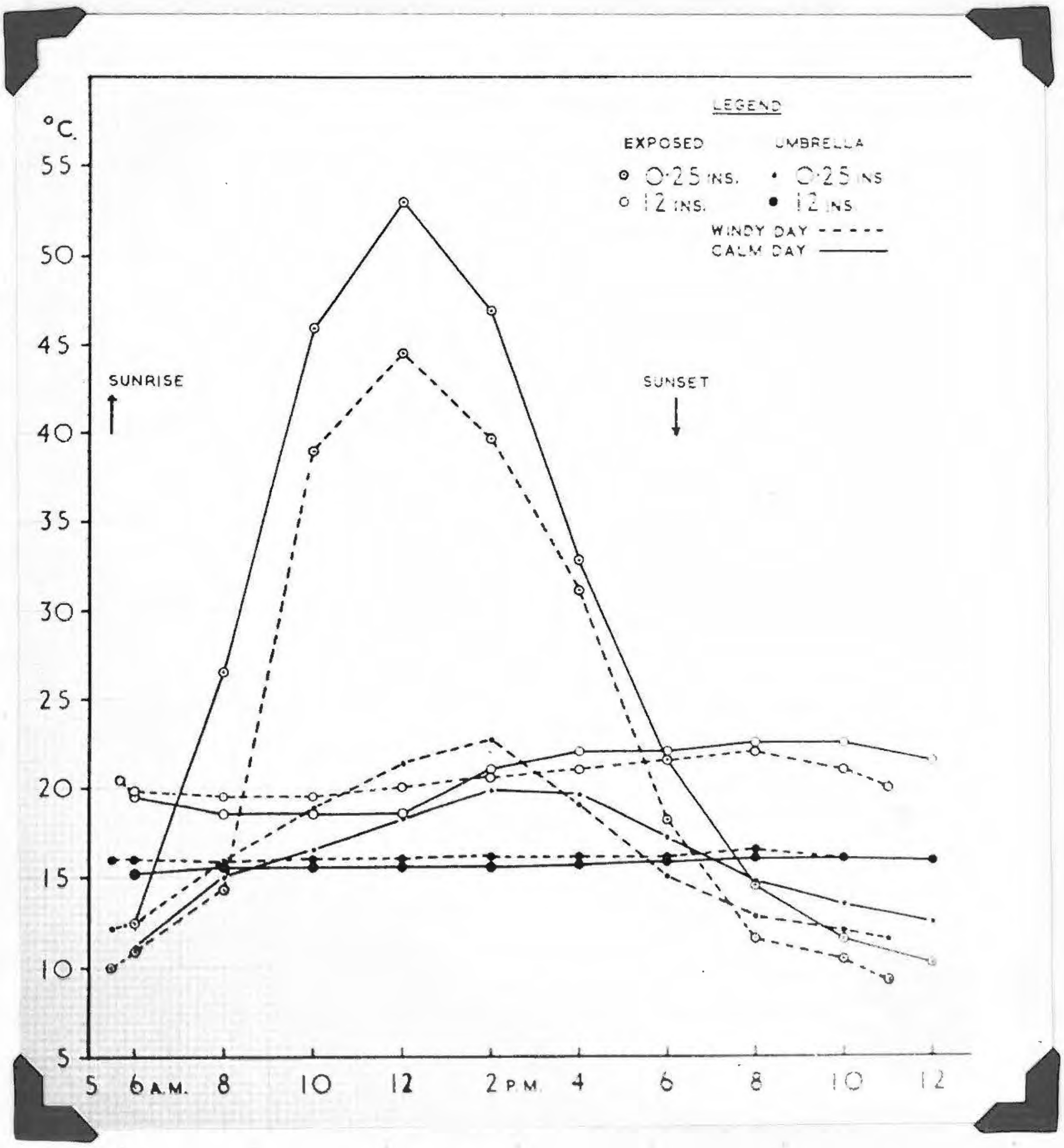

FIGURE 2.

The effect of wind on soil temperatures at 0.25 ins. and 12 ins. depth in open ground and the umbrella.

IV. FACTORS WHICH INFLUENCE THE DISTRIBUTION OF ANTS IN ORCHARDS.

These factors are listed below and will be considered in the order indicated. Each of the three ant species will be dealt with separately, and comparisons will be made between reactions of the three species to these factors.

1. Food
2. Soil conditions.
3. Shade.
4. Irrigation.
5. Insecticides.

(a) Anoplolepis custodiens. Most observations on this ant were made in the Sundays River Valley near Hermitage, in an orchard of over 600 6-year old trees belonging to Mr. I. Mathews. The comments which follow refer mainly to the behaviour of this ant in that orchard. Observations made in the Fish River Valley will also be discussed.

1. Food.

Fig. 3e correlates the distribution of ants with various honeydew secreting Homoptera in the S.R.V. orchard.
From Table 5 it is obvious that less than 50% of the trees were foraged for honeydew. In May, 1956, although the aphid distribution was not recorded, a distinct drop in aphid numbers was noticed. Soft Brown Scale on the other hand showed some local distributional changes, but the number of infested trees was virtually unchanged over almost three months (75; 79). (Fig. 3f, Tables 5 and 6).

Figs. 3e and 3f (March and May, 1956) show that a considerable number of trees were foraged for food other than honeydew. This must consist largely of insects not included in the honeydew complex. It is interesting to note in contrast that all Soft Brown Scale infestations were tended by ants, but this, as Table 5 shows, is not true for aphids.

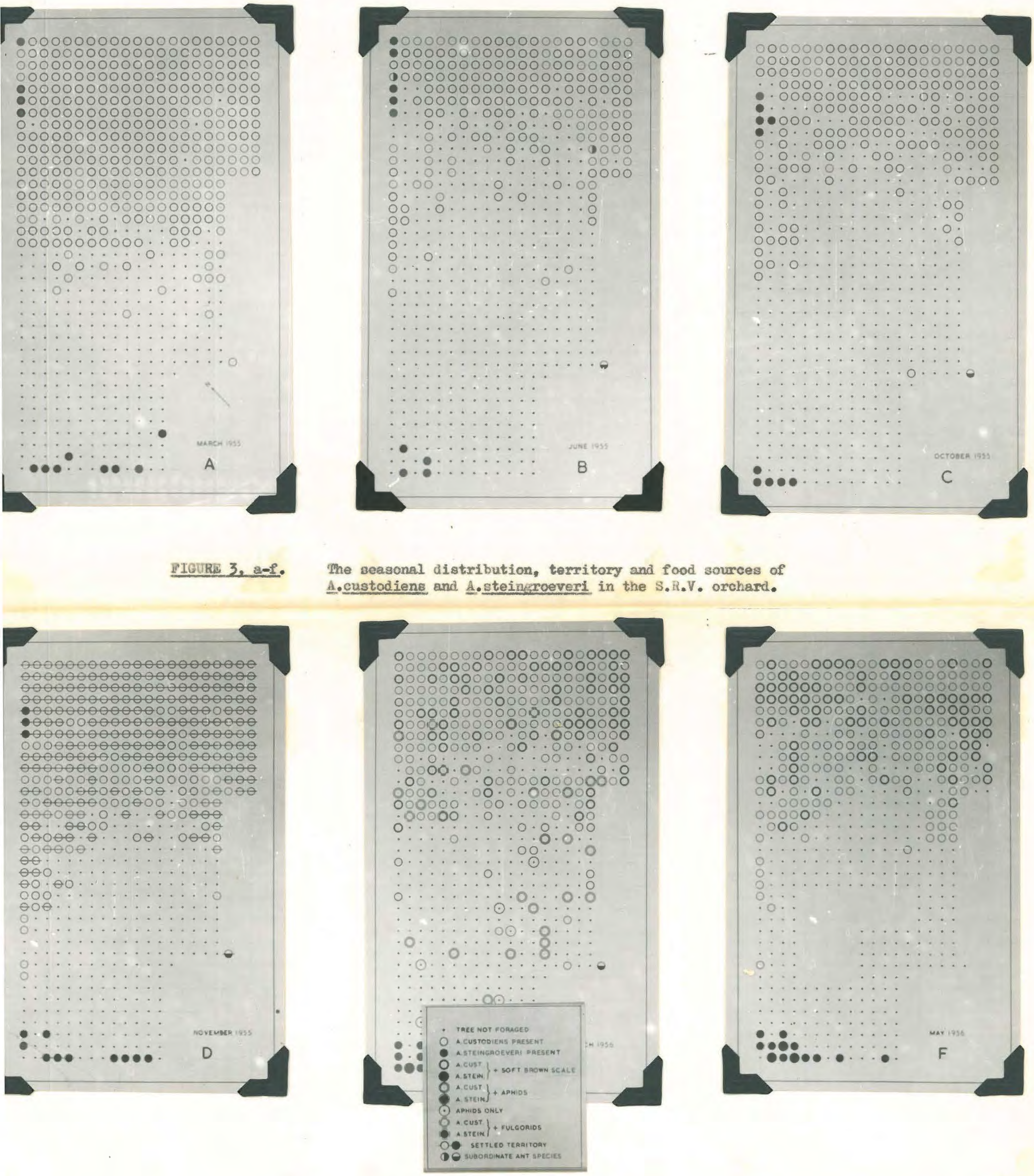

FIGURE 3, a-f. The seasonal distribution, territory and food sources of *A.custodiens* and *A.steingroeveri* in the S.R.V. orchard.

TABLE 4.

Correlation of ant species with number of trees foraged.

1955 1956

Trees	March		June		October		November		March		May	
Total No.	641	%	641	%	641	%	641	%	640	%	640	%
Unforaged.	284	44.3	427	66.6	424	66.1	299	46.6	342	53.4	393	61.4
Foraged	357	55.7	214	33.4	217	33.9	342	53.4	298	46.6	247	38.6
A.cust.	343	96.1	199	93.0	206	94.9	328	95.9	282	94.6	234	94.7
A.stein.	12	3.4	9	4.2	10	4.6	13	3.8	15	5.0	13	5.3
Other spp.	2	0.6	6	2.8	1	0.5	1	0.3	1	0.3	-	-
Totals	357		214		217		342		298		247	

TABLE 5.

Correlation of trees foraged for honeydew and other food sources.

March,1956. Trees foraged for all honeydew sources.

Honeydew source.	*A. custodiens*	*A. steingroeveri*	Total	source not foraged.	% of total foraged (298)
S.B. scale	73	2	75	-	25.2
Aphids	27	4	31	8	10.4
Fulgorids	4	-	4	-	1.3
Totals	104	6	110	8	36.9

Therefore other food sources 63.1 %

TABLE 6.

May, 1956. Correlation of Soft Brown Scale and trees foraged.

Honeydew source.	*A. custodiens*	*A. steingroeveri*	Total	Unforaged	% of total foraged(247)
S.B. scale	76	3	79	-	31.2

Therefore other food sources 68.8 %

Soft Brown Scale is present throughout the year, though population numbers may fluctuate. Applications of insecticide substantially reduce the Soft Brown Scale. In this orchard the first use of insecticides against Soft Brown Scale was made in January, 1956. This,coupled with the unusually cold conditions in 1956, resulted in fewer trees being foraged than at the same time in 1955.

The greatest infestation of scale is found along the orchard borders where the marginal effect is most pronounced. This would seem to indicate that the success of the scale is dependent on the ants. There is no evidence that either _A.custodiens_ or _A.steingroeveri_ actively transport and spread the scales. However, it is certain that crawlers that are not tended by ants appear to have little chance of survival against enemies and desiccation (Stofberg, 1937 a, b).

It is not known to what extent an incipient infestation of scale may attract ants. Ants scout in an exploratory manner, ('exploring', Talbot, 1943a) outside the area which is yielding food on the offchance of finding another food source. Once a food source is found the ants are quick to establish ownership of it (Brian, 1955). After this the ants no longer wander about, but set about foraging in the most expedient manner they know ('trailing', Talbot, 1943a).

The foraging field of these ants is limited by the foraging range of the workers, the number of individuals available for scouting, and the degree of satiation of the colony. It would appear that the foraging drive of _A.custodiens_ is synchronised with the seasonal copiousness of food in summer. In the section dealing with foraging activity it will be shown how _A.steingroeveri_ may forage under adverse climatic conditions in summer, while under similar conditions in winter they remain dormant. This is largely attributable to the presence of brood, which activates the workers (Schneirla, 1944; Vowles, 1955).

During 'drive' periods ants forage all available food to meet the demands of the brood. In this respect they are limited by their own foraging ability, and also by physical obstacles created during farming operations.

From the above observations it appears that Soft Brown Scale infestations do not limit the distribution of ants to infested trees, and A.custodiens also visits trees which do not support insects associated in the honeydew complex. Thus scale infested trees may attract most of the foraging ants to them, but do not restrict the movement of ants to healthy trees which apparently offer other food sources independent of the honeydew complex.

2. Soil conditions.

The orchard situated in the Sundays River Valley shows three distinct zones of ant distribution, the northern densely A.custodiens-populated region, a more or less distinct unoccupied central belt, and a small portion in the southern end occupied by A.steingroeveri (Fig.3a). During the surveys a few colonies of small ants of the genera Monomorium and Tetramorium were found in the central belt.

If we accept Steyn's (1954a) observations that P.megacephala is able to inhabit fine loose sandy soils, while A.custodiens is restricted to compact heavier soils, the presence of these small ants seems to indicate that the soil in the central belt is unsuitable for nest purposes by Anoplolepis. However, it is clearly noticeable in Fig.3e when compared with Fig. 3a, that there was a spread of A.custodiens into this formerly unoccupied area before the winter contraction shown in Fig. 3f took place. No soil texture analysis of this orchard has been made to establish if the distribution of the different ant species is determined by the soil type.

After cultivation in the Sundays River Valley orchards the surface layers of the soil are broken up into fine particles which hamper ant movement and foraging. 'Islands' of uncultivated soil are created around individual trees which are isolated from each other by the loose cultivated soil between them. This is temporary, and once the soil has been moistened by irrigation, rain, or heavy dew-fall, the soil surface particles are once again bound together and the ants are able to move easily over the soil. The uneven soil surface caused by harrowing and construction of basin walls accentuates the difficulties in terms of the antlion-trap principle.

The 'islands' result from the method of cultivation by tractor drawn harrows. A margin is left around each tree so as not to damage its roots. The island is square with the tree occupying the circular central portion, leaving the four corners of the island exposed. The portion covered by the lower branches I have termed the 'umbrella'. Fig.4 shows a plan view of a typical island.

In this orchard the entire border was cultivated. There were no roads or tracks and the only permanent undisturbed consolidated soil was that of the islands. This strip of loose soil around the orchard tended to temporarily disrupt the communication between orchard and extra-orchard mother colonies.

Steyn (1954a) reports that A.custodiens is loath to return to a nest which has been partly dug up. This he attributes to the resulting abnormal waterbalance in the soil after it has been broken down. It would appear then that the only nesting sites available to the ants in this orchard are the islands which are not disturbed by cultivation.

A detailed account is given later showing that 74.3% of the nest entrances of A.custodiens occurred in the northern corner of the tree-islands. No counts were made of the number of nest entrances occurring outside the islands since these were so few in number it was not thought worth while to correlate the number located here with that of island nests.

It is estimated that at least 75% of the nests were located in the consolidated island soil. This indicates that A.custodiens has a marked preference for undisturbed soils, and in this respect the ants are limited in the distribution by the amount of compact soil in the orchard.

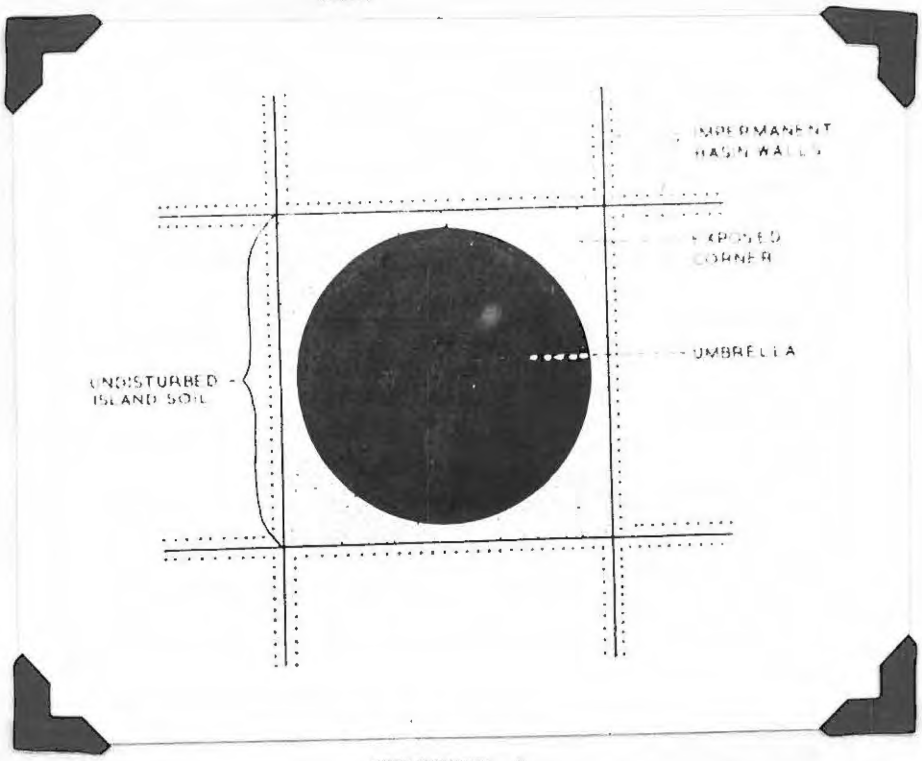

FIGURE 4.

The 'island' of undisturbed soil around a citrus tree, and the shade, or 'umbrella', cast by the tree.

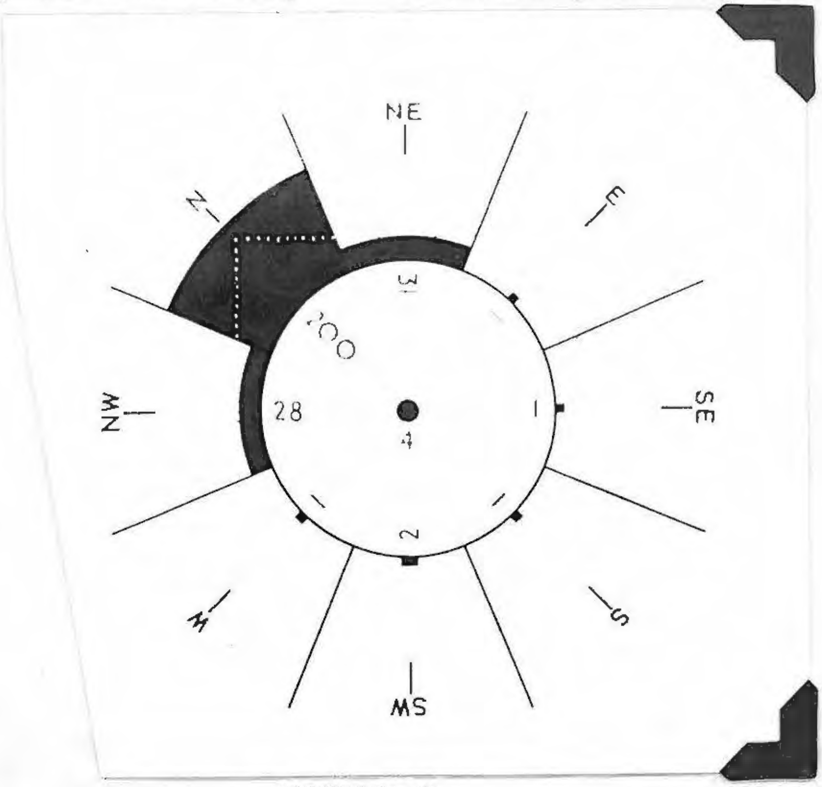

FIGURE 5.

The distribution of ant nests in relation to the 'umbrella' and soil insolation.

This ant is obviously very sensitive to its nests being broken up, and where possible will nest in a place free from such disturbances. Such places are usually found along footpaths, roads, and around human dwellings where the soil cover is kept down, the soil surface is exposed to maximal insolation, and the soil is compacted by vehicles and man. Insolation, compacting and soil stability are all interrelated, and any one of these may act as a limiting factor in the distribution of A.custodiens in orchards.

These facts may be related to orchard conditions. Weed clearance improves soil insolation, but does not disturb the protective deep, or 'mulch' layer, within individual tree-islands. Weeding affects only the immediate surface. Deeper penetration would damage the roots of the trees. Extra-island soil is weeded automatically during cultivation, which involves harrowing. Thus the soil is disturbed to a depth of at least six inches and the mulch layer is broken down.

We may conclude, therefore, that the soil surface influences foraging behaviour while the stability and the amount of insolation received by the mulch layer influences nesting behaviour. No experiments were undertaken to determine how long and to what extent foraging by the ants was interrupted by loose,freshly cultivated soil.

3. Shade.

In conjunction with the selection of islands for nesting sites, the phenomenon of 'cornering' was noticed. Most of the nests were found to be situated in the northern corner of each island. Nest entrances, however, did occur elsewhere. A survey with the view to finding out whether this superficial observation was correct, and its significance, was undertaken.

Each island was divided into eight segments based on the cardinal compass points,and the position of each nest was noted. If there were a group of nest entrances in a segment they were taken to represent one nest. One or more nest entrances located elsewhere on the same island were recorded as being separate. Nine categories were used, the eight compass segments of 45° and that of nests occurring at the base of the tree trunks denoted as 'O'. By chance one corner was almost due North, and 22.5° on either side constituted the 45° for the segment with due North in the centre. Thus segment N. = $337.5^{\circ} - 22.5^{\circ}$, and similarly segments NE. = $22.5^{\circ} - 67.5^{\circ}$; E. = $67.5^{\circ} - 112.5^{\circ}$, and so forth.

The results tabulated below are obviously significant and require no statistical analysis.

TABLE 7.

	N.	N.E.	N.W.	E.	W.	S.W.	S.E.	S.	O.	Total
No.	200	31.	28.	1.	1.	2.	1.	1.	4.	269
%	74.3	11.5	10.4	0.4	0.4	0.7	0.4	0.4	1.5	100.0

The distribution of ant nests within 'islands'.

From these results we deduce that A. custodiens responds to the amount of insolation the consolidated soil receives. By preference the ants select the northern corner which receives most sunlight and heat. This is shown diagrammatically in Fig. 5.

Three distinct stages of umbrella development - 'umbrellisation' - may be recognised in the life of an orchard. Initially, young newly planted trees have a small crown of leaves and cast a small shadow, or umbrella. The stems are long and bear no side branches. Here the umbrella plays no selective rôle as the stem base is exposed and directly illuminated by the sun. Nest entrances are found at the base of the stem. Subsequently, at the age of about 5 years, side branches develop which form the 'skirt' and this grows down to the ground, and prevents the sun from striking the ground. Once a tree is skirted, the ants have to move outside the umbrella, as is the case with A. custodiens. In the last stage with overall tree growth more soil is shaded, and in some cases entire orchards may become unsuitable for brood development.

The overall effect of the final stage depends on the spacing of the trees, and to what extent they have been stunted. Where maximal 'umbrellisation' prevails ants are forced to produce brood outside the orchard, and in this respect shade

(1) limits the area available for brood rearing;
(2) forces the ants to forage from extra-orchard nests, thus their foraging potential is reduced; and
(3) causes the death of a number of established orchard colonies.

'Umbrellisation' is a gradual process. Fortunately I was able to carry out this investigation at the crucial time when the tree skirts dropped, and the nest entrances were shifted from the stem bases to the corners outside the umbrella. Each orchard from the time of its planting until its fullest development has a parallel 'shade life', which is of great significance to the ants.

It would seem logical to assume that when an orchard has full shade, conditions would become more suitable for forest-inhabiting ants, or species adapted to temperate conditions. But for some reason such ants as Pheidole and Crematogaster do not take over this environment in the S.R.V. This is possibly due to the extensive use of insecticides to which both species are highly susceptible.

The significance of 'die-back' in terms of 'umbrellisation'.

'Die-back' is a term applied to citrus trees when through the effects of scale insects there is premature leaf-fall, sometimes culminating in the death of entire branches. These branches are pruned away, from which the term 'cut-back' is derived. The net result is that the tree becomes stunted, and skirt dropping is delayed in young trees. In older trees there is a reversion to the condition found in young trees where the stem and the soil beneath the tree are exposed.

The relationship of the ants, scales, die-back and other impinging factors is best represented diagrammatically: (Fig. 6)

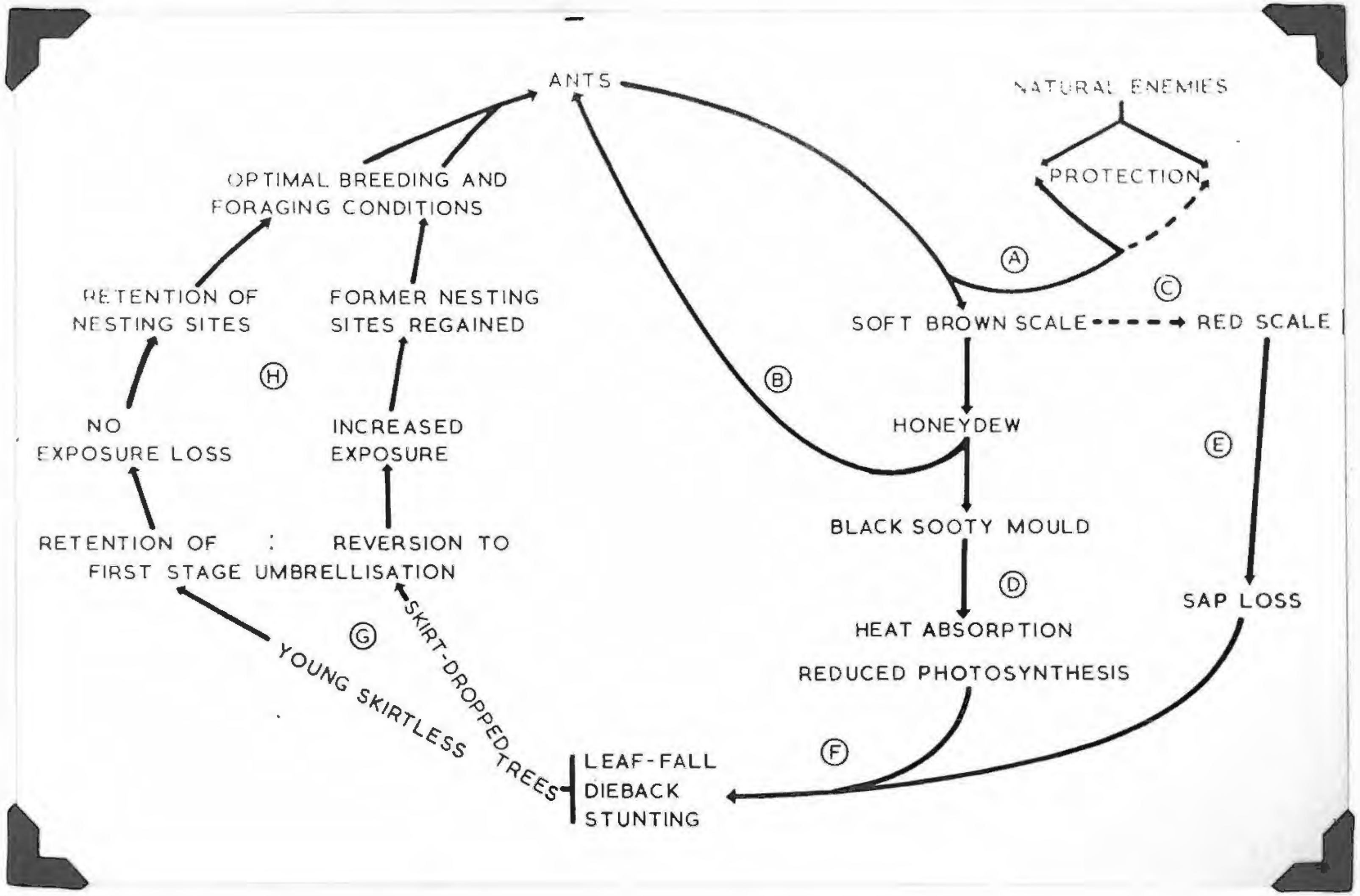

FIGURE 6.

The relationship between ants, citrus scale insects, and die-back conditions.

since there is a chain of interacting factors which have a cyclical mode of operation.

The 'symbiotic', or 'mutualistic' relationship of ants and scale insects is well known (Wheeler, 1910); in this instance the relationship has greater long-term significance than was formerly thought.

(A) The ants foster scale infestations mainly by disturbing and attacking the natural enemies of the scale.

(B) The Soft Brown Scale insects in return 'donate' honeydew to the ants, and at the same time the ants assist in reducing possible scale mortality through asphyxiation by, and fungal infection in, honeydew. Anoplolepis is not such an assiduous forager as Oecophylla (Way, 1954b), and a coating of Black Sooty Mould is found growing on the excess unforaged honeydew. This mould is highly diagnostic and characteristic of Soft Brown Scale infestations.

(C) There is an enigmatical association between ants and the non-honeydew-secreting Red Scale, where the latter is found in pure populations. Where both Soft Brown and Red Scale insects occur in mixed populations, 'coincidental infestations', the latter benefit from the presence of ant whose attention is directed more to soliciting honeydew (Flanders, 1945). The benefit is largely protection from the natural enemies of Red Scale.

(D) Black Sooty Mould has several deleterious effects on the leaves. The black colour of the mould absorbs considerabl radiant heat and the leaves must be cooled by abnormally high transpiration. This is a serious water loss to trees which depend on irrigation for their survival. The mould also filters some of the sun's rays, which results in imperfect and reduced photosynthesis. (Whitnall, 1940).

(E) Red Scale is more pernicious since it lacks the unhygienic habit of secreting honeydew. This enables it to live in more crowded conditions without any fear of suffocation by honeydew. Its main effect on the tree is a general drainage of sap from leaves and branches.

(F) The combined effects of (D) and (E) result in premature leaf-fall, and the die-back of heavily infested branches. These effects culminate in stunting the tree. Dead branches are pruned away in the hope of stimulating new growth, but this is of no avail as both species of scale prefer new succulent growth.

(G) Young trees up to about six years old are particularly susceptible to die-back before and after the onset of skirt-drop. This stage, as I have pointed out, is of great significance with regard to the nesting behaviour of the ants. If no control measures are taken against the ants or scales on young trees, die-back will indefinitely delay skirt-dropping. This allows the ants to enjoy an extended period with an abnormally high level of insolation. These conditions, which resemble first-stage 'umbrellisation' in a healthy tree, may also result from skirt-dropped trees becoming heavily infested with scale and ants and then dying back. The lower branches are most prone to die-back because they are most easily reached by the ants. Also, honeydew secreted by scale higher up in the tree collects on them.

(H) The overall effect of die-back, besides delaying skirt-drop, is that the ants nesting under young trees do not have to change their nesting site. In older trees die-back causes a reversion to conditions of insolation similar to those in first stage umbrellisation. Thus the ants are provided with optimal foraging and breeding conditions. The shadow cast by crown leaves of the tree reduces soil temperature immediately below the tree, while temperatures outside the umbrella become excessive. The removal of the skirt or lateral branches from die-back allows insolation in the early morning and the late afternoon when it is most needed by the ants. This tends to give a more even distribution of heat throughout the day to ant nests situated below the tree. Individual ants also benefit from direct radiation from the sun, which promotes foraging while low air temperatures prevail.

Steyn (1954a) mentions briefly the correlation of die-back with ant-scale infestations. His observations correspond with mine; but he presents no evidence on which to base his conclusions.

Former ant control measures involved banding tree-trunks with a sticky ant-barrier and keeping the tree high-skirted, or the lower branches from touching the ground (Smit and Bishop, 1934). These measures have not proved successful, since the barrier soon becomes covered with debris and is easily crossed by the ants. Some of the banding materials caused bark-burn which stunted the trees. The height to which the trees were skirted varied considerably, but obviously the ants stood to benefit from increased insolation.

An extreme case exists in the F.R.V., where high skirting was maintained by introducing sheep into the orchards to feed from the lower branches and on weeds. Figure 7 shows the orchard in question with maximal exposure; it has the greatest infestation of A.custodiens known to me.

4. Irrigation.

In the Sundays River Valley A.custodiens is confined, because of its temperature and humidity requirements, as expressed by its preference for certain nesting sites, to undisturbed, insolated and therefore warmed northern corners of the tree-islands.

These islands are completely inundated with water to a depth of about six inches during irrigations. This suggests that flooding is of minor importance to the existence of colonies. Steyn (1954a) notes that at Letaba this ant also nests in irrigation basins, but when neighbouring nests are situated on high ground, after the water has subsided, ants from flooded colonies transport their brood to nests above the water level. In the orchard in the S.R.V. no permanent basin banks above the water level were available to the ants. Obviously, <u>A.custodiens</u> must be immune to a greater or lesser degree to the effects of irrigation. This, I think, lies mainly in its method of nest construction, and the wax-lined nest walls.

The nest distribution of <u>A.custodiens</u> was surveyed on the farm 'Brandeston' in the F.R.V. on 12.III.1956, in order to investigate changes in nesting behaviour of this ant in terraced orchards.

Fig.7 shows the orchard in question, which has high-skirted trees allowing good insolation beneath the trees. Thus no true umbrella of shade could be recognised below any of the trees. Furthermore, besides conditions of maximal insolation, little disturbance of the soil was made by the infrequent harrowing, and very high terrace-basin-walls were present. The average skirt height of the trees was found to be 0.813 meters. The results are as follows:-

<u>TABLE 8.</u>

Location of nests	No.	%
At base of trees	39	4.75
In basins	27	3.29
On terrace walls	754	91.95
Totals:	820	99.99

Total number of trees:	61
Average number of nests per tree:	13.4

These results show that <u>A.custodiens</u> prefers to nest in well insolated, flood-free terrace walls, when they are available.

By contrast, in another orchard belonging to Mr. G.McCarthy at the Koenap River (a tributary of the Fish River), two rows of tall, heavily leafed, full-skirted trees running parallel to a typical terrace bank were found. Under such conditions of full umbrellisation there were fewer ant colonies and these occurred on the terrace walls in the most insolated area between the trees. At this place the soil is least affected by tree shade, since the tree rows run NNE to SSW and the ant nests derive full

FIGURE 7.

Highly insolated soil in a terraced orchard on 'Brandeston' farm in the Fish River Valley. Note the high-skirted trees with few leaves, characteristic of dying-back.

benefit from the sun traversing E. to W. Both Anoplolepis species were present in this orchard. In one of the tree rows nearest the terrace, A.steingroeveri nested in 13 of the 19 available interspaces between the trees; A.custodiens occupied the remaining 6. This reflects two things. Both species are restricted to nesting in the most insolated area of the terrace wall, and fewer nest entrances were found, averaging 3 nest entrances per tree. This contrasts with the situation at 'Brandeston' where the entire orchard is highly insolated and no regular pattern in the distribution of nest entrances, in relation to tree shade, could be found.

It is noteworthy that the two species did not nest in alternate interspaces at the Koenap River orchard, but each species occurred in a series. This orchard was discovered too late in the investigation (24.X.56) to undertake a study of what appears to be a very interesting distributional and territorial relationship between the two species. This is the only orchard in the F.R.V. where mixed populations of Anoplolepis ant occur in any density.

The whole hypothesis of nest distribution is based upon the temperature and humidity tolerances and requirements of the adult ants and the brood. It is well known that adult ants are able to withstand adverse conditions for longer periods than their brood. Furthermore, the brood is highly susceptible to bacterial and fungal infection. For this reason some ant larvae hibernate (Brian, 1953), while others, of which A.custodiens is an example, hurriedly undergo their development in summer while the most advantageous conditions prevail. In distribution Anoplolepis is limited to the Ethiopian, Mediterranean and western portion of the oriental region (Wheeler, 1922). Table 2 (after Steyn, 1954a) shows the optimal developmental temperatures for A.custodiens. These figures and the known distribution of this genus suggest that they require fairly high temperatures for successful brood maturation.

In this work in the S.R.V. ant nests were not dug up to ascertain the number of nests containing brood. However, when one considers the large percentage of foraged trees which have nests associated with them (Fig. 3d; A.custodiens 75.61%) it is probable that an equally large number of nests produce brood. If this is not so, then 'cornering' behaviour would have no significance and would be difficult to explain.

In general, these findings parallel those of Way (1953) with regard to shade restricting the nesting of A.custodiens to insolated soils. Pickles (1935), Talbot (1934,1943a) and Brian (1951) have observed the tendency among ants to nest in insolated situations. Headly (1941) shows that still other ants prefer to nest in shady situations. Raignier (1948) shows that, although mound building ants (Formica rufa) enjoy more or less constant temperature conditions within their nests, ants migrate from shaded nests to more exposed neighbouring nests (since there is temperature variation between nests).

There is no doubt concerning the validity of the tenet of Fielde (1905) and Wheeler (1932) that temperature requirements for brood-rearing restricts ants to particular environments to which they are adapted. As Wheeler suggests, "Ants are so extremely sensitive to degrees of temperature and humidity of their environment and to the character of its vegetation that many species or sub-species are confined to narrow ecological habitats". Talbot (1934) has since shown in a comprehensive survey that ant distribution is markedly correlated with the temperature and humidity tolerances of different species. Unfortunately, she does not take into account how brood-rearing requirements may influence the distribution of the various species she considered.

5. Insecticides.

Insecticides have been used on one occasion (January, 1956) only in this orchard. I was not there to witness the direct effects of Malathion on this species.

Direct effects are usually not long lasting and are to a certain extent dependent on the residual toxicity of the insecticide (Malathion, about 3 weeks). The repellent action of the insecticide would tend to warn the ants away from it (Skaife, 1955b). Mortalities incurred by ants are mainly those foragers caught up trees during the spraying. My own experiments (see Appendix II) show that *A.custodiens* and *A.steingroeveri* are resistant to the contact insecticide 'Dieldrin' to which most ants are susceptible (Dürr, 1955; Joubert & Walters, 1955; Stofberg, 1954).

The ants are most affected by the reduction of the Soft Brown Scale population and the 'honeydew complex' fauna. It is almost impossible to estimate the long term effects of the honeydew loss to the ants. This aspect is reflected to a small extent in the comparison of Fig. 3d with Fig. 3e.

It would be interesting and valuable to calculate the reduction in population potential as a result of larval starvation. The diminution of food derived from the honeydew complex forces this dense orchard ant population to revert to feeding under veld conditions. Figs. 3e and 3f show that the colonies do not die, but exploitation of the orchard by ants is brought to a temporary standstill while the scale population gradually builds up.

Furthermore, there is the time factor. The respite from die-back conditions allows the trees to bring out new growth which reduces insolation, the effects of which are discussed later. Any disturbance to the scale insects or ants in the scale-ant-insolation complex by insecticides will cause the complex to break down with detrimental effects to the ants.

(b) *Anoplolepis steingroveri*.

In the Sundays River Valley orchard only a few *A.steingroeveri* colonies were found and these did not yield sufficient data to draw many conclusions. More extensive observations were made at Fort Brown in the Fish River Valley, where *A.steingroeveri* is more widespread. Hence, most of my remarks about this species relate to its occurrence in the F.R.V.

1. Food.

In the S.R.V., *A.steingroeveri* enjoys the same food as *A.custodiens* (Table 5). F.R.V. orchards had a much lower level of animal activity, due to the infrequent irrigations, which support less weed growth. Harvester termites (*Hodotermes mossambicus* Hagen) further reduced the soil cover of weeds and grass, and their associated insect fauna.

On the other hand, the termites form a large portion of the diet of *A.steingroeveri*. Large numbers of termite head capsules may be found in ant cemeteries, together with portions of the bodies of other prey.

It is impossible to estimate to what extent the presence of termites compensates for the loss of a large proportion of the weed fauna. The termites are active in summer, but continue their foraging throughout the other seasons. Foraging in winter necessitates more extensive searching for food, which renders them more prone to attack by *A.steingroeveri*.

Besides termites, the ants were mainly restricted to a diet of honeydew, nectar, and the honeydew-complex fauna.

The distribution of *A.steingroeveri* was not correlated with Soft Brown Scale infestations. However, areas in the orchards occupied by this ant were characterised by die-back trees and by Black Sooty Mould, which would indicate that the marked correlation between *A.custodiens* and Soft Brown Scale in the S.R.V. also exists here.

Most die-back trees were found along the orchard margin, where they received most attention from *A.steingroeveri* colonies, situated amongst them and in the adjoining veld. (Figs. 8a-f and 9a-g).

This evokes the question "is the penetration of the orchard by *A.steingroeveri* restricted to scale-infested trees?"

It has been shown that *A.custodiens* fosters all scale infestations in the S.R.V. orchard, and also visits scale-free trees in addition, which indicates that the scale does not

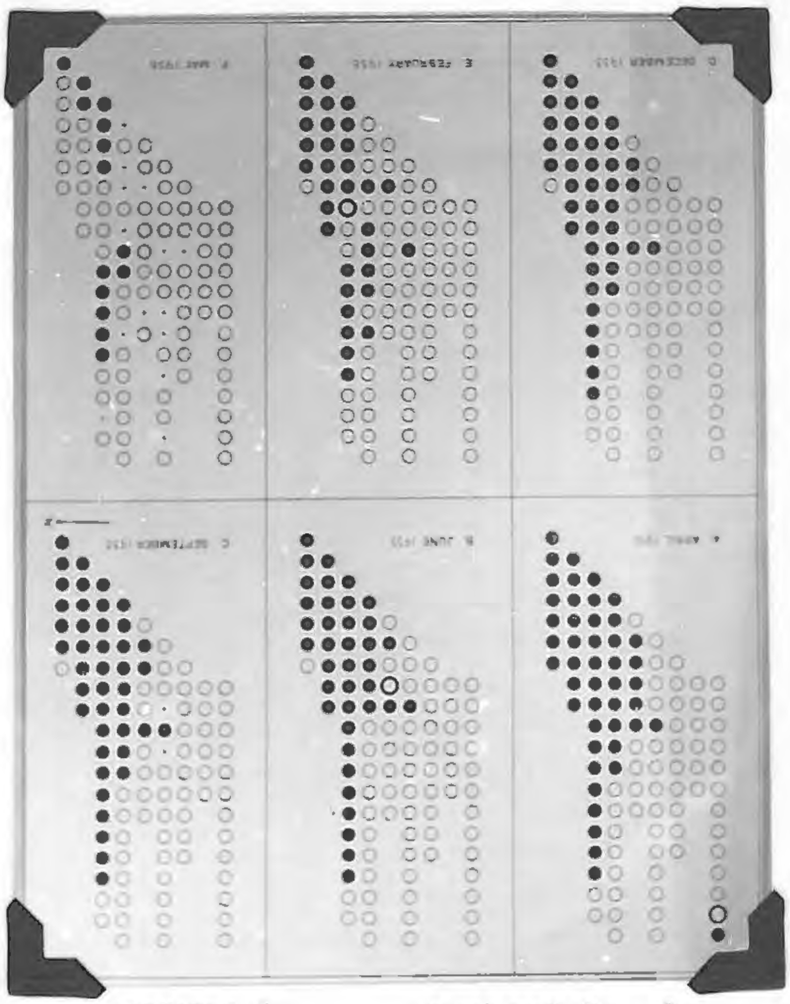

FIGURE 8. Orchard No. 2.

Survey of the distribution and territorial relationships of A.steingroeveri and P.megacephala from April, 1955 until May, 1956. Key in Fig. 9.

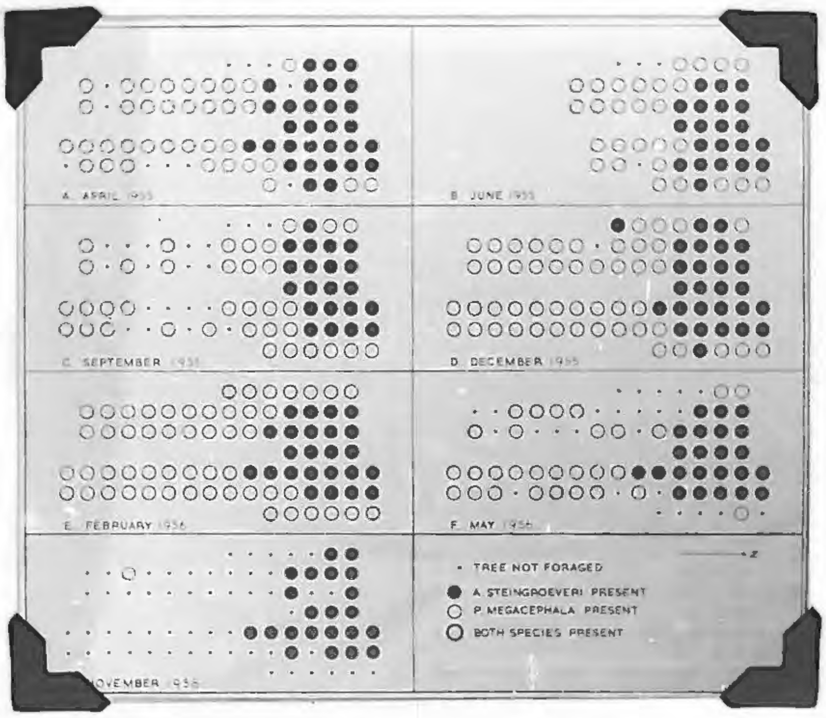

FIGURE 9. Orchard No. 3.

Survey of the distribution and territorial relationships of A.steingroeveri and P.megacephala from April, 1955 until November, 1956.

ORCHARD No.2.

TABLE 9.

Analysis of ant territory in the Fish River Valley.

Trees: Months	April	July	Sept.	Dec.	Jan.	May	Nov.
Total No.	103	103	103	103	103	103	103
Unforaged	-	-	2	-	-	13	101
Foraged	102	103	101	103	103	90	2
A.steingroeveri	46	39	42	42	33	14	2
P.megacephala	56	63	59	61	69	76	-
Coincidental	1	1	-	-	1	-	-
Totals	103	103	101	103	103	90	2

TABLE 10.

Trees occupied as percentages of total no. trees foraged.

A.steingroeveri	44.66	37.86	41.58	30.77	32.03	15.55	100.0
P.megacephala	54.36	61.16	58.41	59.22	66.99	84.44	0.0
Coincidental	0.97	0.97	-	-	0.97	-	-
Totals	99.99	99.99	99.99	99.99	100.0	99.99	100.0

TABLE 11.

Trees occupied as a percentage of the total no. trees.

A.steingroeveri	44.66	37.86	40.77	40.77	36.89	13.59	1.94
P.megacephala	54.36	61.16	57.28	59.22	62.13	73.78	-
Totals	99.02	99.02	99.05	99.99	99.02	87.37	1.94
Unforaged	0.98	0.98	0.95	0.01	0.98	12.63	98.06

ORCHARD NO.3. TABLE 12.

Analysis of ant territory in the Fish River Valley.

	1955				1956		
Trees: Months	April	July	Sept.	Dec.	Jan.	May	Nov.
Total No.	77	53	77	77	77	77	77
Unforaged	10	4	20	1	-	25	54
Foraged	67	49	57	76	77	52	23
A. steingroeveri	30	21	21	27	24	23	22
P. megacephala	37	28	36	49	53	29	1
Totals	67	49	57	76	77	52	23

TABLE 13.

Trees occupied by different species as a % of total no. trees foraged.

A. steingroeveri	44.77	42.85	36.84	35.52	31.16	44.24	95.65
P. megacephala	55.22	57.14	63.15	64.46	68.84	55.76	4.34
Totals	99.99	99.99	99.99	99.98	100.0	100.0	99.99

TABLE 14.

Trees occupied by different species as a % of total no. trees.

A. steingroeveri	38.89	39.64	27.27	35.06	31.16	29.87	28.57
P. megacephala	48.05	52.83	46.75	63.63	68.84	37.66	1.30
Totals	86.94	92.45	74.02	98.69	100.0	67.53	29.87
Unforaged	13.06	7.55	25.98	1.31	-	32.47	70.13

restrict the penetration of this species. However, it will be shown later that A.steingroeveri was prevented from penetrating deeply into the F.R.V. orchard by the conditions prevailing in and around them. The scale, rather, is restricted here to trees visited by the ants.

Although food derived from the honeydew complex is important to the ants, which appear to be the mainspring of the 'honeydew complex', the presence or absence of this food is dependent largely on the ants and not vice versa. Hence the extent of the honeydew complex food source is a function of the attentions of the ants.

2. Soil conditions.

The soil texture was uniform throughout any one of the F.R.V. orchards, and hence this aspect cannot be considered to be a selective factor in the manner described by Steyn (1954a). Both ant species were able to nest in basins and terrace ridges. The soil type may be described as being clay which cracked and flaked after irrigation. The cracks interfere with the foraging of A.steingroeveri. It is described later how the ants bridge the cracks. Thus cracking of the soil surface has only a temporary adverse effect on the ants.

Cultivation is not so thorough as in the orchard in the S.R.V. for the terraces, close-planted trees, and the comparatively greater tree-size reduce the manoeuvrability of tractor-drawn harrows. Cultivation usually follows irrigation. The loose soil surface did not appear to hinder the foraging activities of the ants. Cultivations between the orchard and mother nests out of, and along the orchard margin, breaks down the liaison between the two types of colony.

Border cultivation occurs when the land adjacent to the orchard is put under another crop, such as tobacco. The absence of the population pressure from mother nests definitely weakens orchard nests. The liaison is lost, not so much from the barrier created by harrowing, but the destruction of mother nests on the trails leading to the orchard nests. The first indication of this was given in the western section of orchard No.2, when the land adjacent to the orchard was ploughed up and the rather isolated territory was lost in the western portion of the orchard. (See Figs. 8a, b, c). Similarly, Fig.8f shows the result of extra-orchard ploughing, together with that of fumigation; however, signs of territory loss were showing in Fig. 8e in the north-eastern portion of *A.steingroeveri* territory.

Soil texture does not play an important rôle in the orchards under consideration. If there were markedly different soil types they would appear to have little influence on the nesting behaviour of *A.steingroeveri*. This species nests on the immediate river sandbanks, where the soil is so loose that it may be scooped up by hand and then runs out between the fingers. Here the ants show signs of being hindered by steep slopes of loose sand, but there were a surprisingly large number of colonies along the river bank living quite contentedly under these conditions. Steyn (1954a) suggests "..... it is conceivable that this small ant (*Pheidole*) can successfully nest in finer soil without dislodging the sand particles ...." On the basis of these remarks, the nesting of the ant in river sand may be attributed to the well-differentiated worker sub-castes of *A.steingroeveri*. Minor workers are considerably smaller and more compactly built than those of *A.custodiens*, and the task of pioneering and maintaining the nest in good condition here must fall to them.

The term 'pseudorepletism' is used to denote the storage of large quantities of fat, or greatly enlarged fat bodies, within certain distended individuals which leave the nests only in exceptional circumstances. The crop is not distended with undigested honeydew or nectar, as is the case with true repletes or honey ants. (Wheeler, 1910). When food is required from true repletes they are tapped by workers, which receive regurgitated food from the repletes. In pseudorepletes the food is stored in the form of fat (which has a greater calorific value than sugar) but it is not readily available to the ants in this form. It is logical to assume that pseudorepletes are killed and eaten when the need for food arises.

Pseudorepletism does confer certain advantages. Such individuals are quite mobile, although they take no part in foraging, and should the need arise, as will be described later, they are able to move to new nesting sites. True repletes are completely immobile. Wheeler (1910) states that repletes require a hard compact soil to support their weight while they hang from the ceilings of chambers within the nest.

Pseudorepletes are less distended and cumbersome than true repletes, and should the theory propounded by Wheeler, and subscribed to by Steyn, be valid, then individuals in the former condition would tend to have definite advantages to ant species nesting in loose sandy soils.

The chambers housing the repletes are disc-shaped and much smaller and flatter than those of *A.custodiens*. *A.steingroeveri* nests may extend to the depth of 4 feet into the soil and this is considerably deeper than most *A.custodiens* nests. Otherwise the method of nest construction resembles that of the pugnacious ant. These shallow 'storage' chambers are densely packed with pseudorepletes and the workers serving them; but a few pseudorepletes cling to the ceiling,and those that do derive a certain amount of support by resting on those individuals below them.

The extreme depth of these nests compared to those of *A.custodiens* is another manifestation of adaptation to arid conditions. At a depth of 4 feet there is little possibility of the nests being flooded out, and the singularly constant conditions, together with the sedentary habits of pseudorepletes, makes outpost or basin nests ideally suitable for storage purposes.

Steyn points out that pseudorepletes may occur in any of the worker sub-castes in *A.custodiens*. The same applies to *A.steingroeveri*. Since most minor workers are devoted to honeydew foraging, for which they are the best adapted worker subcaste, pseudorepletes are found mainly in media and major

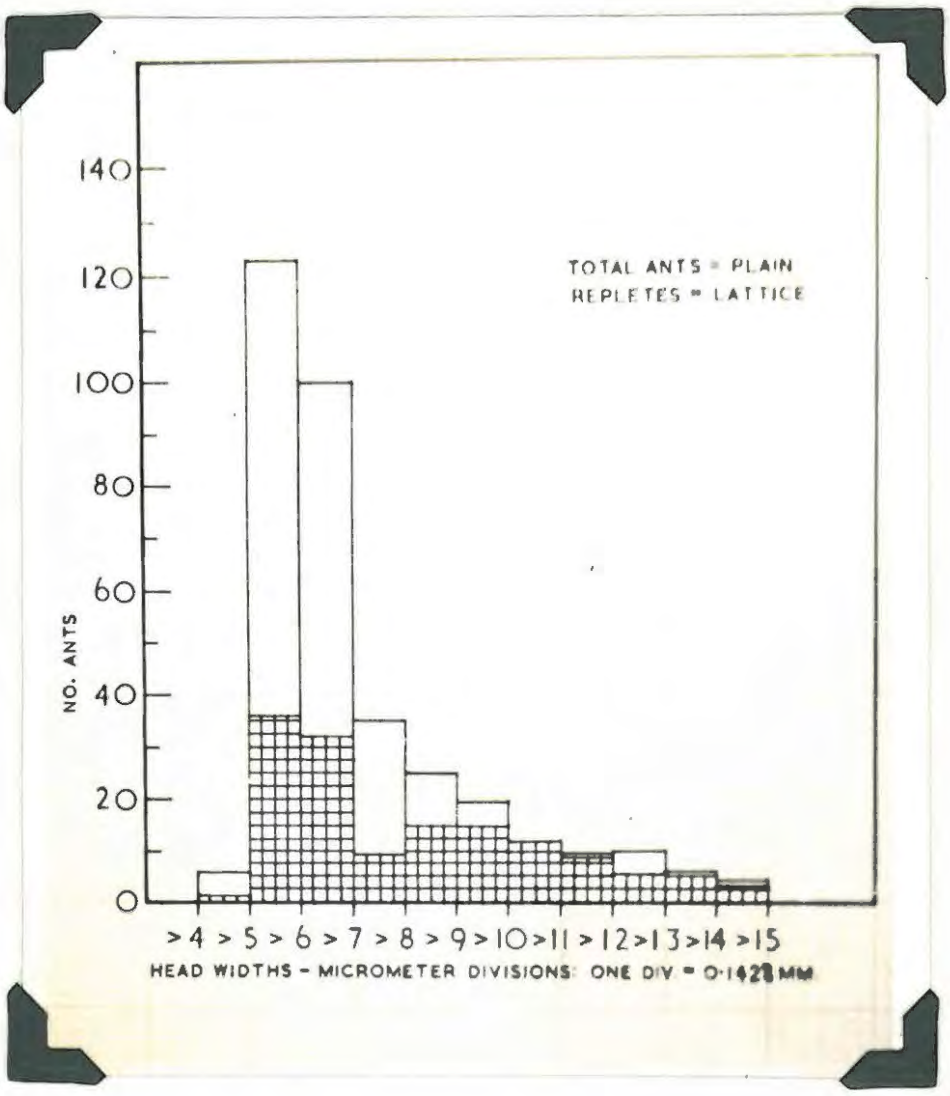

FIGURE 10.

The distribution of pseudorepletes in a sample of ants taken from an A.steingroeveri nest. Micrometer division 6>7 indicates that ants with headwidths greater than, and including, 6 divisions, but less than 7, were placed in this group, and so forth.

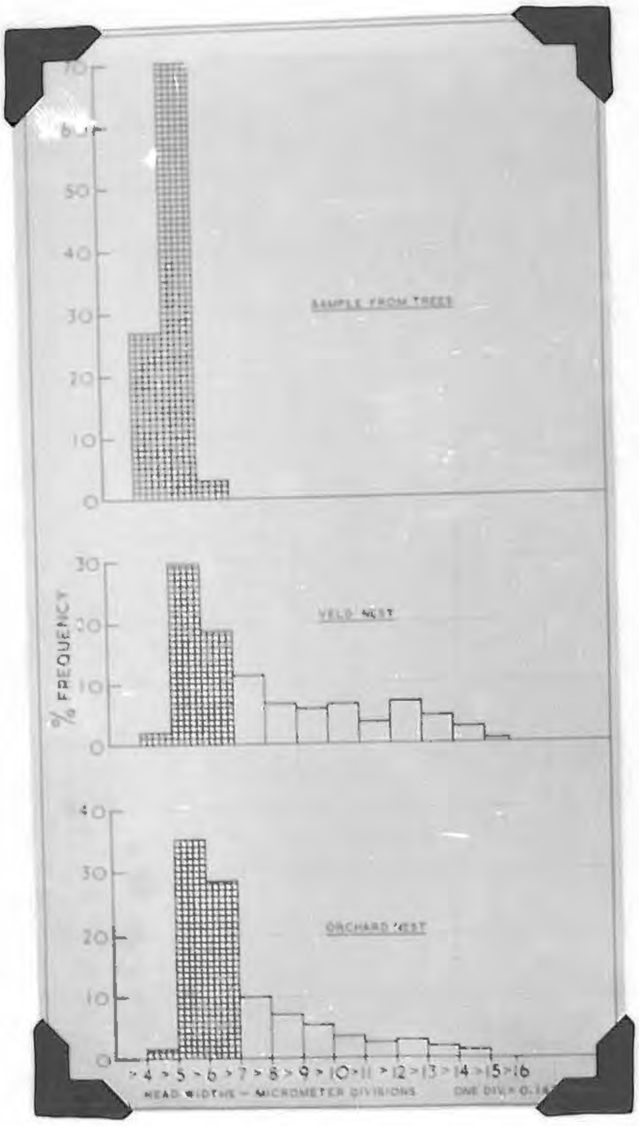

FIGURE 11.

A comparison of the numbers of ants of different sizes in samples taken from trees, orchard and veld nests. It shows that honeydew foraging is done mainly by minor workers (lattice), and the orchard sample contained more minor workers than the veld sample.

workers. The latter sub-castes are obviously more suitable to serve as repletes.

Fig. 10 is a typical histogram of the distribution of the various worker sub-castes in a sample of 350 specimens taken from a mother nest attached to an orchard. Ant numbers are plotted against head width; the latter being grouped into micrometer divisions as indicated. Superimposed in black on the white histogram is the number of pseudorepletes occurring within the different divisions. This shows that proportionally more media and major workers are given over to repletism than minor workers.

This aspect of the study was taken a stage further. Samples of 50 ants from six different trees were collected, measured, and placed into the micrometer groupings. Not a single specimen fell into the divisions above 6, while the majority fell into group 5. Fig. 11 shows the comparison, in percentages, of the frequency of occurrence of ants of different sizes in samples of foraging ants taken from trees with samples from veld and orchard nests. It is quite clear that minor workers do most of the honeydew foraging, while the major and media forms are given over to defence, attack and repletion.

3. <u>Shade</u>.

Terrace, or basin bank, nests are usually located with nest entrances along the ridge of the basin wall, while the subterranean portion of the nests extends downwards parallel to the terrace wall. These nests differ from basin nests by having queens, and brood chambers in the uppermost parts of the nest. The brood chambers lack waterproofing, and because of their superficial dispositions are freely permeated by rainfall and irrigation water. The effects of excess moisture when it does reach the brood have been mentioned above. Humidity balance is of the greatest significance to this species. Veld colonies are located on high ground with a good run-off. Other nests are situated in extremely sandy and porous soil where waterlogging does not occur.

In the polydomous nesting regime of orchard-foraging *A.steingroeveri* ants, brood is placed in extra-orchard mother nests along roads, or in other places with exposed consolidated soil, and within the orchard along highly insolated terrace banks.

Ant nests situated in terrace banks running more or less North to South have an additional advantage; besides being situated above irrigation water-level, they receive more insolation in the early morning and later afternoon, while at midday they receive as much as the level surrounding exposed areas. Mound-building termites and ants create this happy circumstance for themselves. The greatest use or exploitation of insolation is found in the Australian Compass Termite, (*Amitermes meridionalis* Froggatt) (Emerson, 1938; Skaife, 1955a) Similarly, mound-building termites (*Trinervitermes*) in South African grasslands have their mounds higher than the surrounding grass on which they feed.

A.steingroeveri has used the terrace banks for the same purpose, especially those terraces sloping towards the East, for warming of brood chambers is much more important in the early morning than in the late afternoon. Furthermore, early morning skies are more dust-free, and little radiant heat is lost on that account.

Terrace banks running East to West also support some *A.steingroeveri* colonies, especially if the down slope faces northwards.

In both types of orchards, no correlation between nest dispositions and tree shading could be made. The irregular planting of trees on the contour results in a heterogeneous shade patterning in the orchards. The figures which depict the distribution of ants are drawn as diagrammatically as possible to facilitate drawing and interpretation. However, where *A.steingroeveri* nested in terrace banks there was a marked correlation with the presence of adjacent die-back trees.

4. Irrigation.

The results are mentioned above of an investigation into the distribution of brood-rearing nests of A.steingroeveri in relation to their location within the orchard. The data are fully presented below, showing the occurence after rainfall and irrigation of brood exuviae in ant cemeteries.

TABLE 15.

Location	No. Cemeteries.	%
Beneath trees	-	-
Basins (unshaded)	36	14.75
Banks	208	85.24
Totals: ,	244	99.99

These figures are derived from a survey of A.steingroeveri cemeteries in the area depicted in Fig. 9 (Orchard No. 3) on 27.III.56, when brood-rearing reached its peak. The presence of dead brood even on the drier bank ridges substantiates previous observations that A.steingroeveri is extremely susceptible to the effects of excess moisture.

These results confirm the impression that, although a considerable number of nests exist within the basins in exposed situations and beneath trees, these nests are outpost nests. Outpost nests contain, as far as I can ascertain from six nests which I have examined, no queens, infrequently brood, but all have workers and pseudorepletes.

Outpost nests function to establish territory and facilitate foraging in that the workers have to traverse less ground to yield up their honeydew to the pseudorepletes. Furthermore, it is a form of specialisation, since the mother nests can be given over to a greater extent to brood production. Mother nests also have pseudorepletes, but the storage of food in outpost nests, together with the presence of non-pseudoreplete workers, improves the economy and consolidates the territory of this ant.

In the S.R.V. it is noticeable that A.steingroeveri was unable to penetrate at all deeply into the orchard which lacked permanent banks. This is true especially for the A.steingroeveri territory in the south-west corner (Figs. 3a-f), where it did not encounter any opposition from A.custodiens. This shows the extent to which orchard colonies of A.steingroeveri are dependent on extra-orchard mother nests, and suggests that they are unable to inhabit well irrigated land. A.steingroeveri does not line its nests with wax in the characteristic manner of A.custodiens, and this is most likely the reason why A.steingroeveri cannot nest in completely flooded orchards with impermanent basin banks.

5. Insecticides.

Extreme discretion has been used in the application of insecticides at Dunbar. Fumigations with HCN gas (Cyanogas) are made infrequently and only when necessary, but heavy dosages are used when the scale-infested trees are treated. Mainly due to this form of treatment, the scales are still susceptible to HCN, and it has not been found necessary to resort to contact insecticides. Fumigation was carried out on one occasion only during the time of this investigation.

(i) Direct effects of fumigation.

Fumigation is carried out at night, when there are fewer ants foraging in the trees. Smithers (1953) records that A.custodiens individuals were killed by HCN gas in the S.R.V. A.steingroeveri is also killed by this gas, but only the foraging ants in the trees and on the ground beneath the trees are affected. These small losses incurred by outpost nests are easily and quickly replaced from mother nests which are not subject to fumigation.

(ii) Indirect effects of fumigation.

These are due to the killing off of the Soft Brown Scale, which is the ultimate fount of most foods available to A.steingroeveri. Removal of this attractant results in a significant reduction in activity and a change of foraging behaviour from 'trailing' to hopeful 'exploring'. The reduction in foraging intensity is not to be attributed to the lower mortality inflicted on A.steingroeveri through fumigation, but to the absence of food.

(a) Reduction in activity.

This was calculated for A.steingroeveri on the basis of data obtained from other experiments dealing with the activity of this species (in which the ants were provided with a constant, or "ad libitum" food source in some trees, but not in others). To eliminate possible complications due to varying climatic conditions, activity records between 10 a.m. and 8 p.m. were used. Between these times the ants are most active and least affected by adverse climatic conditions.

Using absolute figures of the total numbers derived from counting the ants ascending and descending past a given point on the tree trunk and times at hourly intervals for periods of two minutes, in October, 1955, the relative activity ratio (1.69 : 1) between two scale-infested trees was established. One of the trees contained the ad libitum food source of sugar solution, and the other, 'control', tree had no additional food other than honeydew which was common to both trees.

From the ratio the percentage activity reduction after fumigation was calculated for the control tree. The fumigation was made in early May, 1956, and the calculated percentage reduction in activity was compared with the activity in the previous month (April) before fumigation.

Results.

The data given below are given in some detail to show how the percentage reductions in activity were calculated.

1. Total activity, October, 1955 (before fumigation).

Tree	Control		Ad libitum
	2994		1769 ants/4mins/hour
Activity ratio	1.69	:	1

2. Total activity in May, 1956, on tree with '<u>ad lib</u>' food source, after fumigation.

Tree	Ad lib.
	2424 X activity ratio (1.69) = 4097

therefore theoretical total activity on control tree if fumigation had not taken place =

4097 ants/4 mins./ hour

3. Total activity in May, 1956, after fumigation.

Tree	Control	Theoretical activity on control tree.
	301 (recorded)	4097 ants/4mins./hour

Percentage reduction in activity = 92.55%

4. As a measure of the reliability of the above calculation, it may be stated that a count made in April, 1956 (unfortunately without a corresponding count on the ad lib. tree) gave a value of 6659 ants/4 mins./hour. When this is compared with the value after fumigation (301 ants/4 mins./hour) it gives a percentage reduction in activity of 95.48%, a figure in close agreement with that obtained by using the theoretical ratio. This shows how fumigation of scales reduces the foraging intensity of the ants.

Killing of the Soft Brown Scale reduces the whole level of activity of the entire orchard invertebrate fauna, including the ants, and the atypically dense orchard ant population is faced with having to live under veld conditions. Once again the long term effects from starvation are incalculable and may only be recognisable in the next generation.

(b) Territory.

It is to be expected that the drastic drop in ant activity would be paralleled by a loss of interest in the now barren trees, and the trees would be deserted by the ants.

Orchard No. 3 (see Table 12 and Fig. 9f) shows that only one tree had ceased to be foraged by A.steingroeveri, which means that the foraging of this species is just as widespread as it was before fumigation, but not so intense. These trees are being explored for possible food-sources, or sites of re-infestation by Soft Brown Scale, which, if found, would alter the behaviour of the ants. Since citrus trees are virtually the only flourishing vegetation on this farm, most insect life would be attracted to it, including the ants. Furthermore, hunger would stimulate the ants to forage more extensively in an effort to recoup their food losses.

Retention of territory by A.steingroeveri after fumigation but with reduced foraging intensity, is apparently not true in Orchard No. 2, where 19 trees, or 57.58% of their territory (see Table 9, Fig. 8f) had been lost. This loss had been progressive (see December and January columns) and springs from the disturbance of mother nests in the adjacent virgin veld in the preparation for tobacco. The effects of fumigation are secondary, and may have had a minor rôle in the loss of this territory, since the outpost nest losses could not be readily replaced from mother nests.

For a true picture of the effects of fumigation, we must rely on the observations made in Orchard No. 3.

(iii) Effects of Parathion Sprays.

Late in the investigation (24.XI.56) a final survey of ant distribution in the two F.R.V. orchards was made. Just previously, the trees had been sprayed with parathion to control a heavy infestation of Bollworm (Heliothis armigera Hübner). This was the first occasion on which parathion had been used in these orchards and it had startling results on the ants. I was not present to witness the direct effects of parathion on A.steingroeveri. In Orchard No.3 the ant population was not much affected, if at all, but there had been a marked change in their foraging behaviour. Any new scale infestations which had arisen after fumigation in early May were killed by the parathion Although some ants continued to visit the trees, and such trees were considered to be their territory, most foraging was of the exploratory type and 'trailing' to trees was noticeably absent. A.steingroeveri in Orchard No. 3 (see Fig. 9g) showed an overall loss of 1 tree, when compared with the figures for the previous survey in May (Fig. 9f); it had gained three new trees and lost four which it previously occupied. In Orchard No. 2, A.steingroeveri lost all of its territory with the exception of two trees. This represents a net loss of twelve trees since the previous survey (Fig. 8f). This loss was due, not so much to the effects of parathion alone, but the combined effects of the removal of mother nests from the adjoining veld, and fumigation, then finally parathion. In Orchard No.3, the mother nests had remained untouched.

Thus, insecticides have little direct effect on the ant colonies, but the absence of scale and honeydew-complex changes the ants' foraging behaviour, and substantially reduces their foraging activity.

(c) Pheidole megacephala.

The behaviour of this species was studied only in the F.R.V.,at the farm "Dunbar", in the same orchards as A.steingroeveri.

1. Food.

P. megacephala occupied most of the trees not foraged by A.steingroeveri. These trees were usually situated deep within the orchards and did not bear Soft Brown Scale, or only very light infestations. As a result, most of P.megacephala colonies were weakly populated and had no economic significance. In a few isolated instances P.megacephala colonies did harbour heavy infestations of scale, which resulted in the trees dying back. Such colonies were numerically stronger and more vigorous than the colonies beneath scale-free trees.

Since most P.megacephala colonies did not enjoy the honeydew-complex food their nourishment was most likely derived from scavenging. Harvester termites may have formed part of their diet, but it is not known to what extent P.megacephala draws upon this food source. This ant burrows extensively and possibly attacks termites beneath the soil surface. On several occasions P.megacephala was found occupying characteristic termite tunnels. It appears that colonies of P.megacephala were not limited in their distribution by food, but their numerical strength was dependent on the food available to them.

2. Soil conditions.

The more or less uniform soil texture in Orchards 2 and 3 has been described above and P.megacephala nested in the same soil as A.steingroeveri, as some nests, especially at the base of tree trunks, were occupied by these two ants at different times. P.megacephala also nested in terrace banks, but terrace colonies did not form any part of the honeydew-complex owing to the short foraging range of these ants. Terrace colonies of P.megacephala did, however, constitute a source from which the alates spread into the orchards.

P.megacephala colonies were found in a number of places; in the veld, terraces, and even beneath trees, and not restricted to any one particular soil type. The orchard colonies beneath trees were not affected by harrowing, as the harrows did not reach under the trees. Thus, soil conditions did not play an important rôle in the distribution of this species in the F.R.V.

3. Shade.

The Brown House Ant, as Broekhuysen (1948) has shown, is able to produce brood in a wide range of environments, largely because the brood can develop at lower temperatures than Anoplolepis (Steyn, 1954a). As I have pointed out above, P.megacephala would be able to produce its young even under conditions of complete shade in the F.R.V. Way (1953), when discussing the distribution of Pheidole punctulata, says "The distribution of this ant is not markedly influenced by these factors". (He refers to soil texture and insolation).

Orientation of Pheidole tree trails.

I noticed that P.megacephala trails leading up citrus trees tended to be located on the north-eastern side of the trees. I then decided to take compass bearings of all the mud tunnels and other types of Pheidole trails leading up trees in orchard No. 2 on 29.V.56.

The bearings were then grouped into quadrants of 90° as shown below, and the following results obtained.

Results: TABLE 16.

Quadrant		No. of trails	%
1. N-NE;	0°-90°	48	61.54
2. NE-S;	90°-180°	14	17.95
3. S-SW;	180°-270°	5	6.41
4. SW-N;	270°-360°	11	14.10
Totals:		78	100.00

The ants show an obvious preference for trailing up the N-NE quadrant, while they preferred to a lesser extent the adjacent quadrants (NE-S and SW-N) on either side of it.

The three quadrants represent the arc of maximal illumination by the sun during the course of the day. The sun is the only factor with which the orientation of Pheidole trails could be correlated, and this points to the ants being dependent to a certain extent on the sun. P.megacephala must derive whatever benefit they can from the sun while they are on the trails. The ants have a slight preference for the early morning sun, as more trails are found on the eastern side of the trees.

Most trees occupied by Pheidole had low-hanging skirts and these would tend to reduce the effects of the sun. On the other hand, the ants must benefit to an extent which makes building of their trails on the sunny side of the tree worth while.

4. Irrigation.

P.megacephala appears to enjoy almost complete freedom from ill-effects of irrigation. Like most ant species, some adults are drowned, but since P.megacephala is adapted to raising its brood under colder and more humid conditions, the young apparently were not affected in the same way as A.steingroeveri by excess moisture. This accounts for distribution of P.megacephala at the bases of trees.

5. Insecticides.

(i) Direct effects of fumigation.

The direct effects of the insecticides on those ants caught in or below the tree at the time of fumigation are readily seen in *P. megacephala* by the number of cadavers in cemeteries. This ant appears to be susceptible to fumigation because of its habit of nesting beneath trees, and the structure of its nest with a network of superficial galleries just below soil surface. It is not possible accurately to calculate the mortality in the ant colonies since they are located between the roots of the trees and so cannot be dug up.

(ii) Indirect effects of fumigation.

P. megacephala territory. In Orchard No.2 all trees were fumigated, while in Orchard No.3 only the first five northern rows were fumigated. (More attention was given to *A. steingroeveri* because it fostered infestations of scale). When the condition in Orchard No.2 in Fig. 8f is compared with Figs. 8a and b, it is apparent that, although *P. megacephala* has gained some territory, it lost a number of trees which it formerly held. This loss was due rather to the onset of winter than to fumigation. When a similar comparison is made between the observations in Orchard No.3 (Figs. 9f : 9a, 9c) we can only assume that the territory loss of *P. megacephala* was due to climatic factors, since most *P. megacephala* trees were not fumigated. There may be other factors involved, but they were not seen in operation.

(iii) The effects of parathion sprays.

The effects on ants of parathion sprays are different to those of fumigation. After fumigation the ants would continue trailing up trees, but after treatment with parathion, *P. megacephala* was to all intents and purposes absent from both orchards (Fig. 9g).

Parathion has a marked detrimental effect on this species, largely because the insecticide tends to run down and collect at the base of the tree trunk, where the nests of this ant are situated. In this way, *P.megacephala* was severely affected; only one tree had this ant ascending it, and this tree was the only one in the two orchards to be visited by this species.

(d) Comparisons and discussion.

1. Food.

All three species avidly seek honeydew and exploit honeydew-complex food when it is available to them. These ants, however, are not completely restricted to the honeydew-complex, as they visit and sometimes exist on the food derived from healthy, scale-free trees. In the S.R.V. orchard, well over 50% of *A.custodiens* forag~~ing~~ed territory consisted of healthy trees. *A.steingroeveri* in the F.R.V. continued to retain the trees in its territory, even when the honeydew-complex was eliminated by fumigation and an application of parathion. A large percentage of the trees occupied by *P.megacephala* were free from scale infestations.

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On the other hand, these ants foraged all available honeydew, which suggests that the scale insects are almost completely dependent on the ants for their existence. Those ant colonies which enjoyed a copious supply of honeydew were numerically stronger and more vigorous than colonies without honeydew.

2. Soil conditions.

Soil texture did not appear to restrict the nest distribution of these species in the orchards under consideration. The limited number of soil types in the F.R.V. did not allow me to investigate Steyn's claim (1954a) that the relationships of *A.custodiens* and *P.megacephala* were influenced by the soil type in terms of the 'ant-lion-trap' principle. Loose surface soil in the S.R.V. resulting from harrowing only temporarily disrupted the trailing of *A.custodiens* in the S.R.V. orchard. Cultivations were less thorough, and made more infrequently in the F.R.V. and did not affect *A.steingroeveri* to the same extent. *P.megacephala* was not affected by harrowing because it nested beneath the trees.

The destruction of the soil 'mulch' or consolidated surface soil, during harrowing limited the choice of nesting sites by A.custodiens to the tree islands in the S.R.V. orchard. The less thorough harrowing in the older F.R.V. orchard had no similar effect on A.steingroeveri, partly because of the permanent terraces, but this ant did nest in harrowed soil to a limited extent. P.megacephala was unaffected for the reason stated above.

Steyn (1954a) quotes the observations of eight entomologists on the distribution of A.custodiens. From these, together with those of Way (1953), we may conclude that this species nests in a wide variety of soil types. Most of the observations bear two things in common: A.custodiens nests in (1) well insolated soil, which is (2) compact and undisturbed. These findings confirm my observations in the S.R.V. on the pugnacious ant. A.steingroeveri also occupies similar range of soil types and equally requires insolated compact soil for nesting purposes.

3. Shade and Irrigation.

The phenomenon of 'cornering' was shown by A.custodiens, which preferred to nest in the northern, more insolated corner of the islands. Here higher soil temperatures prevailed, which are necessary for brood maturation. Where other consolidated, undisturbed soil was available (F.R.V.), A.custodiens showed a distinct preference for nesting in it (permanent terrace walls), which indicates its preference for nesting in undisturbed ground, and also freedom from irrigation water. This species, however, was able to nest in completely flooded soil, largely because its nests were lined with waterproofing wax. The distribution of A.steingroeveri nests could not be correlated with shade, owing to the irregular layout of the F.R.V. orchards. However, by noting the position of brood-bearing nests after an irrigation, it was found that most of the brood was reared on the terrace banks. The terrace banks experience greater insolation than the basins, and were more flood-free. Hence A.steingroeveri, which lacks the nest-waxing habit, was apparently very susceptible to excess moisture in its nests and can only penetrate into orchards which have permanent flood-free soil. This explains why A.steingroeveri was not able to penetrate into the S.R.V. orchard.

Where terrace banks and extensive tree shade are present (Koenap River) both A.custodiens and A.steingroeveri are restricted to nesting on the terrace in a small insolated area between the trees. P.megacephala is adapted to live and rear its brood in a wide range of temperature and moisture conditions and was not much affected by shade or irrigation. Those two factors do not appear to hamper the spread of this species in orchards. This suggests that P.megacephala has been relegated the rôle of occupying the areas unsuitable to Anoplolepis for brood rearing and nesting purposes.

4. Insecticides.

Both A.custodiens and A.steingroeveri individuals, which come into direct contact with parathion or are exposed to fumigation, are killed. The number killed in this way appeared to represent only a small proportion of the total colony strength. When A.steingroeveri is deprived of support from mother nests the effect is greater.

The indirect effects are felt by the ants through the lack of food with which the brood is fed, but this is a long term effect which is incalculable. The removal of the honeydew source after fumigation causes a marked reduction in the foraging activity of A.steingroeveri, which must also apply to A.custodiens. P.megacephala, which is well-known for its susceptibility to insecticides, was most affected. It appeared to incur greater losses of adults from fumigation than A.steingroeveri, but no accurate counts of cadavers in cemeteries were made before and after fumigation. An application of parathion severely affected this ant, because the insecticide tended to collect in and around its nest. The result is shown by the number of apparently dead colonies situated beneath trees. (Tables 9 and 12).

(e) INTERPRETATION OF RESULTS IN RELATION TO ANT CONTROL.

In the areas under consideration, of all the ants which occur there, *Anoplolepis* appears to be the most widespread, the most economically important in citrus orchards, and the most difficult to control. *Pheidole megacephala* is equally widespread but is of less economic importance and is easily controlled for extensive periods by insecticides (Stofberg,1954) besides which it is dominated by *Anoplolepis* when there is a coincidental occurrence of the two species.

Previous control measures (Mathews et al., 1933; Smit et al., 1934) have been more concerned with *preventing* ants from gaining access to the trees, and have met with little and temporary success. This calls for a revision of our ideas of an~~y~~t control to one of ant *attack*; of driving the ants from orchards by horticultural means, and then destroying extra-orchard nests. This also entails a change in farming procedures which are not only beneficial to citrus farming, but may also be successfully correlated with ant control.

Young orchard trees are particularly susceptible to stunting when heavily infested with ant-fostered scales, but on maturity - after skirt-drop - the susceptibility is considerably reduced. The following argument deals with young orchards; however, the suggested treatments may be carried through until the orchards have become more mature.

I have shown that some farming operations do exercise a limited control on the distribution of ant nests:-

1. Cultivation restricts ants to rearing their brood in consolidated, undisturbed soil.
2. Shade case by trees further reduces these areas to insolated portions of the consolidated ground.
3. Irrigation does not have a significant effect on *A.custodiens*, but definitely reduces the 'encroachment potential' of *A.steingroeveri* into orchards.

Other farming operations are beneficial to ants:-

1. The dense ant population in orchards stems indirectly from

irrigation, but irrigation cannot be avoided; however, some of its effects may be exploited or reduced to assist in ant control.

2. Weeding of consolidated soil improves insolation and increases breeding potential.
3. Construction of permanent basin walls or terraces provides well insolated and consolidated soil for brood rearing, and a means of encroachment into orchards by ant species which normally suffer during irrigation.

Now we must consider why the various farming operations are practised:-

1. Cultivations are made to break up the soil crust to assist percolation by irrigation water, reduce moisture evaporation from the soil, and free the soil of weeds which compete with the citrus trees for a common water supply. The soil is enriched by ploughing-in of weeds.

2. Other operations cannot be altered to suit our purposes, or alteration is unnecessary.

What is required is a process to take the place of cultivation and simultaneously provide unsuitable conditions for ant breeding.

A heavy application of a grass mulch will fill the rôle most suitably, for the following reasons:-

1. In relation to farming: such a mulch, it is known, maintains the soil in an absorbent, friable condition, significantly reduces soil temperature and the effects of wind, both of which are contributory and sometimes complementary factors in water loss by evaporation from the soil. Reduction in light intensity will tend to inhibit weed growth. The conservation of water resulting from decreased evaporation may warrant fewer irrigations.

The use of mulches is not unknown in agriculture, but the correlation with ant distribution in orchards has not been released. Mulches are being used to a limited extent in both The S.R.V. and the N.E. Transvaal.

Practical difficulties such mulching would entail are the growing of the grass, and the speed of irrigation would be lessened, as the mulch would tend to hinder the flow of water. Where there is subterranean irrigation with porous piping, such a difficulty would not be encountered. Regrettably, this new method of irrigation is practised on a small scale only in the N.E. Transvaal.

Depending on the locality, termites may play havoc with the mulch, but a preliminary systematic poison baiting of the area would probably remove this danger.

Obviously in itself mulching is extremely good farming practice, and one may expect only good to result from such treatment.

2. <u>In relation to the ants</u>: mulching of the soil would entail foregoing harrowing, which disturbs the soil. This is beneficial to the ants, but the absence of high soil temperatures would reduce the breeding and foraging potentials of the ants within the orchards. In other words, the ants would find it extremely difficult to breed in orchards, and would be restricted to rearing their brood outside the orchard.

Extra-orchard nests are more vulnerable since they may be dug out without harming the citrus trees. A systematic digging-up of the nests and the treatment with insecticides of the soil both in and around the nests should exercise satisfactory control of the ant colonies.

The control of ants nesting on orchard terrace-walls constitutes a big problem, but a programme of progressively increasing the shading of the soil will be disadvantageous to the ants and restrict the ground suitable for nesting. However, a minority of orchards are terraced and this need not detract from the general argument.

Mulched orchards would constitute a suitable environment for smaller ants such as <u>Pheidole</u> which do not require very high temperatures for brood maturation. This ant, in my opinion, does not constitute the same menace to citriculture in the

E. Cape Province as Anoplolepis; furthermore, it is easily controlled in its restricted operational territory with insecticides.

It must be borne in mind that these remarks refer to conditions existing in the Eastern Cape Province, and the control measures suggested here may not be applicable in other places with higher temperatures. However, the same behavioural trends in Anoplolepis are noticeable elsewhere (Zanzibar; Way, 1953); N.E. Transvaal; Steyn, 1954).

Mulching must be considered as a temporary measure applied to young orchards to carry them through the initial stages of growth when maximum soil insolation prevails. Once the orchard has grown beyond the age(± 6 years) when it is most vulnerable to the effects of scale/ant activity, mulching may be discontinued. It would be sensible to carry on with mulching for a few years after this stage, to ensure that stunting does not occur as a result of increased ant activity.

Way (1953) sums up the situation, "It seems that A.custodiens and A.longipes could be controlled (in Tanganyika) by encouraging the growth of a thick ground vegetation of grasses and creepers".

V. COMPARISON OF A.STEINGROEVERI WITH A.CUSTODIENS.

Both *A.custodiens* and *P.megacephala* are well-known ants. *A.steingroeveri* is not so well known, although it may have been mistaken on many occasions for *A.custodiens*, which it strongly resembles in many respects. Some points of dissimilarity have been discussed above. To give the reader an appreciation of the physical characters, and behavioural characteristics of *A.steingroeveri*, a comparison between this species and the familiar *A.custodiens* is made below.

The data for sub-sections (a), (b) and (c) below are taken from Arnold's monograph of South African ants (1922).

	A. Custodiens.	*A. steingroeveri.*
(a) *Caste structure.*		
	Polymorphic;	Polymorphic;
	3 worker sub-castes	3 worker sub-castes
(b) *Size of workers* (body length)		
Minor:	3.5-5 mm.	3-3.8 mm.
Media:	5.3-7 mm	4.8-5.8 mm.
Major:	Up to 9 mm.	Up to 7 mm.
(c) *Colouration.*		
	"Head, thorax, legs and antennae dark burnt-sienna or brownish-red, the masticatory margins of the mandibles black, and abdomen dark brown. Densely clothed all over with a pale yellow and silky or slightly golden pubescence."	"Not unlike a smaller, darker and more compact *custodiens*, but without any silk pubescence or pattern on the abdomen. Dark rusty reddish-brown, the tarsi and antennae ferruginous, the thorax darker than the head, abdomen dark brown, apical margins of the segments pale flavous."

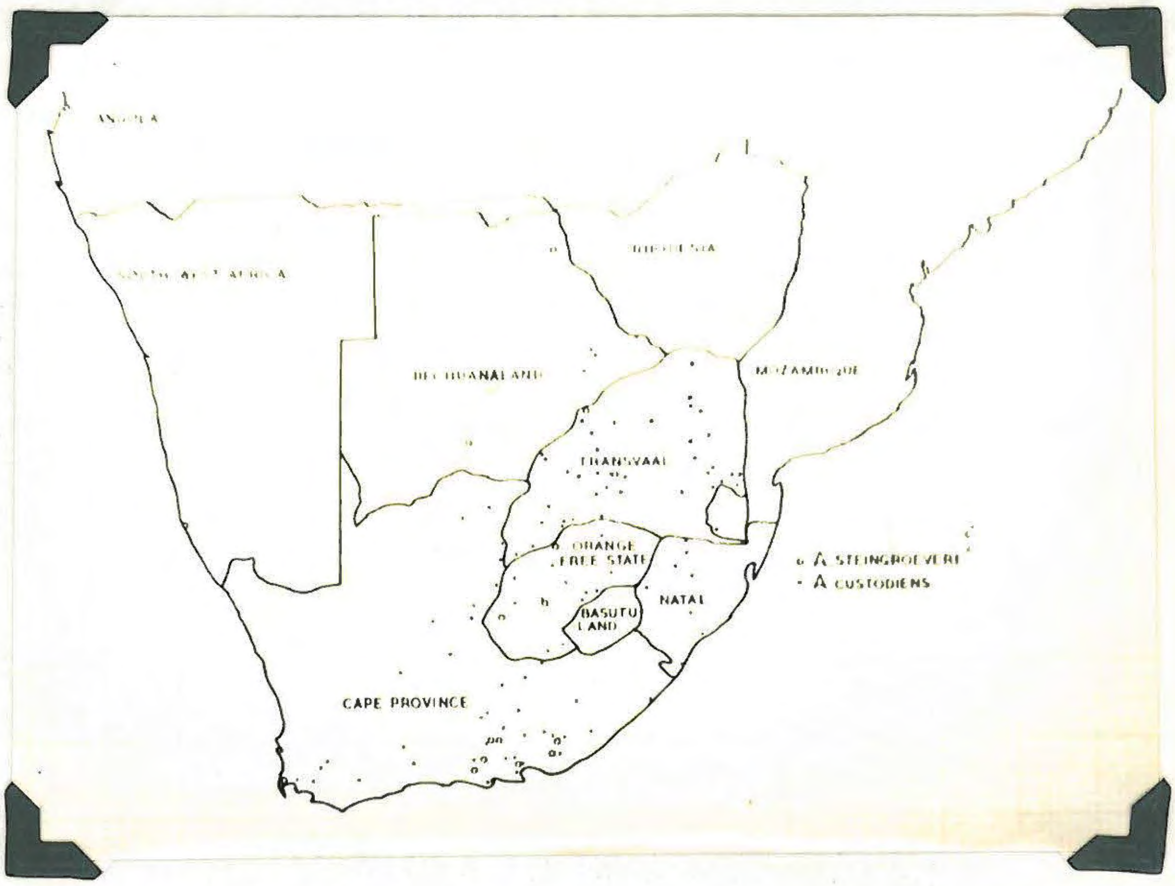

FIGURE 12.

The distribution of A.steingroeveri and A.custodiens.

(d) Distribution.

Fig. 12 shows the distribution of the two species. *A.custodiens* is much more widespread than *A.steingroeveri*. From the known distribution of *A.steingroeveri* one obtains the impression that it prefers drier conditions than *A.custodiens*. Owing to the extreme variability of rainfall in the mountain ranges along the South African coasts, it is not possible to make an accurate correlation between rainfall and distribution of the two species. However, it is noteworthy that *A.custodiens* apparently does not occur along the extremely arid west coast in the North-west Cape and South West Africa (Steyn, 1954), whereas *A.steingroeveri* has been found in several localities in those areas where the mean average rainfall does not exceed 5 inches.

(e) Behaviour.

Some aspects of the biology of *A.steingroeveri* have been discussed above, and later it will be shown that under veld conditions it is more than a match ~~of~~ for *A.custodiens*, 'the pugnacious ant'. The latter is considered one of the fiercest ants in South Africa.

A.steingroeveri reacts in a singular manner to a burning cigarette stub placed near its nest. Most species of ant known to me run away from burning cigarettes. However, *A.steingroeveri* individuals attack the cigarette in a vicious manner, biting and spraying it with poison until it is extinguished.

This behaviour may be an expression of the intrinsic voracity of this species or it may have other origins.

Regardless of the full significance and evolution of this heroic behaviour, it does illustrate the viciousness of this ant since few animals, especially invertebrates, are not afraid of fire. *A.custodiens* reacts to a cigarette in the same way, but only a few individuals make half-hearted attacks on it. There is not the same concentrated attack as *A.steingroeveri* ants, which unhesitatingly fling themselves upon the cigarette end.

Should an animal (man or ox) approach an area with a concentration of ants above ground, these ants make a concerted movement towards the animal and attack it. The mechanism underlying this movement seems to be related to vibrations in the soil. Approaching from different directions relative to the wind does not alter the reactions of the ants. The throwing of stones or tapping with a stick over the ants to the opposite side of approach does, however, create some confusion in the ants. *A.custodiens* behaves in a similar manner. Professor Ewer (1956) informs me that this ant also displays the same 'encircling' behaviour as *A.steingroeveri* which is described below, but I have not observed it in that species.

In this respect another peculiar piece of behaviour of this ant was noticed. Sometimes harvester termites (*Hodotermes mossambicus* Hagen) forage near and among the ants. The relationship of these two species is by no means fixed or constant. Sometimes the ants attack the termites without hesitation, while at other times they appear reluctant to attack, or show a certain degree of tolerance. Before an attack is made by a single ant on an individual termite the ants in the vicinity behave in the usual disinterested 'exploring' manner, frequently shunning the opportunity of attacking when it presents itself. Immediately attack is made, there is an instantaneous reaction from the nearby ants which, regardless of their position relative to the attacking ant, turn towards the place of attack. From the instant of the attack there is a marked behavioural change from 'exploring' to purposive 'trailing' towards, or encircling, the attacked termite where they help overpower it. Once the termite is subdued, the ants resume 'exploring' until such times that the next attack is made.

The 'encircling' behaviour is most striking, and lends itself to speculation. Ants in a circle of about two feet diameter respond to some signal from the attacking ant. The instantaneous response of ants from every compass point suggests that they are reacting to some stimulation which is not windborne. No stridulation was heard, but should this occur, such sound must be above the human auditory range. The explanation of this signalling remains enigmatical; however, it does demonstrate the high degree to which the co-ordination between individuals of this species is developed.

Fly-catching behaviour by A.steingroeveri was first noticed in the S.R.V. and subsequently studied in greater detail in the F.R.V. The large dipteran population in the honeydew-complex may be considered as competitors with the ants for honeydew. I did not witness a single successful attack on a fly, but many flies were seen falling to the ground after the attack had been made by the ants. Many ants made repeated lunges at the flies, which usually managed to evade the attacks. Activity in scale-infested orchards is at an extremely high pitch in summer, with the result that some flies do get caught, usually by minor workers. The first sign of a successful attack is the frantic buzzing of the fly trying to rid itself of the solitary ant clinging to it with its mandibles. The weight of the ant is sufficient to throw the fly off balance and bring it to the ground, where other ants, attracted possibly by the continuous buzzing, subdue the fly in a 'Lilliputian' manner. It is not possible to say whether the encircling response of the ants results from the buzzing of the fly, a signal sent out by the initial attacking ant, or a combination of both. Whatever the cause, the response is immediate, and should the fly not rid itself of the initial attacker quickly, it is overpowered and killed. Sometimes the victim does manage to escape, but only on very few occasions. Accordingly, there are few other insects which are able to forage openly in trees occupied by A.steingroeveri.

The same behaviour prevails in veld nests where ants forage honeydew-secreting Homoptera on veld plants. Although there are fewer flies visiting such small honeydew sources, captures are made in the same manner. This behaviour accounts for the way in which the ants of this species derive their food, both directly and indirectly, from honeydew.

A. steingroeveri is the only ant known to me which indulges in fly-catching, and this is a marked behavioural difference between the two species. Otherwise the two species derive their food from the same sources. Steyn (1954a) has drawn up a comprehensive list of the animals and other food sources included in the diet of *A. custodiens*.

Later, a description of 'entombing' behaviour by *A. steingroeveri* is given, by which this ant covers the nest entrances of *P. megacephala* with small pebbles and clods of earth, and thus avoids direct combats with *P. megacephala*. A more detailed account of entombing behaviour has been published (Myers, 1956).

After irrigation, the upper clayey soil flakes and cracks with drying out, leaving the orchard finely criss-crossed with cracks. The ants quickly set about filling up cracks along their trails with small pebbles and other suitable material. This bridging behaviour may be seen along all the major trails.

With specialisation, one expects and does find that animals become restricted to narrow ecological niches to which they are best adapted. This specialisation confers certain advantages and disadvantages on *A. steingroeveri* colonies living in and around orchards. Some of these have been discussed above; others will be described in the next section.

The two *Anoplolepis* species, as their congeneracy would suggest, bear many common characteristics in structure and behaviour.

VI. TERRITORIAL RELATIONSHIPS OF ORCHARD INHABITING ANTS.

(a) Introductory remarks and the concept of ant territory.

There have been few investigations into the question of territory. Most attention has been directed towards behaviour studies, and to a certain extent the distribution of ant colonies has been considered (Gösswald, 1932; Talbot, 1943).

Pickles (1935) was among the first to consider ant territory in relation to environmental factors under natural conditions. Greater consideration has since been given to ants in their association with Homoptera infesting cultivated food plants. This subject has been reviewed by Nixon (1950) and there is no further need to emphasize the significance of the fact that ants foster infestations of economically important Homoptera. The regular layout of orchards and plantations provides an excellent opportunity to observe territorial behaviour of ants under more or less uniform conditions. The most recent investigation along these lines was undertaken by Way (1953).

Territorial behaviour is well developed among vertebrates, especially birds, where each territory may be controlled by varying numbers of animals ranging from a single pair, or individual, to a group of animals. Territory marking is manifested in several ways. Several different species of animal may occupy the same area, but only a limited number of the same species are found in it.

Frequently migration and breeding are associated with territorial behaviour. This is known in birds and seals. In the main their interest in a particular area has sexual significance, as is the case with male Robins (Lack, 1948), Sticklebacks (Tinbergen, 1953) and Sealions (Matthews, 1952). There is also competition and foraging territories among birds (Lack, 1946).

Among invertebrates, territorial behaviour is not so well marked nor so well developed, especially among insects which are mostly short-lived and structurally incapable of fighting to obtain or hold territory. Among the short-lived insects the males of several species compete for territory; this has been observed in relation to dragon-flies (Jacobs, 1955).

Among pests of stored products and other insects occupying a limited food source, pollution and cannibalism are not to be considered as true territorial competition, but side effects (Rich, 1956).

The exception lies in social insects which, if each colony is considered in terms of the concept of the 'supra-organism' (Wheeler, 1911), are much longer lived.

Fighting in honeybees has been often recorded, and robbing occurs during lean seasons. As a means of defence hive entrances are protected and only those bees having the characteristic odour peculiar to each colony are allowed to enter. This 'odour passport system' is common in most social insects, but the territory interests of bees are confined to the hive. Once away from the main colony a different behaviour pattern operates. Individuals of the same species but from different colonies, which would be antagonistic near a hive, peacefully forage side by side in the field. In this respect they resemble non-social insects.

The odour-passport system prevails equally well among ants, but in contrast to bees, ants forage by walking and leave an odour trail to and from their food sources. Honeybees do mark with scents localised food sources (von Frisch, 1950), but no real territory significance can be attached to this behaviour. Marker scents dropped by bees at food sources are probably used by bees from other nests. The foraging field of honeybees is an expression of their most effective and economical flight range.

Thus there are two systems of marking territory in ants. There is the distinctive common odour of the colony which is produced by thoracic glands, and there is the odour trail which is laid down from an anal secretion.

Trail-marking behaviour is found in most ants regardless of the degree of optical development, and the ability of ants to follow this trail with antennae alone has been shown (MacGregor, 1948). The trail-odour intensity increases the closer one comes to the nest, as more ants cover the approaches to the nest. There is a diminution of odour intensity as the trails radiate away from the nest. Obviously, the trail-odour is of territorial significance. On this point I have satisfied myself by dropping Crematogaster and A.custodiens at various intervals away from the nest of the other species. Close to the nest of the other species frenzied escape activity is shown by the intruding ant. In no-man's-land this is replaced by cautious exploratory movements. At the extremes of home territory the behaviour is exploratory, but lacks any signs of nervousness.

In broad outline, this particular behaviour resembles that of male sticklebacks (Tinbergen, 1953). Similar behaviour between foraging ants has also been recorded by Brian (1955). Thorpe (1956),when discussing ant habituation, summarises the situation: "Many species exhibit antagonism to ants of other species,and even other colonies of their own species .... this antagonism is mainly, if not entirely, due to distinctive odours"

The relationships of different ant species varies in accordance with diet and mode of life. Let us consider species with common food requirements or preferences. When they forage from the same source, there may be partial occupation of a tree. Diver (1935) found ants from different colonies foraging from different branches, or there may be stratification, some species preferring to forage at soil level while others may forage on vegetation above the ground (Brian, 1955). In such an instance foraging behaviour influences the relationships of the ants.

There is no sexual significance attached to the territorial or competitive behaviour of ants. However, the presence of brood exercises a stimulating effect on workers, which forage more vigorously. This aspect will be discussed more fully under the section on foraging activity.

(b) Territory and relationships of A.custodiens and A.steingroeveri.

1. Climatic conditions and territory.

A single orchard of over 600 six-year-old trees, belonging to Mr. I. Matthews in the S.R.V., in which both A.custodiens and A.steingroeveri colonies were present, was selected for this investigation. This orchard was mapped as far as possible at three monthly intervals. The observations were begun in March, 1955, and continued in June, October and November, and in March, and May of 1956.

Results are given as maps, and various symbols are used to indicate the territory of each ant species and their association with different Homopters. The key to the symbols is attached to the maps (Fig. 3).

As is to be expected in a country with well-marked seasonal climatic changes, there is a fluctuation of the insect fauna. Soft Brown Scale reach their greatest density in summer and so do all insects of the honeydew-complex. At this time the ants have to meet the food requirements of the brood (Steyn, 1954a). This results in a more vigorous and widespread foraging, as is seen in Fig. 3a (March, 1955), but in Fig. 3e (March, 1956) fewer trees were being foraged. The significant increase in territory as illustrated in Figs. 3c and 3d in Table 4 (October and November, 1955), where the percentage of foraged trees rose from 33.9% to 53.4%, shows the sudden onset of foraging activity over a period of one month. This is correlated with the production of ant brood in summer.

On the other hand, during winter (Figs. 3b, 3c and 3f; Table 4) there is a distinct reduction in territory, which is coupled with a withdrawal ('winter withdrawal') of ants from output nests to the peripheral or marginal nests. The latter nests are permanent, and the spread of ants at the onset of summer takes place from them.

There are too few A.steingroeveri colonies in this orchard to draw any definite conclusions from the effect of climate on their territory. The variations in territory suggest that the react in the same way as *A.custodiens* to season changes for the same reasons.

2. Territorial relationships of *A.custodiens* and *A.steingroeveri*

The only territory disputed by the two species was located in the north-west corner of the orchard. During winter (Fig. 3b) there appeared to be a 'truce', and a buffer of one tree in depth existed between the territories of the two species. In summer, when competition was intensified, the buffer trees were absorbed into the territory of *A.custodiens.* In one year after the first observations (March, 1955), the *A.steingroeveri* territory had been taken over by *A.custodiens* Later, in November, 1956, it was found that *A.steingroeveri* had recovered one of the trees which it had lost to *A.custodiens*

A.custodiens is extremely tolerant of its own species, but is equally intolerant of other species, whether of the same or another genus (Way, 1953; Steyn, 1954a). Wheeler (1922) quotes a letter from Dr. Brauns, "the nests of *P.(Anoplolepis) custodiens* and *steingröveri*(former spelling) are frequently found close together .... At Willowmore *steingröveri* is showing a tendency to displace *custodiens*." This apparently is the first record of antagonism between these two species.

Superficially *A.steingroeveri* looks to be better equipped as a fighter than *A.custodiens*. However, the results of the surveys show that *A.custodiens* had successfully ousted *A.steingroeveri* from the northern corner of the orchard where the two species opposed each other.

Only one battle between the two species was witnessed. It took place in the northern left-hand section of the orchard in November, 1955. Antagonism is to be expected in this season, when the general activity of the ants is at a high level. This particular engagement was won by *A.steingroeveri*. Individuals of this species approached from a tree in their territory towards a tree held by *A.custodiens* and the battle took place midway between the two trees. Their styles of fighting were contrasting: *A.steingroeveri*, the aggressor, moved forward in a solid phalanx, while *A.custodiens* individuals parried this slow advance by making quick lunges at the advancing column. Once an *A.custodiens* individual grappled with an *A.steingroeveri*, it was quickly overpowered by ants coming to the assistance of the latter.

The combatants were mainly major and media workers of both species. After I had been watching the battle for about fifteen minutes, the engagement was broken off. *A.steingroeveri* carried away both its own dead and living *A.custodiens* individuals as well. *A.custodiens* did not make any captures and were not seen removing their own dead or those of *A.steingroeveri*.

As Brauns suggests, it would appear that *A.steingroeveri* is a fighter superior to *A.custodiens* when they meet on equal terms. This points to an inability of *A.steingroeveri* to contend with orchard conditions. It differs from *A.custodiens* in this respect, in that it lacks the nest-waxing behaviour of the latter. This, I have suggested, is one of the more important factors to which *A.custodiens* owes its success in orchards.

Since *A.steingroeveri* appears to be a desert inhabiting species, it has little need for such a protective mechanism against flooding. *A.custodiens*, with its much wider distribution in tropical areas, has evolved this mechanism to survive the effects of heavy rainfall.

The penetration of *A.steingroeveri* into the orchard is very slight compared with *A.custodiens*. This demonstrates the greater dependency of the former on extra-orchard mother nests situated in flood-free areas. There cannot be extensive occupation of an orchard without building up the ant population within it. From Figs. 3a-f it will be seen that *A.steingroeveri* did not have independent colonies within the orchard as is the case with *A.custodiens*, and this shows that nest founding by budding from mother colonies, or by queens, is hazardous to *A.steingroeveri* within orchards.

It is not known for how long *A.steingroeveri* and

A.custodiens have been established in the S.R.V. orchard. The picture to-day suggests that A.steingroeveri was formerly present as the indigenous ant, but has been superseded by A.custodiens. The inability of the A.steingroeveri colonies at the southern end to exploit and penetrate the orchard, especially when they are free from competition from other ant species, lends weight to the premise that this species is unable to contend with the conditions prevailing in this orchard.

3. The relationship of A.custodiens with subordinate ant species.

The distribution of subordinate ant species is indicated in Fig. 3 by vertical and horizontal half-moons. Trees occupied by these ants were far removed from A.custodiens territory. One species temporarily lived beneath a 'buffer' tree between the territory of the two major competing species (Fig. 3b) during winter, but the colony had disappeared after four months.

By and large, colonies of subordinate species were too few and temporary for any distinct relationship to be established between them and A.custodiens.

(c) Territorial relationships of A.steingroeveri and P.megacephala.

1. Climatic conditions and territory.

Figs. 8a-f and 9a-g present contradictory data. In Orchard No. 3, A.steingroeveri, only a slight, if any, winter withdrawal took place, but in Orchard No.2 in 1956 it appears to have suffered a considerable setback. (Also see Tables 6 and 9). This,I have explained, is due partly to the loss of extra-orchard mother nests and partly to the fumigation and the application of parathion. In all, A.steingroeveri territory shows little seasonal variation.

Conversely, P.megacephala shows a territorial loss in winter in Orchard No.3, which is not evident in Orchard No.2. P.megacephala ants at Fort Brown appear to behave in a different manner to those at Letaba, where, according to Steyn (1954a) they are most active in winter. The reason for this change in behaviour is not clear.

2. Relationships of *A.steingroeveri* and *P.megacephala.*

These two species are highly antagonistic, largely on account of their similar diet. Throughout the year the cemeteries of both species bear remains of the other, and this is indicative of almost continuous conflict. This is particularly noticeable in *A.steingroeveri* cemeteries.

A.steingroeveri is the dominant species and uses its power to encroach into *P.megacephala* territory should it so desire; but it requires special conditions, and when these are absent or disturbed, it has to give ground. *P.megacephala*, on the other hand, (as its cosmopolitan distribution suggests), tolerates a wider range of conditions and is able to exist in single colonies of smaller numbers. *A.steingroeveri* is too dependent on polydomy to exploit with the same success as *P.megacephala* restricted environments with a limited amount of food.

(i) *Food territory.*

The conquest of a *P.megacephala* tree is characterised by a series of steps. First of all, *A.steingroeveri* becomes attracted to a *P.megacephala* tree with a good food source during the summer.

Initially one finds *P.megacephala* in control of the main stem, ascending the tree along a typical trail. Once *A.steingroeveri* scouts approach the tree *P.megacephala* individuals become active around the base of the trunk, and other avenues of access to the tree, such as low-hanging branches and weeds. This is a form of territory claiming and defensive behaviour. Subsequently, if *A.steingroeveri* decides to occupy the tree an anomolous situation results whereby both species forage the same tree, but not amicably. Depending on where *A.steingroeveri* makes its most concerted attacks, it comes to occupy either the main stem or branches round the circumference, while *P.megacephala* uses the avenue of access not occupied by *A.steingroeveri*.

This state is found when either species is gaining or losing territory to the other species. It is a gradual process in which continuous pressure is brought to bear on the species attacked. Eventually the tree is completely taken over by the species which is dominant under the conditions prevailing at that time.

No extensive battles between the two species were seen in this connection, though isolated individuals of *A.steingroeveri* were observed making off with an enemy clasped in their mandibles. *P.megacephala* usually employs several individuals to subdue a single major *A.steingroeveri* worker. *A.steingroeveri* minor workers do most of the ferreting out of *P.megacephala* from its tunnels, for these are too small for major workers to enter. *A.steingroeveri* workers often enlarge the tunnels and galleries of *P.megacephala* nests to reach the brood and queens. For the most part, *A.steingroeveri* media and major workers concern themselves with aiding minor workers when the need arises.

Once *A.steingroeveri* has occupied a *P.megacephala* tree it sets about establishing an outpost nest to consolidate its territory.

This consolidation is highly necessary to neutralise any *P.megacephala* colony remnants persisting in the network of tunnels and galleries beneath the tree. The rapidity with which *P.megacephala* re-occupies its former territory suggestw that, although *A.steingroeveri* temporarily controlled the trees, superficial soil and part of the deeper soil, *P.megacephala* colonies persisted during the occupation. This rapid re-occupation precludes the possibility of its being natural spread. (See Fig. 8f).

One frequently finds that *A.steingroeveri* is wary of strong colonies of *P.megacephala* and also obtains the impression that the possible food gain is not offset by the losses that it must occur to obtain it. A case in point is the isolated *P.megacephala* tree at the western end of the most northerly row in Orchard No.2. This *P.megacephala* colony, hemmed in on all sides by orchard and veld nests of A.steingroeveri, survived for over a year under conditions of extreme jeopardy, since the tree it occupied was heavily infected with scale, yet A.steingroeveri did not appear to 'want' this prize.

(ii) Nesting territory.

An extensive attack was observed on 27.IX.1955, when A.steingroeveri was obviously intent upon wresting a nesting site in a terrace wall from P.megacephala. Fig. 13 shows that members of the attacking party surprisingly not only came from the adjacent territory, but also from far removed nests without any apparent interest in the nesting site. The explanation of this is enigmatical; perhaps it may be another manifestation of the mechanism of polydomy.

In this battle once again P.megacephala was hounded out of its nest by A.steingroeveri, which made off with workers, brood and queens.

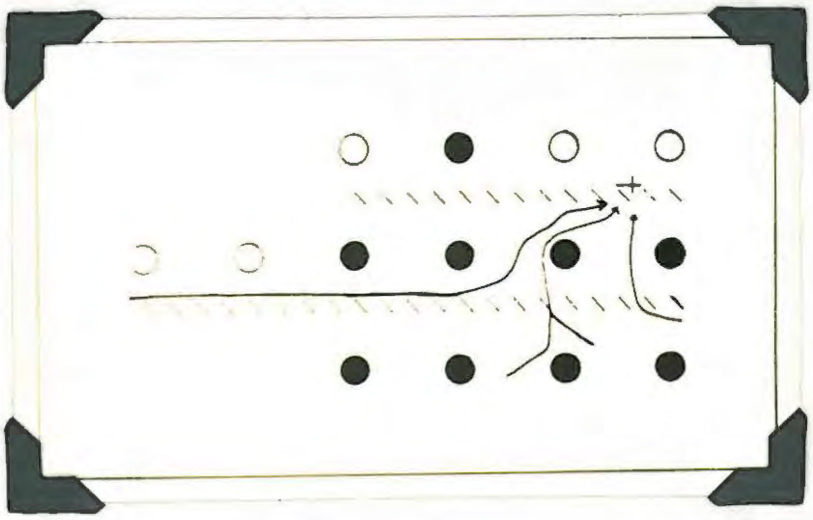

FIGURE 13.

Map showing battle between A.steingroeveri and P.megacephala in Orchard No.3. Routes of former species marked with arrows. Cross shading represents terrace walls.

P.megacephala was seen to attack on one occasion only (22.IV.56). My attention was drawn to large numbers of workers and pseudorepletes of A.steingroeveri moving from one nest to another. When the area around the vacated nest was examined, large numbers of P.megacephala were found harassing the A.steingroeveri rearguard.

It is doubtful whether the change in nesting sites was primarily due to *P.megacephala* aggression. Possibly the change in the sun's orbit may have rendered the one nest too shady and the brood was removed to another more insolated nest. Whatever the circumstances leading to the shift, *P.megacephala* exploited this momentary weakness of *A.steingroeveri*.

(d) Relationship between competitive and non-competitive species.

1. Harvester Ants: (*Messor barbarus* L., r. *capensis* Mayr, v. *decipiens* For.).

In addition to the two species already mentioned, harvester ants were the next most numerous species in the orchards. They are seed eaters, adapted to living under desert conditions, and their nests are characterised by extensive well-defined foraging trails radiating away from them. This species has no interest in honeydew, and in my experience confines itself to seed collecting. Although there is a marked differentiation of the worker sub-castes, the major (soldier) workers concern themselves with foraging and not with defence or aggression. Since this species is the only seed-eating ant it has no real competition from other ants.

It has similar nesting requirements to *A.steingroeveri*. One often finds the two species nesting within a foot or six inches of each other, and their foraging paths often cross over each other. For *A.steingroeveri* to permit Harvester ant nests to survive under such circumstances shows a wide degree of tolerance, but *A.steingroeveri* cemeteries do contain a few remains of *Messor* individuals, and this indicates some aggression by the former species. At the junction of the foraging trails the true relationship may be seen. For the most part, individuals of both species ignore each other, but occasionally *A.steingroeveri* attacks the Harvester Ants. Major *Messor* workers bear the attacks, and it is not uncommon to find a single soldier struggling along with three or four *A.steingroeveri* minor workers clinging to its legs; but it makes no attempt to bite the attackers and goes on its way to the best of its ability. Minor Messor workers behave in a different way to attack. They display a form of kataplexy whereby the attacked individual curls up into a ball, feigning death, and shows no sign of aggression. Media workers alternate between the two types of behaviour depending on the size of the attacking ants.

These forms of defensive behaviour seem to be designed to thwart the aggressiveness of A.steingroeveri. In the first case, major Messor workers are not in any real danger from a few clinging A.steingroeveri minor workers, which eventually fall off. In the second instance, which may be described as 'cowering' behaviour, the lack of response from the attacked individual causes the attacker to lose interest, and after toying with the victim it is released. Sometimes Messor individuals are dragged to the A.steingroeveri nests, dismembered and eaten.

2. Tetramorium setuliferum Em., v. cluna For.

Few colonies of this species are present in these orchards. Like Messor they display the same 'cowering' kataplexy, with the same success, and also live among A.steingroeveri colonies. These ants seem to be scavengers. A significant portion of their diet consists of various seeds. I have not seen them feeding on honeydew.

3. Monomorium albopilosum Em., r. thales For. This ant, although never present in any great numbers, appears to enjoy a certain degree of immunity from attack by A.steingroeveri, largely because of its ability to run quickly. It is also found nesting close to A.steingroeveri colonies, and forages at the base of trees occupied by both A.steingroeveri and P.megacephala. It is omnivorous, and may also be considered as a scavenger.

4. Camponotus rufoglaucus Jerdon, r. vestita Smith.
Camponotus rufoglaucus Jerdon, r. cinctella Gerst.

These two races have a similar behaviour, and are differentiated in the field on a basis of colour. The former race is reddish brown and the latter race is greyish black. This species is a large, extremely agile, fast-moving ant. This allows a modicum of success in foraging honeydew from trees occupied by A.steingroeveri and Pheidole. They play a very small rôle in orchard economy because of their small numbers. Their inability to compete with the other species relegates them to the position of scavengers. This species is mainly crepuscular in habit, but may be found during the day or at night in fewer numbers.

5. Camponotus maculatus Fab.

The familiar'Sugar', or 'Marmalade',ant is markedly nocturnal in habit, otherwise it displays in most respects the furtive behaviour of the camponotines described immediately above.

6. Solenopsis puntaticeps Mayr is a small yellow ant found in the soil surrounding the brood chambers and other superficial portions of the nests of both Anoplolepis species. In most Anoplolepis nests which I have dug up this ant has been present, but it has never been seen above ground.

Surprisingly, there is a strong antagonism between Anoplolepis and this ant. S. punctaticeps has a well developed sting for which Anoplolepis has a great regard. The feeding habits of Solenopsis are not known. The relationship between this ant and the two Anoplolepis species under natural conditions, when the nests are not disturbed and the species not thrown forcibly into contact, is also not known.

Wheeler (1910) states that a number of species of Solenopsis are 'thief ants' (Lestobiotic) which feed on the brood of the larger ant with which they are associated. The thief ants are able to enter the brood chambers of the 'host' ant through small tenuous tunnels, where they move freely among the host ants and carry off brood. In all probability S.punctaticeps is related to the two Anoplolepis species in a similar manner.

(e) Intraspecific relationships between veld and orchard colonies of A.steingroeveri.

Intraspecific tolerance between some ant species is well known. A small investigation was undertaken to ascertain the relationships between both the adults and the brood of orchard and veld colonies of A.steingroeveri. Ants from these two places are tolerant of their own species in the same environment (Steyn, 1954a). However, when one compares the density of the nests in the two environments, one would expect that the veld colonies, which only just manage to eke out an existence in the scrub, would not be so tolerant as orchard ants, which live under more crowded conditions.

By presenting ants from one environment with a sample of brood and adults from the other, it was hoped that any behavioural difference between the ants of the two environments would manifest themselves. These differences would point to the evolution of a new behavioural trend among orchard ants as a result of living in such a concentrated environment.

To this end an experiment along these lines was carried out twice in two different localities on the farm "Dunbar". A sample of brood and adults was taken from one place and set down near the nest-entrance of a colony in the other environment.

Orchard colonies accepted veld adults and brood of veld colonies quite readily. Brood of all ages were quickly taken into their nests, away from harmful conditions above ground. Only one instance of half-hearted fighting, or 'mauling' between adults was seen.

Veld colonies took less kindly to orchard adults and brood which were thrust upon them. The brood was not accepted quite so readily, and they showed a preference for pupae and more mature larvae which would not require much feeding. The younger larvae were taken into the nest last, or even overlooked

Twenty-one instances of fighting between the adults were recorded, but usually strange adults were treated with 'suspicion' at first and then accepted into the new colony,

In all, veld and orchard colonies still retain the basic intraspecific tolerance of individuals from the other environment, but veld colonies did exhibit more reluctance in accepting orchard ants than vice versa.

B. ANT ACTIVITY.

I. INTRODUCTORY REMARKS.

Most investigators of rhythmic behaviour find that ants have thresholds of cold and heat tolerances when cold rigor and heat torpor set in. Bodenheimer and Klein (1930) show that the seasonal shift of peak foraging activity of the Harvester Ant, *Messor semirufus* E. Andrè, in deserts changes to different times of the day. In summer most foraging is done at night, and in winter at midday. Talbot (1943a) remarks that peak activity of the Fruit-eating ant, *Prenolepis imparis* Say, is synchronised with fruit fall in autumn, but its feeding is curtailed by temperatures above 65°C. and below 0°C. She considers air temperature to be the most important controlling factor. Headley (1941) considers the periodicity in foraging by *Lasius niger alienus* var. *americanus* Emery to be positively correlated with the prevailing high relative humidity of the air. The familiar 'Sugar Ant', *Camponotus maculatus* Fab., is a nocturnal forager. Once, however, at Fort Brown, I saw it working industriously during the day after heavy rain and under overcast skies. The nocturnal behaviour otherwise persists and appears to be correlated with high air humidity.

In South Central Florida, Fungus-growing Ants, *Trachymyrmex seplentriolis seminole* McCook, have temperature thresholds above and below which they will not forage, regardless of adequate foraging material (leaves, etc.) being available. This species has a diurnal foraging rhythm. (Weber, 1956).

Lutz (1929) and Hodgson (1955) have studied the well known Leaf-cutting, or Parasol Ant, *Atta cephalotes* L., under tropical conditions in the Panama Canal Zone. Allee (1926) does record slight fluctuations in environmental conditions. However, Hodgson does not record air temperature fluctuations greater than 2°C. and the relative humidity did not fall below 70%. Illumination was the only significant variant, and this Hodgson proves triggers off the foraging pattern at dawn.

Under similar, more or less constant conditions, Schneirla (1944) finds that the Army Ants of the genus Eciton carry out their complex manoeuvres in response to trophallactic stimulation by the larvae. The regular cycle of nomadism, followed by a sessile 'statary' phase, is a reflection of the state of brood development in a series of consecutive broods, which in turn arise from regular egg production by the queen, the'pacemaker'. During nomadism workers are active diurnal food foragers and at night the brood is carried to a new bivouac. But at the statary phase (while the brood is pupating) diurnal foraging drops in intensity and there is little nocturnal activity. Only the equable and almost constant environmental conditions permit such behaviour, and above ground nesting, to evolve.

To summarise: one finds foraging by ants may be correlated with a number of factors, some of which are described above. In localities with a continuously available food supply (seeds, etc.) where extreme climatic conditions prevail, the ants forage when conditions are most suitable to them. As Bodenheimer points out, this may lead to seasonal changes in their foraging behaviour. But where in temperate zones the climatic fluctuations are not so sharply defined, diurnal foraging is commonly the rule.

Under most constant conditions in well canopied tropical rain forests, the diurnal foraging rhythm persists in Atta cephalotes, while Eciton may be active at night and/or in the day-time, depending on the particular phase of brood development in the colony.

Most noticeable of all is the variety of habitats occupied by ants to which they in turn have to adapt themselves to feeding on the foods available to them. When several ants compete for a similar food and habitat, a change in foraging behaviour, for example, from diurnal to nocturnal, may open up a new niche for such a species, or, as Steyn (1954a) suggests, this gives them a distinct advantage over another species with a different inherent activity rhythm. Periodicity in activity is of obvious significance in territorial behaviour, and conveys advantages, or disadvantages, to different species at different times of the day, or at different seasons.

A study of activity rhythms of ants serves several functions:- (1) A purely academic contribution to our knowledge which may be further extended to (2) include correlations of activity with environmental and physiological factors. This would give a greater and more detailed understanding as to which of the numerous factors possible are most intimately correlated with their activity. (3) Where such an ant is economically important, a knowledge of its foraging behaviour allows us to evaluate its importance relative to other species feeding from the same food source.

Anoplolepis steingroeveri is such an ant. Some aspects of its territorialism and biology are discussed in the previous section, and a study of its foraging behaviour may be usefully compared with the known foraging behaviour of *Anoplolepis custodiens* (Steyn, 1954a). Furthermore, additional factors not considered by Steyn but with a possible bearing on the activity of *A.steingroeveri*, were investigated to clarify contentious issues.

The term 'activity' may apply to several states or conditions of movement, carried out by ants either within, or outside, the nest. By defining the various ways in which the term activity may be used, I want to clarify the aspect of activity I have considered:-

(1) *General movement* within the nest, including nursing of the brood, excavation of soil, soliciting of food, etc., in the sense used by Barnes (1941).

(2) *Irregular mass movements* outside the nest, including shifting nesting sites, raiding parties, together with protective patrolling or guarding of the area around the nest entrances.

(3) *Thermokinetics, or speed of movement,* is usually expressed in terms of distances travelled by ants in a set time in

relation to temperature (Shapley, 1920).

(4) <u>Concerted movement or 'trailing'</u>, by ants outside the nest to a food source which is being exploited to the greatest extent of their inherent ability under the prevailing conditions.

The latter is the type of foraging activity in which foraging rhythms, or periodicity in feeding, manifest themselves. It is measured by the number of ants present at a food source (Broekhuysen, 1948), present in a given area (Talbot, 1943b), or passing a given point for a set time (Holt, 1955), at different times of the day and year. This gives an assessment of the relative numbers of ants concerned with foraging at different times, and in this way the daily and seasonal foraging rhythms for a particular ant species in a certain locality is determined.

This is the type of ant activity I have considered. Speed of movement is usually positively correlated with increased foraging activity, but this aspect has not been considered in this study.

II. THE FORAGING ACTIVITY OF ANOPLOLEPIS STEINGROEVERI.

(a) Location.

The investigation of the foraging activity of A.steingroeveri was carried out at the farm 'Dunbar', near Fort Brown in the F.R.V. The climate and some of the other conditions of the locality are described in a previous section.

(b) Significance of orchard microenvironmental conditions.

It is important to differentiate closely which environmental factors impinge upon the ants once they are outside their nests. In tropical forests with a dense canopy, soil temperatures are very constant and have no great significance to ant behaviour. However, in deserts and other localities with sparse vegetation, the effects of soil surface temperatures are of paramount importance in terms of the 'film' or microclimate, through which the ants move to and from their food sources. This 'film' lies immediately above the surface of the soil. It is least affected by winds and most affected by the radiant heat of the sun which the soil absorbs, and also by convection currents rising from the soil (Parry, 1951). It is in this 'film' that the ants have to move when walking over exposed soil. During foraging excursions ants pass through many microenvironments, and at different times of the day each of them may have good or bad effects on the foraging behaviour of the ants.

Microclimates may arise from a number of factors, such as shade, exposure, air temperature, humidity, etc., some of which blend to form the microenvironment. Some factors dominate more than the rest, depending on the extent to which they are able to exert themselves. For instance, wind has no visible effect on ants beneath stones or moving through grass, but it has a striking effect, as will be shown later, on ants ascending a die-back tree.

For our purposes we may restrict ourselves to considering three main microenvironments which most affect the foraging of A.steingroeveri at Fort Brown.

1. Nests.

Although ant nests are not on the foraging trails and the ants are not exposed to the above-ground climate, nests are microenvironments in themselves with particular characteristics for which the ants select them. They are the place from which activity originates. For that reason it is necessary that the conditions prevailing within the nests are considered.

Nests are found in three different places within these orchards: (1) terraces; (2) basins; and (3) in the umbrella, or beneath trees. The first two have more or less the same conditions prevailing at the same time; however, as I have pointed out (p.56), terrace nests are warmer than basin nests. The conditions prevailing in umbrella nests vary from tree to tree, depending on the amount of insolation received by the soil beneath each tree.

The method employed for assessing foraging activity did not take into consideration the contribution each type of nest made to the overall foraging pattern. I have shown that the umbrella nests are only of occupational significance, and that there are fewer basin nests than terrace nests. Thus the terrace and extra-orchard mother nests supply the major portion of the foraging ants, and it is the conditions within and above the terrace nests which have been taken into consideration. The conditions prevailing below trees were recorded in connection with the activity of P. megacephala, and these data may be used to represent the conditions to which A. steingroeveri in umbrella nests were subjected.

The data recorded were soil temperatures at depths of 0.25 and 12 ins. There was no apparatus available to record soil humidities and evaporation rates.

There is very little difference between day and night temperatures in nests at a depth of 12 ins. Paradoxically, they may be warmer at night than during the day. This is caused by the lag in the conductance and accumulation of heat in the soil. The actual difference between day and night temperatures at this depth is very small and the conditions are surprisingly constant. At night surface temperatures fall below those at 12 ins. depth.

There are definite daily and seasonal variations in both exposed and shaded soils at depths of 0.25 and 12 ins. The variation is more marked in exposed soils, but is still recognisable in shaded soils. In both places and at both depths highest temperatures are recorded in summer and the lowest in winter.

When the lowest temperatures recorded at night (Table 17) are considered, it is obvious that in exposed places soil temperatures at 12 ins. depth are always greater than both the air soil surface temperatures. The lowest temperature recorded at 12 ins. was 11.5°C. in day-time, when the soil surface and air temperatures were respectively 22.0° and 15.8°C. at the corresponding time (11 a.m. on the 24th May, 1956). Thus even in this extreme case the nest conditions would not inhibit activity. In point of fact, the low nest temperatures may stimulate the ants to move out of the nest into the warmer air at soil level.

The protective effect of the nest has for ants was well shown on the 29.V.1956, in winter, before sunrise, when I dug into a nest (A. steingroeveri) in an exposed position. The ants were not active above the surface but at a depth of approximately one foot the soil was warm to the touch and the ants moved freely and quickly at the bottom of the hole. Some ants were thrown onto the surface, where they quickly suffered cold rigor, their movements became awkward, their speed of walking dropped significantly, and they lost their aggressiveness.

Thus the conditions prevailing in the nest in no way restrict the foraging of A. steingroeveri, and we must look elsewhere for restricting factors.

2. Foraging trails.

The foraging trails considered here lead from nests to trees. Here the factor most likely to affect the ants is soil surface temperatures. This is influenced by the amount of

TABLE 17.

Comparison of air temperatures with those of the soil of exposed ground and umbrella at depths of 0.25 ins. and 12.0 ins.

			Sept. 1955	Oct. 1	Oct. 2	Oct. 3	Dec.	Jan. 1956	Feb.	Mar.	Apr.	May.
EXPOSED °C.	0.25 ins.	H	29.0	44.6	30.5	53.0	56.0	65.0	34.0	24.0	37.0	25.0
		L	11.5	9.2	12.0	10.2	8.5	17.0	16.0	12.3	4.3	5.0
		D	17.5	35.4	28.5	42.8	47.5	48.0	18.5	11.8	32.8	20.0
		m	20.3 ± 8.8	26.9 ± 17.7	26.3 ± 14.5	31.6 ± 21.4	32.3 ± 23.8	41.0 ± 24.0	25.3 ± 9.3	17.6 ± 5.4	20.6 ± 16.4	15.0 ± 10.0
	12.0 ins.	H	20.0	22.0	21.4	22.5	23.3	-	26.8	20.0	20.5	13.8
		L	18.0	19.5	20.0	18.5	19.0	-	25.5	17.5	17.0	11.5
		D	2.0	2.5	1.4	4.0	4.3	-	1.3	2.5	2.5	2.3
		m	19.0 ± 1.0	20.8 ± 1.3	20.7 ± 0.7	20.5 ± 2.0	21.1 ± 2.1	- -	26.1 ± 0.6	18.8 ± 1.3	18.3 ± 1.3	12.6 ± 1.1
UMBRELLA °C.	0.25 ins.	H	20.0	22.6	-	20.2	22.5	-	21.5	16.4	20.3	-
		L	11.5	11.5	-	12.2	13.0	-	18.5	15.3	9.3	-
		D	8.5	11.1	-	8.0	9.5	-	3.0	1.2	11.0	-
		m	16.1 ± 4.3	17.1 ± 5.6	- -	16.2 ± 4.0	17.8 ± 4.8	- -	20.0 ± 1.5	15.8 ± 0.6	14.8 ± 5.5	- -
	12.0 ins.	H	17.5	16.5	-	16.0	17.0	-	21.8	19.0	18.0	-
		L	16.5	15.8	-	15.2	16.0	-	21.1	18.5	17.0	-
		D	1.0	0.8	-	0.8	1.0	-	0.7	0.5	1.0	-
		m	17.0 ± 0.5	16.1 ± 0.4	- -	15.6 ± 0.4	16.5 ± 0.5	- -	21.4 ± 0.3	18.8 ± 0.3	17.5 ± 0.5	- -
Air temp. °C.		H	20.0	24.9	20.0	26.1	24.5	32.0	23.5	20.4	24.2	18.1
		L	13.0	10.0	11.0	9.4	10.0	19.0	16.0	14.3	3.3	3.3
		D	7.0	10.9	8.9	16.5	14.5	13.0	7.5	6.1	20.9	14.8
		m	16.5 ± 3.5	15.5 ± 5.5	15.6 ± 4.5	17.7 ± 8.3	17.3 ± 7.3	19.5 ± 6.5	19.8 ± 3.8	17.4 ± 3.1	13.8 ± 10.5	10.7 ± 7.4

Where H = highest temperature recorded; (usually recorded during the day).

L = lowest temperature recorded; (usually recorded at night).

D = difference between H. and L;

m = mean temperature and range.

soil cover or shade provided by weeds and grass. Since there is so little vegetation at Fort Brown, I have decided not to take shade into account and only used the records from exposed soils.

In the early morning in winter I observed behaviour which I term 'sunbathing' being practised by both A.steingroeveri and P.megacephala. The ants laze about nest entrances displaying no drive or trailing incentive. A.steingroeveri, in particular, because of its black colour, was absorbing more radiant heat from the early morning sun than the lighter coloured soil.

The sunbathers may also be looked upon as weather scouts, for as soon as the activity threshold is reached, some return into the nest and probably stimulate the rest of the colony. This results in a 'flush' or sudden outpouring of ants from the nest. Lutz (1929) observed similar behaviour being displayed by Atta cephalotes.

The question of the rate of heat absorption by insects in sunlight has had little investigation. The findings of different workers vary, but most authors show that insects exposed to sunlight have a body temperature well in excess of the air temperature, and the rate of absorption is surprisingly rapid.

It would be unwise to predict which factor, or group of factors, contributes to produce the activity threshold. It is largely a temperature mechanism, but the way in which the ants are affected cannot be stated with any certainty. It may be the warming of the soil surface and the creation of the 'film'. It may be the ants are able to absorb sufficient radiant heat themselves to throw off the effects of cold rigor, or a combination of both.

The threshold is sharply defined, and once it is reached trailing starts and progressively increases in intensity until the maximum rate is reached.

Between noon and 4 p.m. there is usually a slight fall off of ant activity. There are two possible explanations for this:

(1) the ants have grown tired, which may be a reflection of (2) adverse climatic conditions causing heat torpor. If the concept of the 'film' is considered, soil surface temperatures, together with low humidity, might be the cause of reduced activity. This reduction is usually slight, and we cannot place too much emphasis on it, but it does represent to a small degree what happens to desert ants (Bodenheimer and Klein, 1930; Minchener, 1941).

After sunset in winter there is a rapid reduction in both air and soil surface temperatures which is roughly paralleled by a fall off in ant activity. During summer it is not so marked, as the temperatures rarely drop below the threshold. This enables them to forage throughout the night. Few ants are seen on trails once the threshold is reached in winter. Those ants which are still engaged in foraging usually elect to spend the night in the tree,where it is more sheltered than on the open ground.

3. Beneath and within trees.

The conditions prevailing about any one tree are dependent on the die-back conditions of the tree and its position in relation to other trees. Obviously trees along the orchard border are more exposed to the effects of the sun and wind than trees situated in the middle of the orchard. Thus no two trees have the same climate, and each tree may be looked upon as a separate microenvironment. Steyn (1954a) has shown this to be the case.

Healthy, heavily-leaved trees have a moderating effect on extreme climatic conditions, such as temperature and wind. Since this type of tree is not typical of the trees foraged by *A.steingroeveri*, my remarks will be confined to die-back trees.

Few ants are found up trees early in winter mornings, and these usually return to the nest as soon as the air temperature has risen above the threshold. By the time foragers have reached the trees the air temperature has exceeded the threshold value and their activity is not impeded by low temperatures.

Die-back trees with high skirts allow the ants to enjoy heating by the sun for a longer period, as the early morning sun strikes the tree trunk and the soil beneath the tree over which the ants move. The same effect is obtained in the later afternoon, when the sun shines on the tree from a low angle.

At midday, the shadow cast by the tree prevents the soil from heating up to the same level as that of exposed ground. Thus the ants are not subjected to very high soil surface temperatures, and it is unlikely that the ants beneath and on the tree suffer any ill-effects from the high temperatures prevailing at, and after, noon.

During the evening and at night, trees offer little shelter to the ants, which experience more or less the same conditions prevailing at tree height.

In the text which follows, what has been said above must be borne in mind and considered in relation to the data as they are presented.

(c) Methods.

A die-back tree with a heavy infestation of Soft Brown Scale and Red Scale was selected for the investigation. This tree was typical of the trees foraged by the ants with regard to the conditions prevailing both in and around it. Since there were few lateral branches, the ants passing through the gap in a band of tangle-foot around the tree could be easily seen and counted. Furthermore, none of the lateral branches touched the ground, and weeds around the tree were removed. In this manner the ants were compelled to forage the tree through the gap. The gap was wide enough not to restrict the number of ants passing up and down the tree, and at the same time sufficiently narrow for the human eye accurately to observe the ants passing over a line drawn across the gap.

The use of a single tree may appear to be unscientific, but in subsequent experiments four trees were employed, and little, if any, difference was noted between the foraging activkty of the ants attending each tree.

An alarm clock was modified to chime every minute, and the numbers of ants ascending and descending the tree for a period of two minutes at hourly intervals were counted as they crossed over the line. This auditory method of registering time is far superior to looking at a watch while counting ants simultaneously and allowed one to give full concentration to the counting. Counting, except for when only a few ants were active, was done with the aid of a hand tally counter.

Counts were made at hourly intervals for a day (24 hours) in each month during the period of the investigation from June, 1955 until May, 1956. When the ants ceased to ascend the tree, no further observations were made for the remaining part of the 24 hours, as the cold rigor threshold had been reached. Activity would only be resumed at, or after, sunrise the following morning. Observations at night were made with an electric torch with a red filter to minimise the effect of light on the ants.

(d) Environmental factors considered and techniques.

Several environmental factors were recorded, some of which were considered late in the investigation as a deeper appreciation of the problem developed.

1. Air temperature and relative humidity were measured with a sling hygrometer (psychrometer) at a height of 1 meter above ground level. Dry bulb readings were taken to represent air temperature, and the relative humidity was derived from tables (Marvin, 1941).

2. Soil temperatures. Both the method and the localities where these temperatures were recorded have been described above (p.20)

3. Light intensity or illumination was recorded with a photographer's exposure meter. The readings from the exposure meter were subsequently reduced to meter-candles. The photometer was held on a lug-box with the sensitive plate vertical, and then the readings of the light intensity at the four cardinal compass points were made; the average of these four readings was then calculated. After the observations on the activity of *A.steingroeveri* had been completed, it was realised that the

exposure meter had been incorrectly used, and the recorded data were of no value. (The sensitive plate should have been held horizontally.)

Later, it is shown how the ants forage throughout the night in summer, when the light intensities at night would appear to be of the same order as those experienced in winter when the ants do not forage through the night. Furthermore, it will be shown that on overcast mornings in winter the start of foraging was delayed after sunrise. The light intensity on such mornings was considerably greater than that at and immediately after sunset, when the ants were still active. For these reasons, I attach more significance to radiant heat than light intensity as the component on sunlight which affects ants most.

4. Solar radiation.

Light intensity may be used as a rough relative indicator of the radiant heat given off by the sun. A more accurate estimate of radiant heat was obtained with a black bulb thermometer, or pyrheliometer.

This instrument consists of a thermometer with the mercury bulb painted black. The entire thermometer is encased in an air-tight jacket of thin glass to eliminate the effect of ambient air. A black painted cradle was constructed to house the thermometer. The black paint would tend to prevent reflection of light from the cradle which might disturb the functioning of the black bulb thermometer.

A period of at least half an hour of exposure to direct sunlight was allowed before the readings were considered to be valid. Thus the first morning readings were usually made an hour after sunrise. During the hours of darkness the black bulb thermometer gave readings comparable with the air temperature, but these readings were not taken into account.

5. Wind velocity was judged by eye in terms of the modified Beaufort Scale of wind force (Sutcliffe, 1940), and is indicated in the appropriate Figures and tables as 'B' (e.g. B.3).

6. Cloudiness was estimated by eye and recorded in tenths;

10/10ths being completely overcast, and 0/10ths cloudless.

7. Sunrise and sunset times were recorded.

8. Time. All times are given in South African Standard Time, and were obtained by synchronising my wrist watch with wireless 'pips' immediately before each count.

All observations on environmental factors were made at hourly intervals in the orchard close to the tree on which the activity of *A. steingroeveri* was being studied. This more laborious method of recording environmental data was preferred to using a thermohygrograph, which was considered to be too inaccurate. Owing to the time taken in obtaining readings it was found that the ant activity on only one tree could be satisfactorily correlated with the conditions prevailing at the same tree.

When four trees were used in experiments, ant activity on two trees was first recorded, then the climatic data, after which the remaining two trees were considered. Twenty-five minutes were taken to make all these observations. Thus the counting on the first two trees was begun ten minutes before each hour. When only one tree was under observation, the count of patrolling ants was begun on the hour and was followed immediately by reading the various instruments. One complete observation took ten minutes. Readings of the various instruments were taken in the same sequence throughout all the observations.

9. Analysis.

In the statistical analysis of ant activity with climate factors, both total and partial correlations are given. The significance of the total correlations may easily be seen in the tables showing the results of the analysis, and unless it is necessary, they will not be discussed. This will save a considerable amount of repetition. Partial correlations are more relevant to the question of what factors influence the foraging behaviour of the ants, and will present more valuable data for discussion.

The values of both the total and partial correlations (r) are expressed in terms of the significance of 'P' and with asterisks. A value of 'P' greater than .05 ($P = > .05$; no asterisk) is not significant. Where P. is smaller than .05 ($P = < .05$; one asterisk) it is just significant. When P. is much smaller, .01 ($P = < .01$; two asterisks) it is very significant. P. is highly significant, at .001 and beyond ($P = < .001$; three asterisks).

The following symbols are used in the correlations:-

At = combined, or total, activity of ants going up and down the tree over a period of two minutes.
Au = ants ascending the tree in two minutes.
Ad = ants descending the tree in two minutes.
H = relative humidity.
T = air temperature.
S = soil surface temperature of exposed ground.

In my opinion, the calculation of correlations between ant activity and climatic factors are only valid while the ants were engaged in foraging. Thus throughout the periods when the ants had ceased foraging, the climatic data for those times were neglected in the correlations, although it is mathematically possible to include these data in the calculations.

The total correlations between the climatic factors (rHT) are given only once for each table under the subheading 'combined activity', although they are applicable to, and necessary for, the calculation of the total correlations of ants ascending and descending. Since the correlation 'rHT' remains constant throughout for each table and is not affected by ant activity, it is not repeated. When a new climatic factor is introduced (S) the total correlation rHS is used only for the calculation of the correlations for ants ascending the tree. Correlation rHT remains valid for the other two types of activity.

The partial correlations between climatic factors when the activity is excluded (i.e. rHT.A) are significant throughout and are not included in the tables of any of the correlations.

10. Graphic correlations.

In the figures showing the graphic correlations of ant activity with climatic factors, histograms of ants ascending, descending, and the combined activity are shown in the upper halves of the figures. The combined activity is reduced by a factor of 2 to the same proportion as the histograms for ants ascending and descending.

Black histograms represent ants ascending; open histograms show the number of ants descending; histograms with a ladder of horizontal lines indicate the combined or total activity.

The lower half of each figure contains the air, and sometimes the soil surface, temperature and the relative humidity data. The upper portion of the lower half shows the state of the skies in tenths, represented by inverted black histograms. Between the upper and lower halves, immediately above the sky histograms, are the wind force data in numbers. Directly above these numbers are the times of day at which the observations were made.

(e) Seasonal foraging behaviour of A.steingroeveri.

Monthly observations were made on the foraging activity of A.steingroeveri over the period June, 1955 until May, 1956, with the exception of July and November, 1955.

Four months (August, 1955, winter; October, 1955, spring; February, 1956, summer; and May, 1956, autumn) have been selected to represent the four seasons, and to show the activity pattern prevailing at those times. The observations made during these four months are the most complete and free from mishaps. All the data resulting from monthly counts appear in the text, or at the end of this section.

1. Winter: (26-27:VIII:1955).

Table 19 and Fig. 14 present a typical example of winter foraging by A.steingroeveri. The ants were active only after sunrise, and stopped foraging shortly after sunset. Only a few ants were engaged in foraging, and the rate of foraging never exceeded the low level of 200 ants/2 mins. This is an example of discontinuous foraging, where the ants are not active throughout the night, most of the foraging being done during day-time. Thus, in winter the ants have a strictly diurnal foraging rhythm, and foraging is at a very much lower intensity.

Very low temperatures were experienced, and as Table 18 of the partial correlations of ant activity, air temperature and relative humidity shows, the activity of ants descending is largely determined by air temperature. The remaining partial and total correlations are of very low values, thus the combined and ascending activity have no significant correlation with temperature or humidity.

The morning wind did have a slight effect on the ants ascending the tree, and when it decreased in force more ants ascended the tree.

2. <u>Spring</u>: (25.X.1955).

At this time solar radiation and also the soil surface temperature at 12 ins. and 0.25 ins. depth of exposed and umbrella soil were recorded (Table 21). The records of radiant heat are valid during the hours of sunlight, and as such could not justifiably be correlated with ant activity which persists after sunset. The same may be said of light intensity, which is only truly valid in a total correlation with ant activity during the hours of daylight. It is, in my opinion, not justifiable to enter into partial correlations between one factor whose effects are discontinued (light intensity, radiant heat) and another which persists over the entire period of the observation (air temperature and relative humidity).

Radiant heat does have the effect of heating up the soil, which gradually loses this heat after sunset by convection. The soil surface does retain, and show, some of the effects of radiant heat. It was found that soil surface temperatures had approximately the same correlation as air temperature with ant activity. Thus the soil surface temperature of exposed ground

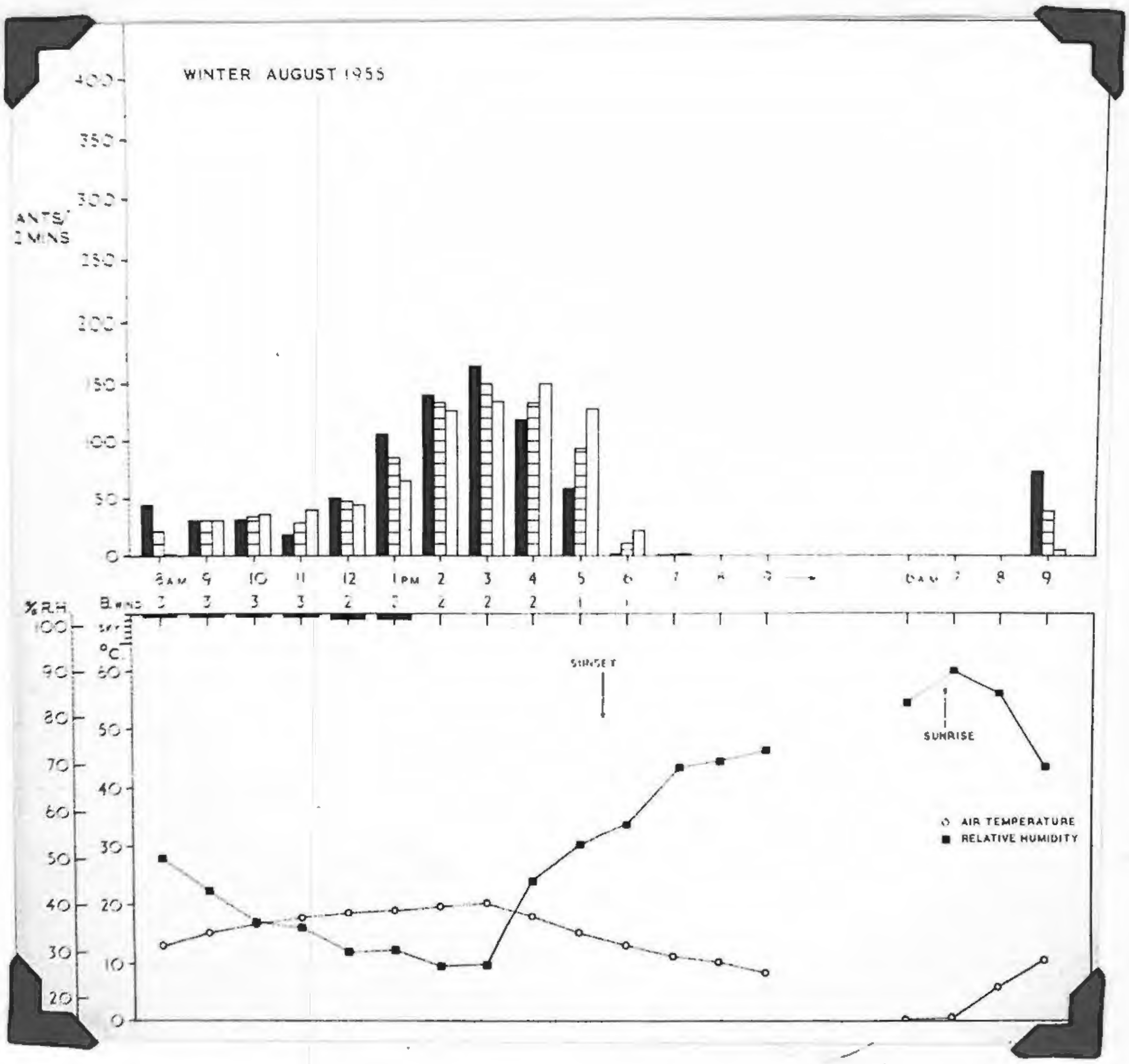

FIGURE 14.

Graphic and statistical correlations of climatic conditions with ant activity from observations made on 26-27.VIII.1955.

TABLE 18.

Combined Activity	rAtH = -.479;	P = >.05
Total correlations	rAtT = +.614;	P = <.03 >.02*
	rHT = -.854;	P = <.0004 * * *
Partial correlations	rAtH.T = -.109;	P = >.05
	rAtT.H = +.449;	P = >.05
Ants ascending	rAuH = -.502;	P = >.05
Total correlations	rAuT = +.564;	P = <.03 >.02 *
Partial correlations	rAuH.T = -.047;	P = >.05
	rAuT.H = +.300;	P = >.05
Ants descending	rAdH = -.475;	P = >.05
Total correlations	rAdT = +.674;	P = <.02 >.01*
Partial correlations	rAdH.T = -.262;	P = >.05
	rAdT.H = +.585;	P = <.04 >.03*

TABLE 19.

Monthly observation from 8 a.m. on 26.VIII.1955 until 9 a.m. on 27.VIII.1955.

Time	Sky in tenths	Comments.	Air temp. °C.	% R.H.	*A. steingroeveri*		*P. megacephala*	
					up	down	up	down
8 a.m.	1	Fairly strong N.W. wind. B3	13.0	50.0	45	2	30	16
9 a.m.	1	" " " B3	15.0	43.0	31	31	13	17
10 a.m.	1	" " " B3	16.6	36.0	32	37	18	22
11 a.m.	1	" " " B3	17.7	35.0	18	40	13	28
Noon	2	Gusty - not continuous as above. B2	18.5	30.0	51	45	24	23
1 p.m.	2	Wind not so strong, few isolated clouds. B2	19.0	30.5	107	66	14	20
2 p.m.		" " " B2	19.8	27.0	141	127	24	20
3 p.m.		B2	20.3	27.5	165	135	35	31
4 p.m.		B2	18.0	45.0	119	150	44	23
5 p.m.		Wind dropped, but nippy S.S.W. breeze blowing. B1 Sunset 5.25 p.m.	15.3	53.0	59	128	33	24
6 p.m.		Slight breeze B1	13.0	57.0	2	23	39	39
7 p.m.		Calm and cloudless -	11.3	69.0	1	2	25	22
8 p.m.		" " "	10.3	71.0	0	0	18	18
9 p.m.		" " "	8.5	73.5	0	0	13	16
10 p.m.		" " "	7.0	82.0	0	0	19	18
11 p.m.		" " "	6.0	85.0	0	0	18	12
Midnight		" " "	4.0	85.0	0	0	5	10
1 a.m.		" " "	3.3	87.0	0	0	1	1
2 a.m.		Dew fall; calm	3.3	87.0	0	0	0	0
3 a.m.			3.1	96.0	0	0	0	0
4 a.m.		Calm.	1.5	91.0	0	0	0	0
5 a.m.		"	0.8	91.0	0	0	0	0
6 a.m.		6.30 dawn; 6.50 sunrise; some frost. Both *spp.* sunbathing at nest entrances.	0.3	83.0	0	0	0	0
7 a.m.			0.5	90.0	0	0	0	0
8 a.m.			6.0	85.0	0	0	0	0
9 a.m.			10.3	69.0	74	5	39	10

was preferred to air temperature in the calculation of both partial and total correlations for ants ascending the tree. In this way it is hoped that some measure of the radiant heat as it affected the ants travelling to the tree was taken into account. Air temperatures were correlated with the activity of ants descending the tree,as they were obviously not affected by the soil surface temperatures. Combined activity gave slightly better correlations with air temperature than the soil temperature, and for that reason the former is preferred, and used in the calculations.[1]

In Table 20, the partial correlations show that the ants climbing up the tree were significantly affected by air humidity, while soil surface temperature had no significant effect.

The effects of humidity and air temperature on combined activity and the ants going down the tree could not be distinguished from each other, and apparently had no significant effect.

Although the period covered by observations does not show complete cessation of activity at midnight, there are indications that it was imminent. The diurnal foraging rhythm still persisted, but over a longer period of time, and a greater number of ants were active than in winter. (Table 21, Fig. 15).

3. Summer. (22.II.1956).

The effects on ant foraging activity of the climatic conditions prevailing in summer are shown in Fig. 16 and Table 23. Significantly more ants were recorded at the same times during the day than in winter and spring; thus activity in summer was at a much higher level. A continuous foraging pattern prevailed, whereby the ants were active throughout both the day and night. The same behaviour prevailed in the previous two months

[1] There was not sufficient time to calculate partial correlations of four variates. Only three variates - ant activity (including combined, ascending and descending), relative humidity, and soil surface, or air, temperatures were taken into account.

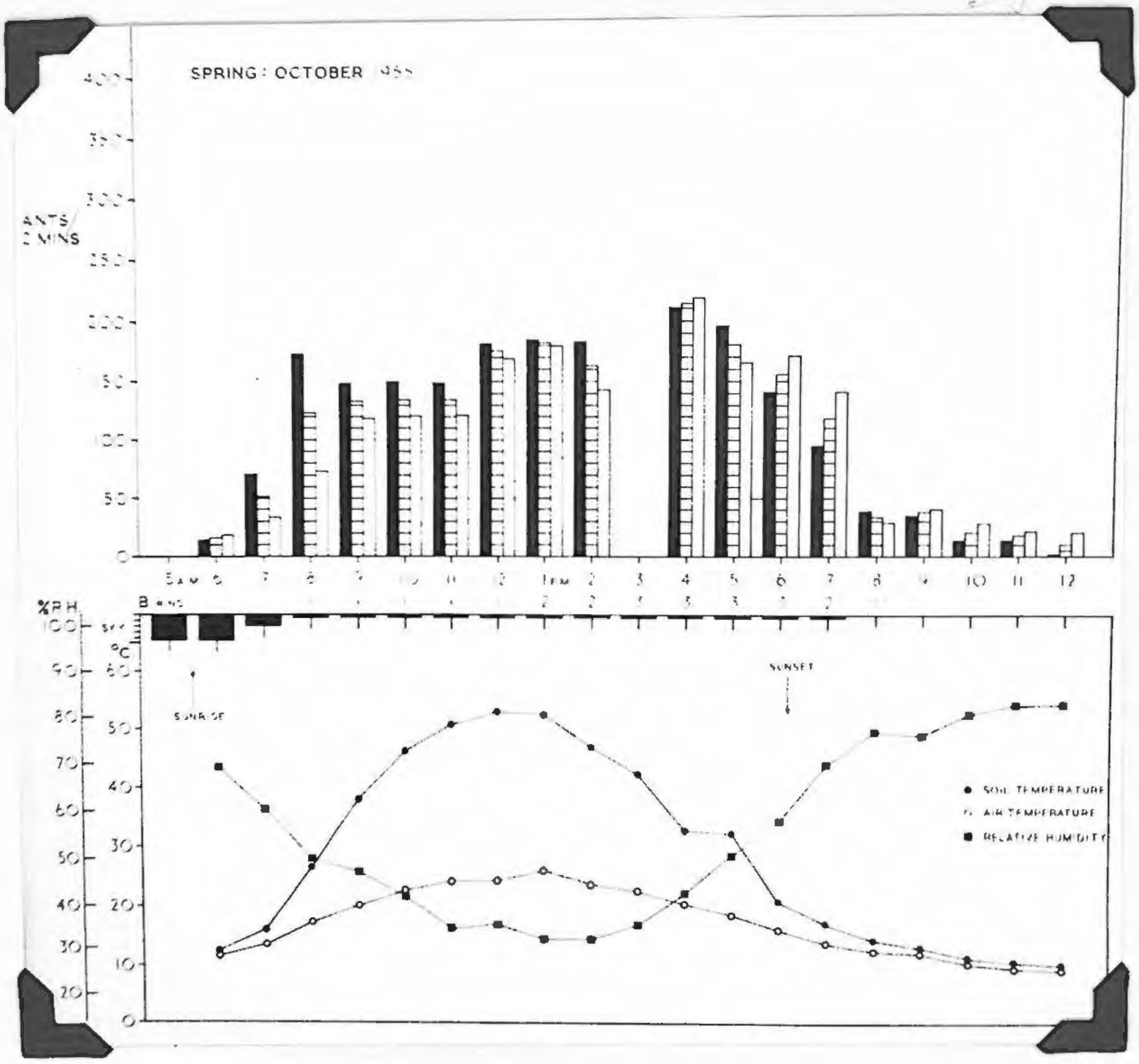

FIGURE 15.

Graphic and statistical correlations of climatic conditions with ant activity from observations made on 25.X.1955.

TABLE 20.

Combined activity: Total correlations	rAtH = -.864;	P =<.0004 * * *
	rAtT = +.857;	P =<.0004 * * *
	rHT = -.970;	P =<.0004 * * *
Partial correlations	rAtH.T = -.272;	P =>.05
	rAtT.H = +.154;	P =>.05
Ants ascending: Total correlations	rAuH = -.906;	P =<.0004 * * *
	rAuS = +.824;	P =<.0004 * * *
	rHS = -.949;	P =<.0004 * * *
Partial correlations	rAuH.S = -.640;	P =<.005 >.001 * *
	rAuS.H = +.265;	P =>.05
Ants descending: Total correlations	rAdH = -.760;	P =<.0004 * * *
	rAdT = +.775;	P =<.0004 * * *
Partial correlations	rAdH.T = -.050;	P =>.05
	rAdT.H = +.241;	P =>.05

<u>TABLE 21</u>. Monthly observations on 25th October, 1955, from 6 a.m. until midnight, together with a comparison of the activity of ants provided with an <u>ad.lib.</u> food source.

Time	Comments	Sky in tenths	Solar Radiation °C.	Air temp. °C.	Soil temperature °C exposed		umbrella		% R.H.	*A.* stein. control		A. stein. ad.lib.		*P.* megacephala	
					12"	0.25"	12"	0.25"		up	down	up	down	up	down
	Sunrise ± 5.30 a.m.														
6 a.m.	Very overcast - cannot feel warmth of sun. Ants not being heated up.	10	13.9	11.7	19.5	12.5	15.2	12.2	69.0	14	18	26	20	24	21
7 a.m.	Sun full strength - broken through.	4	41.9	13.6	19.5	16.0	15.5	13.0	60.5	71	33	79	68	38	42
8 a.m.	" " " " "	1	50.3	17.2	18.5	26.5	15.5	15.0	50.0	173	73	108	52	36	59
9 a.m.	Fine - slight breeze. B1.	1	56.9	20.0	18.5	38.0	15.5	15.7	47.0	149	119	109	78	37	36
10 a.m.	" " " B1.	1	57.7	22.8	18.5	46.1	15.5	16.5	42.0	150	121	95	84	35	24
11 a.m.	" " " B1.	1	58.6	24.2	18.5	50.8	15.5	17.2	34.0	149	122	71	73	29	37
Midday	B1.	1	58.3	24.3	18.5	53.0	15.5	18.3	35.0	182	169	53	61	24	23
1 p.m.	S.E. wind - weak. B2.	1	60.5	26.1	21.5	52.5	15.5	19.1	32.0	185	180	75	80	30	28
2 p.m.	S.E. wind - slight. B2.	1	58.9	23.9	21.5	47.0	15.5	19.8	32.0	183	143	94	95	30	30
3 p.m.	S.E. wind - fairly strong. B3.	1	-	22.8	22.0	42.3	15.5	20.2	35.0	Broken tally counter				31	35
4 p.m.	East wind - fairly strong. B3.	1	46.4	20.6	22.0	32.8	15.6	19.6	43.0	211	218	133	147	41	46
5 p.m.	S.E. wind - fairly strong. B3.	1	35.8	18.9	22.0	32.2	15.8	18.7	51.0	197	166	141	130	46	34
6 p.m.	S.E. wind. Sunset 6.20 p.m. B3.	1	27.2	16.1	22.0	21.5	15.8	17.2	58.0	141	172	121	112	39	57
7 p.m.	B2	1	-	14.1	22.5	17.2	16.0	15.7	70.0	95	142	61	65	42	29
8 p.m.	Very light breeze. Moonlight. B1.	0	-	12.8	22.5	14.5	16.0	14.7	77.0	39	29	32	36	43	23
9 p.m.			-	12.2	22.5	13.2	16.0	14.2	76.0	35	41	9	30	25	18
10 p.m.			-	10.6	22.5	11.5	16.0	13.5	81.0	14	28	27	31	22	26
11 p.m.			-	9.7	22.0	10.8	16.0	13.2	83.0	14	22	15	20	26	35
Midnight			-	9.4	21.5	10.2	15.8	12.5	83.0	2	21	15	16	24	23

(December, 1955, Table 35; January, 1956, Table 36); and in the following month (March, 1956, Table 37).

During summer the air and soil surface temperatures are well in excess of 10°C., which appears to be the temperature at which ant foraging stops in winter and spring. This is not true for observations in December, 1955 (Table 35), when temperatures at and below 10°C. were experienced, but the ants continued to forage albeit at a low intensity. The reason for this will be given later.

In most of the daylight hours the sky was completely overcast on the 22.II.1956, but it does not appear to have influenced the activity of the ants in any respect. A comparison of the intensity of activity in the previous month (January, 1956, Table 36) with February shows that there was little difference in foraging intensity, although in the January count the sky was clear, except for a few hours in the early morning, and the radiant heat was almost double that recorded in February. This would seem to indicate that once the temperature threshold is passed the sun does not play such an important rôle in governing ant activity. There is no recognisable heat torpor reducing the number of ascending ants. There is a slight fall off in activity at 4 p.m., but this is common to most observations and is not only a summer phenomenon.

For all types of activity (combined, ascending and descending) there is a very strong negative partial correlation with humidity, while other factors (air and soil temperatures) did not have any significant effect (Table 22).

4. <u>Autumn</u>. (22.5.1956.)

The foraging activity pattern of <u>A. steingroeveri</u> during the onset of winter is graphically correlated with climatic conditions (Fig. 17) and tabulated (Table 25). The discontinuous foraging pattern had once again manifested itself, there being a distinct peak of activity between sunrise and sunset The ants were active from dawn until midnight, when the temperature fell below 10°C. and foraging stopped. This count

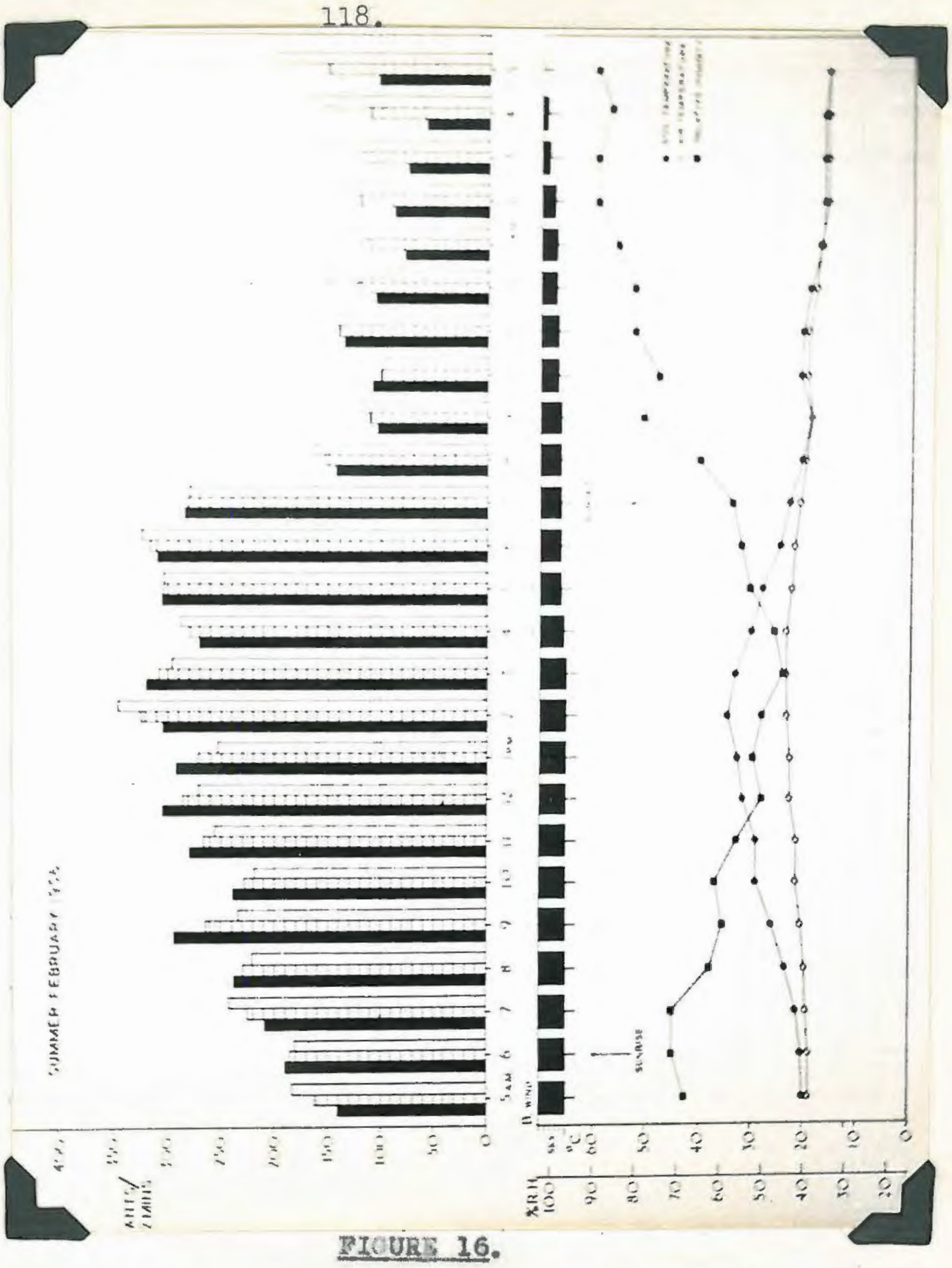

FIGURE 16.

Graphic and statistical correlations of climatic conditions with ant activity from observations made on 23-23:II:1956.

TABLE 22.

Combined activity.	rAtH = -.911;	P =<.0004	* * *
Total correlations	rAtT = +.841;	P =<.0004	* * *
	rHT = -.940;	P =<.0004	* * *
Partial correlations	rAtH.T = -.652;	P =<.0004	* * *
	rAtT.H = +.107;	P =>.05	
Ants ascending	rAuH = -.946:	P =<.0004	* * *
Total correlations	rAuS = +.915;	P =<.0004	* * *
	rHS = -.927;	P =<.0004	* * *
Partial correlations	rAuH.S = -.645;	P =<.0004	* * *
	rAuS.H = +.312;	P =>.05	
Ants descending	r rAdH = -.815;	P =<.0004	* * *
Total correlations	rAdT = +.738;	P =<.0004	* * *
Partial correlations	rAdH.T = -.526;	P =<.01 >.005	* *
	rAdT.H = +.142;	P =>.05	

TABLE 23.

Monthly count from 5 a.m. on 22nd until 5 a.m. on 23rd of February, 1956.

Time	Comments	Sky in tenths	Solar Radiation °C.	Air temp. °C.	% R.H.	Soil temperature °C.				*A. steingroeveri*		*P. megacephala*	
						exposed		umbrella					
						0"	12"	0"	12"	up	down	up	down
5 a.m.	Sky completely overcast.	10	-	19.1	68.0	20.0	26.8	19.5	21.5	142	184	37	21
6 a.m.	(Sunrise not observed: ± 6 a.m. (Mild, windless, ants not very (active.	10	-	19.1	71.0	20.3	26.8	20.0	21.8	190	182	35	32
7 a.m.		10	21.1	19.3	71.0	21.3	26.8	20.0	21.8	209	243	37	30
8 a.m.		10	24.2	19.7	62.0	23.5	26.5	20.0	21.8	238	222	29	30
9 a.m.		10	26.1	20.5	59.0	26.0	26.3	20.0	21.8	294	234	52	34
10 a.m.		10	32.7	21.1	61.0	29.0	26.0	20.3	21.5	238	218	49	31
11 a.m.		10	31.1	21.6	56.0	29.0	26.0	20.5	21.5	279	256	49	46
Midday		10	34.4	22.7	50.0	31.5	26.0	20.8	21.5	304	271	39	40
1 p.m.		10	35.6	22.7	52.0	32.5	26.0	21.0	21.3	292	253	40	32
2 p.m.		10	38.9	23.2	50.0	34.5	26.0	21.5	21.5	304	347	42	46
3 p.m.		10	37.9	23.6	45.0	33.0	26.0	21.5	21.5	319	297	37	38
4 p.m.	Sky clearing in W. First sunlight seen. S. breeze. B.2	9	35.6	23.6	47.0	30.0	26.0	21.5	21.5	270	288	57	39
5 p.m.	Sky clearing in W. E. breeze. B.2	9	34.4	22.7	53.0	28.0	26.0	21.5	21.5	305	303	45	35
6 p.m.		8	30.0	22.0	55.0	24.8	26.3	21.2	21.3	309	324	58	42
7 p.m.	Sunset 6.56 p.m.	8	23.3	21.0	57.0	23.0	26.3	21.0	21.3	284	279	36	39
8 p.m.		8	-	20.0	65.0	20.5	26.3	20.5	21.3	143	163	33	35
9 p.m.		8	-	18.9	78.0	19.0	26.3	20.3	21.3	104	120	29	32
10 p.m.		7	-	19.7	74.0	21.0	26.3	20.3	21.3	108	96	54	32
11 p.m.		7	-	20.0	80.0	20.5	26.0	20.1	21.3	136	148	38	29
Midnight		6	-	18.5	80.0	19.3	25.8	20.0	21.3	106	152	35	28
1 a.m.		6	-	17.4	84.0	17.3	25.5	19.5	21.3	78	148	31	27
2 a.m.		5	-	16.3	89.0	16.5	25.5	19.3	21.3	88	156	25	23
3 a.m.		3	-	16.2	89.0	16.5	25.5	19.0	21.3	76	161	42	32
4 a.m.		2	-	16.1	86.0	16.5	25.5	18.5	21.3	58	166	42	32
5 a.m.	Sky streaked with light. Sunrise 6 a.m.	0	-	16.1	89.0	16.0	25.5	18.5	21.1	104	200	45	41

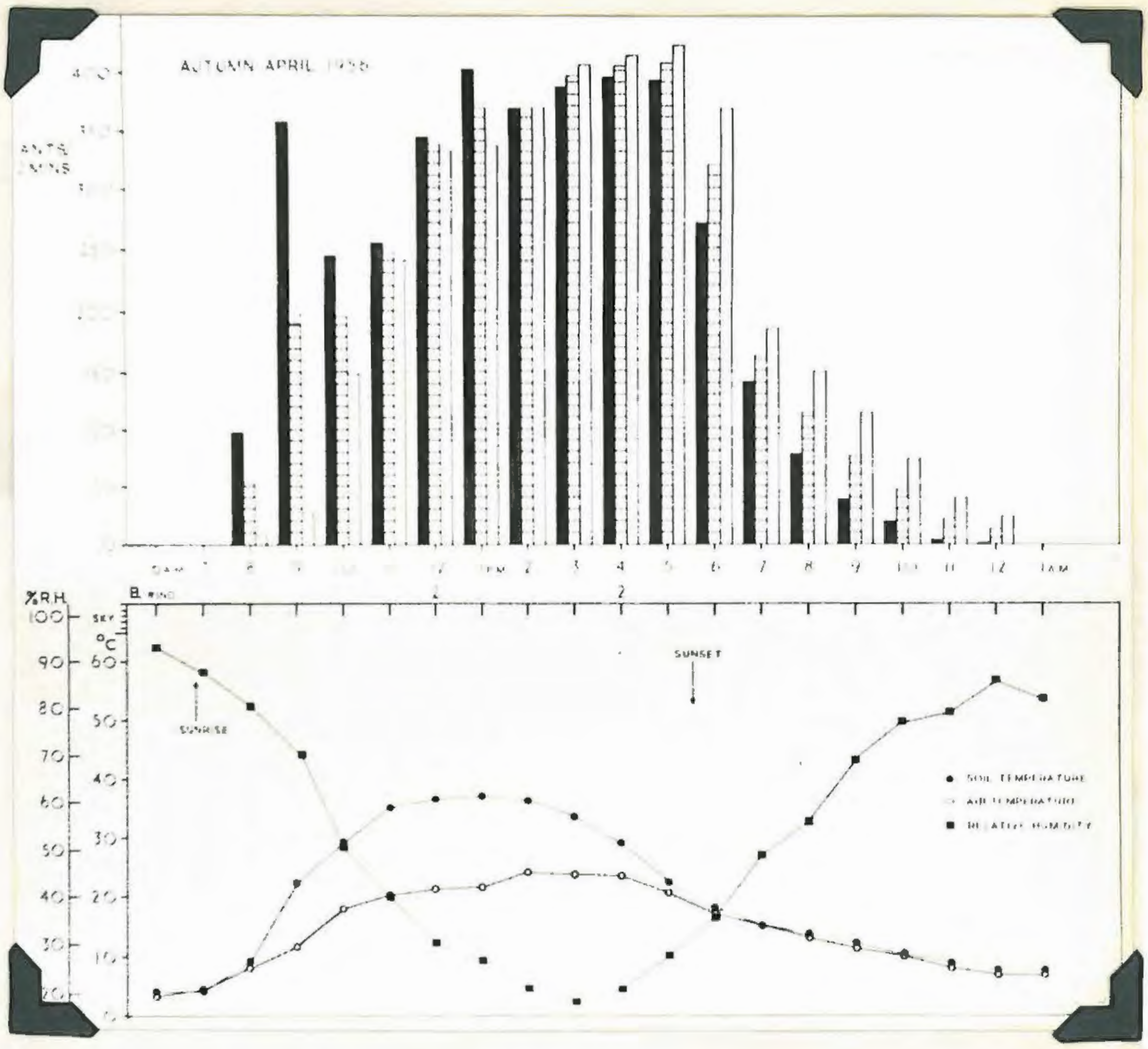

FIGURE 17.

Graphic and statistical correlations of climatic conditions with ant activity from observations made on 22.IV.1956.

TABLE 24.

<u>Combined Activity:</u>	rAtH = -.966;	P = <.0004 * * *
Total correlations	rAtT = +.952;	P = <.0004 * * *
	rHT = -.972;	P = <.0004 * * *
Partial correlations	rAtH.T = -.569;	P = <.02 >.01 *
	rAtT.H = +.213;	P = >.05
<u>Ants ascending:</u>	rAuH = -.861;	P = <.0004 * * *
Total correlations	rAuS = +.854;	P = <.0004 * * *
	rHS = -.836;	P = <.0004 * * *
Partial correlations	rAuH.S = ∓.514;	P = <.04 >.03 *
	rAuS.H = +.480;	P = >.05
<u>Ants descending:</u>	rAdH = -.971;	P = <.0004 * * *
Total correlations	rAdT = +.938;	P = <.0004 * * *
Partial correlations	rAdH.T = ∓.938;	P = <.0004 * * *
	rAdT.H = +.011;	P = >.05

TABLE 25. Monthly count from 6 a.m. on the 22nd until 1 a.m. on the 23rd April, 1956.

Time	Comments	Solar Radiation °C.	Air temp °C.	% R.H.	Soil temperature °C.				*A. steingroeveri*		*P. megacephala*	
					exposed		umbrella					
					0"	12"	0"	12"	up	down	up	down
	Previous few days overcast and cold.											
6 a.m.	Clear, cold and dewey	-	3.3	93.5	4.3	18.3	9.3	17.0	0	0	0	0
7 a.m.	Sunrise 6.50 a.m. Both spp. sunbathing.	-	4.7	87.5	4.3	18.0	9.4	17.0	0	0	2	0
8 a.m.	Clear, cloudless day. No breeze - bit of a nip in the air.	35.8	8.2	80.5	9.3	18.3	11.0	17.0	98	8	19	13
9 a.m.	" " " " "	47.8	11.7	70.0	22.2	17.5	13.4	17.0	357	27	1	2
10 a.m.	" " " " "	54.3	18.1	51.0	29.3	17.3	16.0	17.0	245	149	3	2
11 a.m.	" " " " "	55.6	20.3	40.0	35.0	17.3	19.0	17.0	255	241	2	11
Midday	Slight breeze from S. to N. B2.	56.7	21.4	31.0	36.5	17.0	18.0	17.0	344	331	-	-
1 p.m.		58.9	21.7	27.0	37.0	17.3	18.5	17.0	402	336	-	-
2 p.m.		57.4	24.2	21.0	36.3	18.0	19.5	17.0	368	368	-	-
3 p.m.		54.3	23.9	18.0	33.5	18.5	20.0	17.0	387	405	-	-
4 p.m.	Slight breeze S. to N. B2.	47.5	23.6	21.0	29.2	19.2	20.3	17.3	395	413	-	-
5 p.m.	5.20 p.m. sun no longer shining on soil.	20.6	20.9	28.0	22.6	20.3	19.3	18.0	392	421	-	-
6 p.m.	Sunset 5.35 p.m. Moonrise 6.16 p.m. Still calm and equable.	-	17.4	36.0	18.3	20.3	17.6	18.0	271	368	-	-
7 p.m.	Very moonlight.	-	15.3	49.0	15.3	20.5	16.6	18.0	142	186	-	-
8 p.m.		-	13.5	56.0	14.0	20.5	15.2	18.0	78	150	-	-
9 p.m.	Ants' movements slow and deliberate	-	11.7	69.0	12.5	20.5	15.0	18.0	38	114	-	-
10 p.m.		-	10.3	77.0	10.7	20.0	14.2	18.0	20	74	-	-
11 p.m.		-	8.6	79.0	9.3	19.5	13.0	18.0	4	40	-	-
Midnight		-	7.4	86.0	8.3	19.3	12.0	18.0	2	24	-	-
1 a.m.		-	7.4	82.0	8.0	19.0	11.5	17.5	0	0	-	-

Note: Perfect day: no cloud, winds slight and did not affect ants.

was one of the few during which the foraging intensity exceeded 400 ants/2 mins.

The day on which the observations were made may be described as perfect; the sky was cloudless throughout the day, and there were only very slight breezes on two occasions.

The data from Table 24 relating the activity of A.steingroeveri with climatic factors show that the combined ant activity was affected by humidity, while the partial correlations for ants ascending the tree were only just significantly correlated with humidity; air and soil temperatures had no apparent effect.

Ants ascending the tree were most significantly affected by humidity, as the strong negative correlation shows.

TABLE 26.

Summary of analyses of observations on ant activity.

		1	2	3	4
Combined activity Total correlations	rAtH	--	-***	-***	-***
	rAtT	+*	+***	+***	+***
	rHT	-***	-***	-***	-***
Partial correlations	rAtH.T	--	--	-***	-*
	rAtT.H	--	--	--	--
Ants ascending Total correlations	rAuH	--	-***	-***	-***
	rAuT/S	+*	+***	+***	+***
	rHS		-***	-***	-***
Partial correlations	rAuH.T/S	--	-**	-***	-*
	rAuT/S.H	--	--	--	--
Ants descending	rAdH	--	-***	-***	-***
	rAdT	+*	+***	+***	+***
Partial correlations	rAdH.T	--	--	-**	-***
	rAdT.H	+*	--	--	--

Where 1 = winter; 2 = spring; 3 = summer; 4 = autumn.

From Table 26, the following conclusions may be drawn:-

(i) Combined or total activity had, during summer and autumn, a significant negative partial correlation with the relative humidity, which appears to be the most important factor governing ant activity. The partial correlations of air temperature and humidity in winter and spring are not significant, and ant foraging behaviour does not appear to be influenced by any one factor in particular.

(ii) Ants ascending in winter (air temperature) were not affected by temperature or humidity, but the partial correlations for the remaining three seasons show significant negative correlations with humidity.

(iii) Ants descending showed a marked negative partial correlation with humidity in spring, summer and autumn. Air temperature was apparently only significant during winter, as the factor influencing the foraging activity of *A.steingroeveri*.

With the exception of the summer months, activity appears to be determined by:-

(a) a temperature threshold;

(b) humidity.

There is no activity when the temperature is low, but once the threshold has been passed and the level of activity established, it is reduced or controlled by high humidities.

When these analyses are viewed as a whole, they do not present very consistent results. This is partly due to the ants being affected by more environmental factors than were considered, and also by these agents being more effective at certain stages of the journey as ants pass from their nests to and from the tree.

Furthermore, it is thought that counts of ant activity made on one day in each month are not sufficiently valid to represent the conditions prevailing throughout each particular month. Obviously, observations must be made at more frequent intervals to eliminate and determine the day to day variations in the climatic conditions as they affect the foraging behaviour of ants. These unsatisfactory results may have had other origins, and several other factors were investigated which may have influenced the ants. It is clearly noticeable in my observations that there is frequently a difference in the intensity of activity at the same times on two consecutive mornings (Figs. 14 and 16), which were due to changes in environmental conditions.

(f) Additional factors affecting the foraging behaviour.

1. Seasonal behaviour.

(i) Trophallactic stimulation.

It has been mentioned that the ants foraged throughout the night at low temperatures in December, 1955, but ceased to forage at the same temperatures in winter. To elucidate this, a table has been drawn up in which the foraging behaviour was compared with the prevailing conditions. Foraging behaviour is divided into two categories - continuous and discontinuous. The times, soil surface and air temperature, and relative humidity are given when foraging activity ceased, or the lowest intensity of activity was recorded. (Table 27).

When Steyn's (1954a) data regarding the life history of *A.custodiens*, showing the numbers of larvae present in colonies at different times of the year, are included in Table 27, several interesting facts emerge. (*Note:* My observations on times of brood development of *A.steingroeveri* show that they are more or less the same as *A.custodiens*).

TABLE 27.

Showing the effect of 'trophallactic stimulation' on ant foraging behaviour.

Month	Foraging pattern.	Air temp. °C.	Soil temp.	% R.H.	Time	% Larvae (Steyn).	Lowest temp. °C	
							Air	Soil
June	discont.	7.8	-	86	01.00	0.0	-	-
July	-	-	-	-	-	0.3	-	-
Aug.	discont.	11.3	-	69	19.00	2.4	-	-
Sept.	discont.	14.5	15.0	65	24.00	3.3	-	-
Oct.(1)	discont.	11.1	11.5	60	20.00	3.6	-	-
Oct.(2)	discont.	11.1	12.0	72	24.00	"	-	-
Oct.(3)	discont.	9.4	10.2	83	24.00	"	-	-
Nov.	-	-	-	-	-	6.6	-	-
Dec.	contin.	12.5	9.8	93	01.00	9.1	10.0	9.3
Jan.	contin.	22.0	20.3	65	02.00	17.9	19.0	17.0
Feb.	contin.	16.1	16.5	86	04.00	19.9	16.1	16.0
March	contin.	14.4	12.5	88	05.00	33.7	14.4	12.3
April	discont.	7.4	8.3	82	24.00	2.4	-	-
May	discont.	10.2	7.8	64	23.00	0.5	-	-
June	discont.	-	-	-	-	0.5	-	-

Environmental conditions at the time when foraging ceased ('discont.'), or the lowest foraging intensity recorded during continuous ('contin.') foraging. Lowest temperatures prevailing during summer counts are also given.

(1) Continuous foraging prevails in summer (December, January, February and March), and the ants apparently are not affected by low temperatures at which they cease to forage at other times. This may be explained in terms of Schneirla's (1944) 'trophallactic stimulation' hypothesis, in which he suggests that the larval exudate stimulates the workers to change their foraging behaviour. This may also manifest itself in A. steingroeveri workers which are apparently willing to forage at low temperatures only when large numbers of larvae are present. Fewer workers are involved in foraging at these low temperatures at night than during the day; however, they are sufficiently numerous to show a distinct change in foraging behaviour from discontinuous in winter to continuous in summer.

These data show that the presence of brood modified foraging behaviour, and it may be assumed that low temperatures are subordinate in effect to larval stimulation of the ants during summer. It is not known what rôle humidity plays under these conditions. Although high humidity was experienced in December, it is not typical of the other three months during which humidities of the same order as those prevailing in the other seasons were recorded. Thus the humidity data in Table 27 do not lend themselves to speculation.

(2) During the remaining three seasons (spring, autumn and winter) when no or little brood is present in the colonies, the ants only forage for part of the night. At these times the ants appear to be more responsive to adverse conditions and lack the 'drive' which characterises summer foraging.

2. Diurnal behaviour.

(1) Overcast skies or heavy mists.

In the early mornings there was a sudden and marked increase in ant activity at about sunrise. This is true regardless of the prevailing foraging pattern, and occurs in all seasons.

An increase in activity of 20, or more, ants per 2 minutes over the previous hourly count in the early morning constituted a 'flush' of activity from the effects of the sun on the ants.

Many of the monthly observations were made on days when the sunrise was obscured by heavy cloud formations or mists. The approximate times of sunrise on such days were estimated from records of sunrise times on the preceding day or the day after the counts were made. In the field one gained the impression that the absence of direct sunlight on the ants caused them to start foraging later, or, in other words, the flush was delayed. All the available data of the conditions prevailing at and around flush time were collected to evaluate the effect of overcast skies and the filtering of sunlight on ant foraging activity.

In Table 28 the foraging patterns,state of the early morning skies, and times of the flush relative to sunrise, are compared with air and soil temperatures, and relative humidities prevailing at the times of the flush and the previous observations. For further comparison, the air and soil temperatures are given at which foraging ceased or was lowest in intensity.

Most emphasis will be placed on surface temperatures of exposed soil, which are more applicable here than air temperatures, in terms of the ground surface 'film', as the ants are ascending the tree. It would have been valuable if records of solar radiation could have been included in the table, but there are few valid observations available of the early morning.

Two observations were made, on the 23rd and 25th of October, 1955. These are a useful starting point, since the ants showed a flush of activity at different times on two days in a short space of time on the same tree, which means that ants from the same colonies were involved.

Although the ants on the first day were subjected to winds of force 'B.3' and low temperatures, they 'flushed' 33 minutes after sunrise, when the sun was only partly obscured by clouds. On the third day (25th) the ants had no wind with which to contend and the prevailing temperatures were much higher (soil: 10.9 : 16.0°C; air: 11.6 : 13.6°C.), but the sky was completely overcast, and the flush of activity took place 90

TABLE 28.

The effect of overcast skies on early morning foraging activity.

Month	T.1 Flush temp. °C.	T.2 Previous temp. °C.	Diff. T1-T2	Temp. when foraging ceased.	Lowest temp. if continuous.	Flush time after (+) before(-) sunrise in mins.	Sky Overcast = 0 Clear = C
				Air temperatures.			
June '55	9.4	6.7	+ 2.7	7.8	-	+ 68	?
July "	-	-	-	-	-	-	-
Aug. "	10.3	6.0	+ 4.3	11.3		+130	C - frost.
Sept. "	15.5	13.0	+ 2.5	14.5	-	+ 70	0
Oct.(1)	11.6	11.0	+ 0.6	11.1	-	+ 33	Partly 0.
Oct.(3)	13.6	11.6	+ 2.0	9.4	-	+ 90	0
Nov. "	-	-	-	-	-	-	-
Dec. "	16.0	11.0	+ 4.0	-	10.0	+ 50	C
Jan. '56	19.0	19.0	0.0	-	19.0	+ 2	0
Feb. '56	16.1	16.1	0.0	-	16.1	- 60	0
Mar.(1)	16.7	15.0	+ 1.7	-	14.4	+ 90	0
Mar.(2)	15.8	14.4	+ 1.4	-	14.4	+ 28	C
April "	8.2	4.7	+ 3.5	7.4	-	+ 80	C
May "	13.3	8.5	+ 4.8	10.2	-	+165	0
				Soil surface temperature.			
June '55	-	-	-	-	-	+ 68	?
July "	-	-	-	-	-	-	-
Aug. "	-	-	-	-	-	+130	C - frost.
Sept."	16.5	12.0	+ 4.5	15.0	-	+ 70	0
Oct.(1)	10.9	10.0	+ 0.9	11.5	-	+ 33	Partly 0.
Oct.(3)	16.0	12.5	+ 3.5	10.2	-	+ 90	0
Nov. "	-	-	-	-	-	-	-
Dec. "	15.5	8.5	+ 7.0	-	9.3	+ 50	C
Jan. "	-	-	-	-	17.0	+ 2	0
Feb. "	16.0	16.5	- 0.5	-	16.0	- 60	0
Mar.(1)	18.0	15.5	+ 2.5	-	12.3	+ 90	0
Mar.(2)	13.0	12.3	+ 0.7	-	12.3	+ 28	C
April"	9.3	4.3	+ 5.0	8.3	-	+ 80	C
May "	15.5	12.3	+ 3.2	7.8	-	+165	0
				Relative humidity.	Highest R.H.		
June '55	70.0	85.0	-15.0	86.0	-	+ 68	?
July "	-	-	-	-	-	-	-
Aug. "	69.0	85.0	-16.0	69.0	-	+130	C - frost.
Sept."	76.5	71.5	+ 4.5	65.0	-	+ 70	0
Oct.(1)	81.0	78.0	- 3.0	60.0	-	+ 33	Partly 0.
Oct.(3)	60.6	69.0	- 8.6	83.0	-	+ 90	0
Nov. "	-	-	-	-	-	-	-
Dec. "	70.0	84.0	-14.0	-	96.0	+ 50	C
Jan. '56	85.0	70.0	+15.0	-	85.0	+ 2	0
Feb. "	89.0	86.0	+ 3.0	-	89.0	- 60	0
Mar.(1)	91.0	93.0	- 2.0	-	-	+ 90	0
Mar.(2)	81.0	85.0	- 4.0	-	93.0	+ 28	C
April"	90.0	80.5	+ 9.5	86.0	-	+ 80	C
May "	71.0	100.0	-29.0	64.0	-	+165	0

minutes after sunrise. This suggests that the ants (which are black in colour) were dependent on direct sunlight to increase their body temperature. The possibility of optical stimulation by sunlight triggering off activity remains. However, on overcast mornings at sunrise there was sufficient light for the observations to be made without the aid of a torch.

In September, higher air temperatures and almost identical soil temperatures to those recorded in the third October count were registered at the time of flush when the sky was completely overcast. There is only a difference of 20 minutes in flush delay between the two observations in different months. The delayed flush of over an hour in September may also be contrasted with the short delay in the first October count when the sky was only partly clouded.

In the months of June and August, although the skies were clear, the flush was delayed for one and two hours, respectively, but in both cases the flush took place when the air temperatures had reached the temperature threshold. The same applies to the April observations, when low temperatures prevailed.

The ants forage continuously in December, January, February and March. In December, the flush was delayed for almost an hour, largely on account of the low temperatures, since the skies were clear at sunrise. The observations in January and February were also made on cloudy, overcast mornings, but in both cases the temperatures were high. The flushes took place at, and an hour before, sunrise, which suggests that the ants were stimulated by increased light intensity at dawn, especially in February when there was little, if any, increase in soil and air temperatures.

In March, low temperatures and overcast skies delayed the flush for almost half an hour. Similar soil temperatures and conditions prevailed at sunrise in May, but the air temperatures were lower. In May, foraging was delayed for over two hours in contrast to the half-hour in March. This additional delay in time may be attributable partly to the lower air temperatures in May, and partly to the absence of 'drive', since few larvae were present then (see Table 27).

The data in Table 28 suggest that the presence of dense cloud on cold mornings, especially in winter, autumn and spring, at sunrise delays the time in relation to sunrise at which there is a marked increase in ant activity. Drummond and van Deventer (1954) show that when there is average cloud (5.4 tenths), 19% of the solar energy is absorbed by cloud, and 29% is scattered outwards by water vapour molecules. Thus a loss of about 48% of solar energy going directly to the earth's surface is incurred, and even more is lost when it is completely overcast.

The filtering effect of the clouds on sunlight as it affects the ants is difficult to explain satisfactorily. It is improbable that the ants are responding to optical stimulation, except for the two instances in summer when the soil and air temperatures were well in excess of the threshold. 'Sunbathing' was frequently observed on cold mornings, when the ants showed no desire or drive to forage, and appeared to wait until a temperature threshold had been reached. This threshold may be their own body temperature as it is directly affected by the sun, or may result from the creation of suitable environmental conditions in the 'film'.

It is difficult to assess the effects of air humidity on the ants. It is to be expected that high humidities will prevail in the mornings, but no correlation with the delay times is obvious in Table 28.

(ii) Periodic honeydew excretion.

It stands to reason that if the activity of A.steingroeveri is controlled by environmental factors, the Soft Brown Scale may be equally affected, and honeydew excretion would be a function of temperature. If this were the case, the foraging behaviour of ants could not only be correlated with environmental factors, but also with the presence or absence of honeydew. Thus at certain times and under certain conditions the ants would be stimulated or deterred from foraging by the availability of honeydew.

TABLE 29. Comparison of A.steingroeveri foraging activity in veld and orchard: 24th October, 1955, 12.00 noon - 12.00 midnight.

Time	Comments		Sky	Solar Radiation °C.	Air temp. °C.	Soil temperature °C. exposed		% R.H.	veld colony control		veld colony protein		veld colony carbohydrate		control tree		ad.lib. tree	
						12"	0"		out	in	out	in	out	in	up	down	up	down
Midday	Fairly overcast. Wind from W. Fairly strong.	B3.	6/10	47.5	20.0	20.0	30.5	41.0	7	9	5	2	14	15	-	-	-	-
1.p.m.	Few drops of rain. Wind W.	B4.	7/10	41.0	19.3	20.1	29.5	45.0	9	8	3	6	21	10	-	-	-	-
2 p.m.	" "	B4.	7/10	48.2	18.1	20.2	27.0	47.0	9	7	5	3	8	4	-	-	-	-
3 p.m.	Few drops of rain. " "	B4	5/10	53.3	18.1	20.5	28.5	32.0	3	6	6	1	9	11	-	-	-	-
4 p.m.	" "	B4	4/10	46.6	18.1	20.5	26.5	26.0	5	2	8	10	5	6	-	-	-	-
5 p.m.		B4		29.7	15.3	21.2	21.5	65.0	0	0	meat removed by fowls.		1	4	102	48	88	88
6 p.m.	Sunset 6.22 p.m.	B3		16.7	13.3	21.2	18.0	44.0	0	0			0	1	52	58	77	88
7.30 p.m.	Wind dying down.	B3		-	12.4	21.4	16.0	69.0	0	0			0	0	7	20	34	25
8.30 p.m.	" " "	B3		-	11.1	21.2	13.8	71.0	0	0			0	0	5	11	22	24
9 p.m.	" " "	B2				-	-	-	-	-			-	-	-	-	-	-
10 p.m.	Breeze just fluttering leaves.	B2		-	9.4	20.8	12.0	72.0	0	0			0	0	11	19	20	16
11 p.m.				-	11.1	21.0	12.8	72.0	0	0			0	0	6	6	17	13
Midnight				-	11.1	20.5	12.0	72.0	0	0			0	0	8	4	15	2

On 24.X.55, the effect of the presence of honeydew on the ants was investigated. This involved a comparison of the activity up two orchard trees, one of which had constant or '*ad lib*.' source of sugar solution, and ants' nests in the veld which normally did not feed on honeydew. Three veld colonies were used: a control colony with no extra food, a colony with a piece of meat, and a colony with an '*ad lib*'. source of solution near at hand. Activity in the veld colonies was measured by placing a transparent plastic lid with a small hole over the entrance to each colony, and the numbers of ants going in and out in two minutes at hourly intervals were counted. A 24-hour conditioning period was allowed to the ants during which the '*ad lib*.' food sources were present, before the observations were made, both in these and subsequent experiments.

The food source was presented to the ants by employing the same technique as poultry farmers, by inverting a bottle of water in a dish where a constant water-level is maintained. In this case, 2-lb. fruit canning jars containing sugar solution were inverted into petri-dishes and tied into the '*ad lib*.' trees. It was found that a jar of sugar solution lasted for 3 days, although spilling and wastage occurred. The spilling resulted from wind shaking the trees, and heating of the air and sugar solution within the jar. The sugar solution ran down the branches and presented the ants with a large drinking surface, and there was no question of there being a limited number of ants being able to feed.

Table 29 shows there was little difference in the time when foraging stopped between the control veld colonies and the nest with sugar solution available. The same applies to the two trees in the orchard, especially since the ants of control tree which was situated near the margin of the orchard were more subject to the effects of the wind than the '*ad lib*.' tree. This accounts for the decrease in the number of ants ascending the control tree. There is a significant difference between the times when the veld and orchard ants ceased foraging. This

TABLE 30. Monthly observation, showing the effect of an '*ad lib.*' food source on ant activity from 5.30 a.m. until 11.0 p.m. on the 23rd October, 1955.

Time	Comments	Sky in tenths	Solar rad. °C.	Air temp. °C.	Soil temperature exposed		Soil temperature umbrella		% R.H.	Control A. stein.		Ad lib. A. stein.		Control A. stein.		Ad lib. A. stein.		P. mega.	
					12"	0"	12"	0"		up	down	up	down	up	down	up	down	up	down
5.30 a.m.	Sunrise 5.27 a.m. Sun partly obscured. Cold breeze from S.W. Ants active.	6	-	10.4	20.4	10.0	16.0	12.1	78.0	40	18	-	-	-	-	-	-	11	16
6 a.m.	B2.		10.7	11.6	19.8	10.9	16.0	12.5	81.0	76	16	-	-	-	-	-	-	42	8
7 a.m.	B2.		35.8	14.0	19.8	18.5	15.8	14.0	81.0	165	51	-	-	-	-	-	-	40	25
8 a.m.	Slight wind. B2.		51.1	16.6	19.5	19.3	15.8	15.8	66.0	141	102	-	-	-	-	-	-	35	29
9 a.m.	Increasing wind strength. B3.		59.1	19.0	19.5	38.4	15.8	17.0	58.0	212	199	-	-	-	-	-	-	30	29
10 a.m.	Skies clear.		56.1	21.1	19.5	39.0	16.0	18.0	36.0	276	156	-	-	-	-	-	-	23	30
11 a.m.	Veld ants not active. Wind v.strong; ants descending trees - difficulty in B4		58.6	22.7	19.5	43.2	16.0	20.5	29.5	142	205	-	-	-	-	-	-	15	17
	climbing. ~~B4~~	9	56.7	23.9	20.0	44.6	16.0	21.3	27.0	212	89	73	131	65	123	120	153	14	13
Midday	" " " " " B5																		
1 p.m.	Wind v. strong. B5	10	58.3	23.9	20.2	43.5	16.0	21.1	24.0	153	84	109	73	55	137	145	167	2	16
2 p.m.	" " " B5	10	56.6	24.2	20.5	39.8	16.0	22.6	18.0	158	154	75	67	61	94	136	110	34	6
3 p.m.	" " " B5	10	50.8	19.1	21.0	37.2	16.0	20.0	41.0	155	141	69	97	52	130	117	162	16	6
4 p.m.	" " " B4	10	47.2	18.5	21.0	31.2	16.1	19.0	38.0	145	100	59	84	24	46	119	146	22	5
5 p.m.	Wind dropped. B3	10	40.2	15.8	21.5	25.0	16.1	17.4	48.5	58	58	39	38	53	22	109	52	9	13
6 p.m.	Sunset 6.15 p.m. B3	10	29.1	13.5	21.5	18.1	16.1	15.5	55.0	37	29	3	14	27	37	45	61	21	19
7 p.m.	Wind died down. B2	10	-	11.8	21.5	12.0	16.1	13.8	52.0	6	6	1	0	10	21	6	15	17	28
8 p.m.	B1	9	-	11.1	22.0	11.5	16.5	12.8	60.0	2	1	0	0	4	4	3	7	5	15
9 p.m.	Wind dropped, almost calm. B1	8	-	10.8	21.8	10.6	16.3	12.5	62.0	1	0	0	0	3	1	8	5	21	7
10 p.m.			-	10.5	21.0	10.3	16.1	12.0	62.0	0	4	0	0	0	0	5	3	4	7
11 p.m.			-	10.0	20.0	9.2	16.0	11.5	61.0	0	0	0	0	0	0	4	3	5	5

TABLE 31. Monthly observation and the effect of an '*ad lib*' food source and artificial light on ant activity on the 29th May, 1956, from 7 a.m. until midnight.

Time	Comments	Sky in tenths	Solar rad. °C.	Air temp. °C.	% R.H.	Soil temp. °C exposed		control		*ad lib.* & light		control		*ad lib.*	
						0"	12"	up	down	up	down	up	down	up	down
7 a.m.	Very misty. Sunrise ± 7.15 a.m.	10	-	3.3	100.0	5.0	12.0	0	0	0	0	0	0	0	0
8 a.m.	Still misty; hygrometer dry bulb clouding.	10	8.9	4.2	100.0	5.0	12.0	0	0	0	0	0	0	0	0
9 a.m.	Mist clearing.	8	31.9	7.5	100.0	12.3	11.8	1	0	0	0	1	1	104	52
10 a.m.		6	43.5	13.3	71.0	18.5	11.8	6	5	21	11	1	2	76	52
11 a.m.		6	43.1	16.8	60.0	22.0	11.5	6	2	76	38	0	0	88	80
Midday	N.W. wind. Large branches moving - affecting ants. B4.	5	43.9	22.2	29.0	22.7	11.5	4	18	86	54	2	3	196	106
1 p.m.	Wind strong - ants coming down. B4	7	49.7	23.6	29.0	25.0	11.8	6	14	130	104	0	8	206	124
2 p.m.	Sun obscured by cloud. Wind dropped. B3.	9	29.7	22.2	30.0	21.0	12.3	24	16	110	118	6	2	182	152
3 p.m.	Soft breeze. Sky clearing. B2.	3	25.5	22.2	30.0	19.5	12.5	32	12	155	84	4	4	185	143
4 p.m.	Sky cleared - sun shining. No wind.	2	23.1	21.8	29.0	18.5	13.0	27	18	125	113	8	6	146	193
5 p.m.	Sunset 5.05 p.m.	1	16.3	19.4	37.0	15.3	13.3	16	22	86	94	6	4	106	132
6 p.m.	No moonlight.	0	-	16.9	41.0	12.3	13.3	14	22	22	41	4	5	48	57
7 p.m.			-	13.7	46.0	11.3	13.5	15	17	22	29	3	1	41	46
8 p.m.			-	12.7	54.0	10.4	13.8	13	2	20	16	1	0	33	34
9 p.m.			-	11.9	58.0	9.1	13.5	-	6	15	12	0	1	27	33
10 p.m.	Moonrise 9.45 p.m.		-	10.8	62.0	8.3	13.5	2	0	2	6	0	1	22	28
11 p.m.	Faint breeze. B1.		-	10.2	64.0	7.8	13.5	6	2	0	0	0	0	7	21
Midnight	" " B1.		-	10.2	64.0	7.8	13.3	0	0	0	0	1	0	2	8

Note: The first '*ad lib.*' tree was given a light source (two 500 candle-power pressure lamps) from 4 p.m. onwards.

suggests that orchard ants are stimulated and attracted by honeydew. This result confirms a general observation that veld colonies tend to end their foraging activities at night much sooner than orchard colonies.

On the previous day, 23.X.1955, a similar experiment was carried out on four orchard trees, two of which were used as controls,and the remaining two contained an 'ad lib'. food source of sugar solution. Table 30 shows there is no significant difference in the foraging intensity of the ants on the four trees.

This experiment was repeated on the 25.X.1955, but only two trees were used, one as a control and the other with the 'ad lib. food source. Once again the ants foraging from the two trees displayed typical diurnal activity patterns, and the ants visiting the 'ad lib.' food source did not continue to forage with the same intensity at night as they had during the daylight hours (Table 21).

Another experiment using the same technique was undertaken on 29.IV.1956 in the same orchard, with the same four trees. This orchard had been fumigated just before the counts were made; in addition, the sugar solution was replaced with a strong honey solution. In this instance, besides being hungry, the ants had been provided with a more attractive food source, which should have induced them to forage for as long as possible.

From Table 31, it may be seen that more ants visited the two trees with the honey solution, but their foraging rate fell to almost the same as that on the two control trees at 10 and 11 p.m. The ants visiting the second tree with the 'ad lib.' food showed a tendency to persist in foraging, but this was due to the relatively greater number of ants visiting this tree. The number of ants which persisted in visiting the second 'ad li tree at 9 and 10 p.m. were so small in relation to the number at peak activity at 1 p.m. that no significance may be attached to them.

The results of this series of 'ad lib.' experiments suggest that periodicity in the secretion of honeydew by the scale insects does not influence the foraging behaviour of the ants. Air and soil temperatures appear to exercise a greater control over foraging activity of _A.steingroeveri_. Honeydew does, however, induce the orchard ants to forage for longer periods than veld ants, when temperatures above 10°C. prevail.

(iii) Light.

It will have been noted that in the last '_ad lib._' experiment (May, 1956) a light source was provided around the first '_ad lib._' tree (Table 31) and two experiments had been carried out concurrently.

The light came from two 500-candlepower paraffin pressure lamps suspended about 1 meter above the ground by poles between the tree and the terrace wall in which nests of _A.steingroeveri_ were situated. The distance between the terrace wall and the tree was about 2 meters. Thus the ants, although both the nests and the trees received light, were not affected by the heat from the lamps, as it would tend to rise upwards.

The lamps were placed in position at 4 p.m. and maintained at maximum illumination until midnight, when observations were brought to an end.

The observations show (Table 31) that the presence of light did not alter the foraging rhythm of _A.steingroeveri_. Hodgson (1955) also found that leaf-cutting ants could not be stimulated to forage by giving them an artificial light source at night; however, they did respond to the light stimulation in the early morning.

It appears that even when two stimulants (light and honey solution) are given to _A.steingroeveri_ ants there is no observable alteration in their normal foraging behaviour. From this we may conclude that it is the falling temperature which controls their activities to a large extent.

(iv) Wind.

Very strong winds in July, 1955, almost completely stopped ant activity and there was no recognisable 'flush', although the temperature was well in excess of the threshold. In point of fact the rate of foraging dropped as the wind increased in force (Table 32).

Apart from this extreme example, it is difficult to assess to what extent less strong winds affected ant foraging. This depends on wind direction and the amount of shelter the 'count' tree received from other trees. In the early morning of the winter count (August, 1955; Table 19, Fig. 14), the ant activity was retarded by fairly strong winds. Other examples have been given above.

Gusty winds clearly show the effect of wind on the ants. During each gust of wind the ants cease moving and cling to the tree trunk. Once the gust has passed they continue walking. At a wind force of 'B.3' this behaviour may be seen. Depending on the type and force of the winds the rate of ant foraging is reduced to a lesser or greater degree.

The physical action of wind on ants, as it affects their foraging activity, cannot be correlated with other climatic data. This is because there is not the same close relationship existing between wind force and other climatic data, as there is between light intensity, temperature and relative humidity under natural conditions. There is no regular daily cycle of winds, and they may blow at any time of the day from any direction and at any velocity. The cause of the wind may be some meterological disturbance many miles away.

TABLE 32.

Count made on 31.VII.1955, showing the effect on activity of strong wind.

Time	Comments	Wind force	Air temp. °C.	% R.H.	*A. steingroeveri*		*P. megacephala*	
					up	down	up	down
8 a.m.	Gusty winds	B3	17.0	46.0	10	15	40	40
9 a.m.		B4	18.5	32.0	10	0	35	70
10 a.m.		B5	19.5	38.0	5	10	3	23
11 a.m.	Winds became very strong, carrying a lot of sand. Ants not reacting normally - more clinging than climbing. Stopped counting at 11 a.m.	B6	22.0	31.0	-	-	-	-

III. SUMMARY AND COMPARISON WITH A.CUSTODIENS AND P.MEGACEPHALA.

There are two main foraging patterns displayed by A.steingroeveri at Fort Brown, called 'continuous' and 'discontinuous'. During the summer the diurnal activity rhythm is not marked and the ants forage throughout the night, albeit at a reduced intensity. During the other three seasons A.steingroeveri forages discontinuously, and peaks of activity are registered during the early afternoon.

The results of the ad lib.feeding experiments, together with the indications that C.hesperidum continues to excrete honeydew at low temperatures, suggest that the foraging activity of A.steingroeveri is not controlled by the availability of honeydew. The presence of honeydew does, however, stimulate orchard ants to forage for longer periods than ants in the veld. This aspect is not considered by Vowles (1955) when he discusses the factors which influence ant foraging activity. Further evidence was provided by the count made in May, 1956, after fumigation. It showed a considerable reduction had taken place in the activity of the ants attending trees without scale infestations and ad.lib. food. Those trees with ad.lib. food were visited by almost twice as many ants (Table 31).

A light source of a thousand candle power in conjunction with ad.lib. food did not influence the foraging behaviour of A.steingroeveri in the early evening and at night.

There is evidence to suggest that overcast skies in the early morning in winter delay the 'flush' of activity. This, it is believed, is due to the filtering effect of clouds which reduces solar radiation (Drummond and van Deventer, 1955). It retards the warming up of the ants (Gunn, 1942) and the creation of the soil surface 'film'. During summer this retardation is not evident, largely because of the higher temperatures prevailing at night, together with the possible trophallactic stimulation of worker ants by the larvae. The data from Table 27 suggest that trophallactic stimulation occurs in summer when most larvae are present. The larvae, according to Schneirla's hypothesis (1944), cause the workers to alter their foraging behaviour whereby they forage intensely throughout the entire day. Even when temperatures are experienced in summer below those at which the ants cease foraging in winter, they continue working.

Steyn's (1954a) data show that A.custodiens' foraging is never brought to a complete halt at night in any season. The same increases and decreases in foraging intensity at different seasons exhibited by A.steingroeveri were also manifested. However, the lowest air temperature recorded by Steyn at Letaba in winter was 11.1°C., while temperatures approaching freezing point were registered at Fort Brown. This difference in temperature may explain why A.custodiens did not display a discontinuous foraging pattern at Letaba.

It is suggested that A.custodiens workers must be similarly affected by larval stimulation in summer, although the two foraging patterns - continuous and discontinuous - are not so clearly seen from Steyn's observations.

Broekhuysen (1948) reports that P.megacephala is a nocturnal forager under domestic and laboratory conditions. Carnegie (1954) observed that in citrus orchards P.megacephala has a diurnal foraging rhythm with a peak activity at sunset during summer. In winter the foraging intensity is lower and no marked rhythm was established, as a series of small peaks of activity occurred during the day and night.

In the course of my observations on the foraging of A.steingroeveri, the activity of P.megacephala was also recorded as a comparison. In the first observation, on 4th June, 1955, the P.megacephala colony was fairly strong and foraged a tree with a heavy infestation of Soft Brown Scale. Table 33 indicates that P.megacephala has a diurnal foraging rhythm in winter, but continued to forage when A.steingroeveri was no longer active. In the subsequent observations on another Pheidole colony, the ants had little or no honeydew available to them, which resulted in a more erratic foraging behaviour. However, it is noticeable (Tables 33 and 34) that P.megacephala has a distinct diurnal foraging rhythm in winter, while in summer more ants are active, but the foraging rate remains more or less constant throughout the day and night (Tables 23, 35 and 36).

The important point is that P.megacephala is able to forage at lower temperatures than A.steingroeveri. This would appear to offer an advantage to P.megacephala; however, in the previous section it was shown that this ability to forage at lower temperatures did not affect the territorial relationships of the two species, and P.megacephala was not seen attacking A.steingroeveri nests at night. The reason for P.megacephala not achieving greater success at Fort Brown is enigmatical.

TABLE 33.

Counts of ants ascending one tree over a period of five minutes at hourly intervals from 9 a.m., 4.VI.55 to 9 a.m., 5.VI.55.

Time	Comments	Air temp. °C.	% R.H.	*A. steingroeveri*	*P. megacephala*
9 a.m.		17.6	73.5	127	32
10 a.m.		15.6	48.0	133	-
11 a.m.		20.6	39.0	234	188
Midday		20.8	37.5	312	124
1 p.m.		21.7	37.0	411	132
2 p.m.		21.9	36.5	368	135
3 p.m.		22.8	35.0	406	123
4 p.m.		21.7	37.0	447	91
5 p.m.	Sunset 4.54 p.m.	16.9	57.0	379	74
6 p.m.		16.7	45.0	221	148
7 p.m.		11.1	81.0	55	148
8 p.m.		10.6	68.0	43	92
9 p.m.		11.7	69.0	24	89
10 p.m.		11.1	69.0	11	93
11 p.m.		9.2	79.0	9	97
Midnight		8.9	79.0	4	60
1 a.m.		7.8	86.0	1	39
2 a.m.		7.8	86.0	0	37
3 a.m.		8.3	79.0	0	20
4 a.m.		6.4	88.0	0	23
5 a.m.		6.5	85.0	0	18
6 a.m.		4.7	92.0	0	7
7 a.m.	Sunrise 7.22 a.m.	5.3	88.0	0	29
8 a.m.		6.7	85.0	4	210
8.30 a.m.		9.4	70.0	288	-
9 a.m.		10.6	68.0	226	212

a comparison of

TABLE 34. ~~A comparison of~~ Monthly observation, and also/the activity of a veld colony of *A. steingroeveri* with that in an orchard on 26th September, 1955, from 6 a.m. until midnight.

Time	Comments	Sky in tenths	Soil temperature °C. Exposed 12"	Soil temperature °C. Exposed 0"	Soil temperature °C. Umbrella 12"	Soil temperature °C. Umbrella 0"	% R.H.	Air temp. °C.	tree *A steingroeveri* up	tree *A steingroeveri* down	veld colony *A. steingroeveri* out	veld colony *A. steingroeveri* in	*P. megacephala* up	*P. megacephala* down
6 a.m.	Fairly cold, due to previous day's rain. Heavy mist and cloud. Sunrise obscured. 6.50 a.m. sun shining through clouds.	10	19.0	11.5	17.5	11.5	71.5	13.0	4	5	7	1	7	18
7 a.m.		9	19.0	12.0	17.0	12.0	71.5	13.0	9	8	10	6	8	10
8 a.m.	Overcast, shifting clouds, slight, gusty winds.	7	18.5	16.5	17.0	14.5	76.5	15.0	44	22	27	28	10	17
9 a.m.		7	18.5	19.0	17.0	15.5	84.0	16.0	62	49	22	28	21	8
10 a.m.		7	18.0	26.5	17.0	17.0	61.5	17.7	57	63	45	21	13	11
11 a.m.		6	18.0	27.0	16.5	17.5	57.0	18.5	46	77	22	21	27	20
12 midday			18.0	27.0	16.5	17.5	55.5	19.0	72	84	24	18	12	12
1 p.m.			18.0	26.4	16.5	18.0	54.0	19.0	75	68	27	25	12	8
2 p.m.			18.5	29.0	16.5	18.5	49.0	20.0	70	112	16	13	23	15
3 p.m.			19.0	27.0	16.5	20.0	51.0	19.8	83	118	51	11	31	17
4 p.m.			19.0	28.0	16.5	18.0	49.0	19.8	179	210	9	6	32	29
5 p.m.			19.5	23.4	16.5	17.2	52.0	18.0	109	236	19	28	33	18
6 p.m.	6 p.m. sunset.		20.0	18.0	17.0	16.5	56.0	16.2	60	149	1	5	14	10
7 p.m.			20.0	15.0	16.5	16.0	67.0	15.0	10	18	0	2	7	7
8 p.m.			20.0	15.5	16.5	15.5	65.0	15.0	8	22	0	0	8	10
9 p.m.			20.0	15.8	16.5	15.5	64.0	14.9	10	24	0	0	9	6
10 p.m.			19.5	15.0	16.5	15.0	64.0	14.8	6	10	0	0	6	6
11 p.m.			19.5	15.0	16.5	15.0	64.0	14.5	3	5	-	-	7	4
Midnight			19.5	15.0	16.5	15.4	65.0	14.5	2	2	-	-	4	7

Summary: Day of unstable conditions - passing clouds: variations in light intensity. Gusty winds: variation in temperature. *Pheidole* very sensitive to changes in both above.

Note: 8 a.m. - 3 p.m. the count on the *A. steingroeveri* tree was inaccurate due to some ants ascending the tree by crossing the grease barrier.

TABLE 35. Monthly observation from 5 a.m. on 7th December until 5 a.m. on 8th December, 1955.

Time	Comments	Sky in tenths	Solar rad. °C.	Air temp. °C.	Soil temperature °C				% R.H.	A. steingroeveri		P. megacephala	
					exposed		umbrella						
					0"	12"	12"	0"		up	down	up	down
5.a.m.	Sunrise 5.10 a.m.	1		11.0	8.5	19.0	16.0	13.0	84.0	20	56	41	23
6 a.m.	Many black ants roosting and sun-bathing in trees - must have spent night there.		39.2	16.0	15.5	19.0	16.0	14.0	70.0	50	83	33	53
7 a.m.		4	40.3	16.0	22.0	19.0	16.0	14.8	68.0	98	119	55	43
8 a.m.		0	47.2	17.0	30.5	19.0	16.0	15.0	58.5	148	167	44	32
9 a.m.			57.2	19.0	39.8	19.3	16.0	16.0	53.0	211	144	54	46
10 a.m.			59.4	20.4	47.0	19.3	16.0	17.3	54.0	189	162	36	36
11 a.m.	Very hot - ants driven into nests where exposed, but active beneath trees.		59.4	21.3	53.5	20.0	16.0	17.5	49.0	212	208	43	56
Midday.			57.8	22.0	55.8	20.0	16.0	19.0	40.0	204	222	80	49
1 p.m.	" " " " " "		59.4	23.5	56.0	21.0	16.0	19.5	38.5	171	130	51	47
2 p.m.	Wind freshening from S. B2.		62.2	24.5	55.3	21.0	16.5	20.3	34.0	188	190	70	52
3 p.m.	S.S.E. wind getting stronger. B3		60.0	23.5	42.5	22.0	16.5	22.5	42.0	244	216	87	63
4 p.m.	Ants becoming more active in field.	0	46.1	20.5	53.5	23.0	16.8	19.3	51.0	227	192	95	45
5 p.m.	Sun obscured by clouds.	6	25.3	19.0	26.0	23.0	16.8	18.0	46.0	229	198	56	38
6 p.m.		1	21.2	18.4	22.5	23.0	17.0	17.3	54.0	176	191	45	46
7 p.m.	Sunset 6.58 p.m.	0	-	17.5	19.8	23.0	17.0	17.0	60.0	165	180	46	60
8 p.m.			-	17.0	19.0	23.3	17.0	16.5	64.0	100	112	46	58
9 p.m.			-	-	-	-	-	-	-	-	-	-	-
10 p.m.			-	15.3	15.3	23.3	17.0	16.0	78.0	27	46	46	29
11 p.m.			-	14.3	13.5	23.2	17.0	15.1	77.0	33	56	45	42
Midnight			-	-	-	-	-	-	-	-	-	-	-
1 a.m.			-	12.5	12.3	22.8	16.8	14.3	85.0	20	42	36	47
2 a.m.	Dewfall.		-	-	-	-	-	-	-	-	-	-	-
3 a.m.			-	-	-	-	-	-	-	-	-	-	-
4 a.m.	Getting light, 4.30 a.m.		-	10.2	9.8	22.0	16.1	13.5	93.0	31	52	43	38
5 a.m.	Sunrise 5.07 a.m.		-	10.0	9.3	22.0	16.1	13.0	96.0	40	66	45	41

TABLE 36.

Monthly observations from 6 a.m. on 28th until 6 a.m. on 29th January, 1956.

Time	Comments	Sky	Solar Radiation °C.	Air temp. °C.	% R.H.	soil temp. °C. exposed.		A. stein.		P. meg.	
						0"	12"	up	down	up	down
6 a.m.	Sunrise obscured by cloud and mist. Faint drizzle.	10/10	19.4	19.1	90.0	20.3	22.0	192	181	35	31
7.a.m.	6.55 a.m. light drizzle.	9/10	22.1	19.3	90.0	21.6	22.4	179	213	30	24
8 a.m.	Drizzle stopped.	8/10	25.5	20.2	93.0	24.7	23.0	245	256	37	32
9 a.m.	Getting hotter.	0/10	46.1	22.5	74.0	31.3	23.0	259	236	18	28
10 a.m.	" "		62.2	25.8	63.0	51.3	23.0	255	260	27	24
11 a.m.	Slight E. breeze B1.		63.2	27.5	60.0	59.6	23.5	266	280	24	14
Midday	Calm.		63.9	29.3	52.0	65.5	23.8	280	276	27	43
1 p.m.	E.Breeze gaining in strength B2.		65.0	31.0	49.5	61.8	24.8	327	289	45	38
2 p.m.	E. breeze steady; light. B3.		62.2	31.3	51.0	63.8	25.5	258	289	18	30
3 p.m.			62.2	32.0	50.0	60.0	25.5	266	298	63	31
4 p.m.			46.1	31.4	52.5	52.5	25.8	319	257	35	29
5 p.m.			-	-	-	-	-	-	-	-	-
6 p.m.			45.0	29.5	60.0	40.0	26.5	335	304	37	29
7 p.m.	Slight E. breeze 7.D8 sunset. B2.		32.7	28.3	63.0	30.5	26.5	234	265	41	34
8 p.m.			-	27.0	62.0	27.0	26.0	144	182	39	36
9 p.m.			-	-	-	-	-	-	-	-	-
10 p.m.			-	24.5	77.0	25.0	26.0	105	170	40	35
11 p.m.			-	-	-	-	-	-	-	-	-
Midnight			-	23.5	71.0	22.0	25.0	106	176	43	56
1 a.m.			-	-	-	-	-	-	-	-	-
2 a.m.			-	22.0	70.0	20.3	24.0	100	140	29	30
3 a.m.			-	-	-	-	-	-	-	-	-
4 a.m.			-	-	-	-	-	-	-	-	-
5 a.m.	Sunrise 5.58 a.m.		-	-	-	-	-	-	-	-	-
6 a.m.	Nippy, calm morning.		-	19.0	85.0	17.0	24.0	148	200	16	21

Note: Observations made two days after irrigation during drought.

TABLE 37. Monthly observation from 6 a.m. on 27th March until 7 a.m. on 28th March, 1956.

Time	Comments	Sky in tenths	Solar rad. °C.	Air temp. °C.	% R.H.	Soil temperature °C. exposed 0"	Soil temperature °C. exposed 12"	Soil temperature °C. umbrella 0"	Soil temperature °C. umbrella 12"	**A. steingroeveri** up	**A. steingroeveri** down	**P. megacephala** up	**P. megacephala** down
	Overcast, with very light rain - does not impede ants. Calm, no wind.												
6 a.m.	Sunrise obscured, ± 6.30 a.m.	9	-	14.3	93.0	14.5	17.5	15.5	19.2	191	233	15	14
7 a.m.	Clouds breaking through - sun not through yet.	8	16.5	15.0	91.0	15.5	17.8	15.5	19.0	192	198	13	15
8 a.m.		8	23.6	16.7	81.0	18.0	18.5	16.0	19.0	218	238	25	20
9 a.m.	Still overcast. Wind S.W. moving highest branches. Activity leisurely. B3.	8	32.9	17.8	65.0	21.0	18.0	15.5	19.0	273	270	23	20
10 a.m.	" " " " " B3.	8	34.2	19.0	63.0	23.0	18.5	16.0	19.0	286	278	16	13
11 a.m.	Still overcast. Wind dropped - calm. Activity frenzied.	8	35.0	19.4	62.0	24.0	18.8	16.4	19.0	253	272	7	21
Midday	Activity frenzied. Still overcast. B2	9	28.0	18.9	59.0	22.3	19.0	16.0	19.0	310	295	11	12
1 p.m.	Wind dropped - calm. Activity frenzied. B2	9	28.0	20.4	54.0	22.3	19.3	16.3	19.0	300	321	17	12
2 p.m.	Wind freshening S.S.W. - highest branches moving. B3	10	31.1	19.8	53.0	23.0	19.5	16.1	19.0	279	297	15	14
3 p.m.	Slight S.S.W. wind - highest branches moving. B2	10	25.0	19.2	61.0	21.0	19.5	16.0	19.0	330	334	18	11
4 p.m.	No comments.	10	21.4	18.6	61.0	18.6	20.0	16.0	19.0	312	291	16	12
5 p.m.	Slight wind - upper branches moving; activity 'sub-frenzied' B2	10	18.9	17.9	65.0	17.5	20.0	15.5	19.0	290	288	13	12
6 p.m.	Calm - faint evening breeze. Sunset ± 6.05 p.m. B1	10	17.2	17.6	69.0	16.8	20.0	15.5	19.0	274	329	14	11
7 p.m.		10	-	16.9	74.0	16.0	20.0	15.5	19.0	202	237	7	13
8 p.m.	Slight breeze. Moon fairly bright. B1	7	-	16.7	76.0	16.0	19.5	15.5	19.0	188	221	6	11
9 p.m.	" " " " B1	7	-	16.4	78.0	15.8	19.0	15.5	18.8	170	203	9	12
10 p.m.	Sky clearing.	6	-	16.1	81.0	15.5	19.0	15.5	18.8	181	205	10	8
11 p.m.			-	15.8	83.0	15.3	18.5	15.5	18.5	143	187	9	11
Midnight			-	15.5	86.0	15.0	18.5	15.5	18.5	120	159	7	12
1 a.m.			-	15.5	86.0	15.0	18.5	15.5	18.5	113	162	5	13
2 a.m.			-	15.5	86.0	15.0	18.0	15.5	18.5	117	155	6	11
3 a.m.			-	15.8	86.0	15.0	18.0	15.5	18.5	119	173	4	10
4 a.m.	Sky clear - heavy dew - moon very bright.		-	15.0	89.0	13.3	18.0	15.3	18.5	117	158	6	5
5 a.m.			-	14.4	88.0	12.5	18.0	15.3	18.5	114	140	10	5
6 a.m.		1	-	14.4	85.0	12.3	18.0	15.0	18.5	130	212	9	7

IV. HONEYDEW EXCRETION BY COCCUS HESPERIDUM L.

(a) Introduction.

Apart from the fact that C.hesperidum excretes honeydew, there is no record known to me of observations on the periodicity of honeydew production by this insect. An investigation into this matter was made in relation to the rhythmic foraging behaviour of A.steingroeveri. The problem is to what extent may the excretion of honeydew by the scales influence the foraging of the ants. Since the activity of the ants is primarily restricted by a temperature threshold, the possibility exists that the scale insects are similarly affected and cease excreting honeydew at low temperatures; in which case the cessation of ant foraging may be synchronised with the absence of honeydew.

Herzig (1937) found increased sap uptake and respiration took place in aphids attended by ants. My investigations were confined to the study of honeydew excretion by Soft Brown Scales without ant stimulation, with a view to finding if (a) there is a diurnal or periodic excretion of honeydew, and (b) to what extent it is controlled by temperature.

Bodenheimer (1951) reports that C.hesperidum ejects honeydew forcibly. My observations, made independently and without the knowledge of Bodenheimer's findings, confirm this. Pesson (1933) has examined the internal anatomy of some species of Pseudococcinae, and suggests that honeydew is squirted out in the following way. The rectum is sac-like, chitinous, and bound by both longitudinal and transverse bundles of muscle. When the rectum is full the muscles contract, compressing the rectum, which causes the honeydew to be shot out. A similar mechanism possibly operates in C.hesperidum. Smith (1937) found that Myzus persicae F. (Aphididae) kicks away its honeydew with its hindlegs. Both of these mechanisms are obviously designed to prevent accumulation of honeydew, which could suffocate the insects or create unhygienic conditions around them. (Way, 1954).

FIGURE 18.

Scatograph set up in position to record.

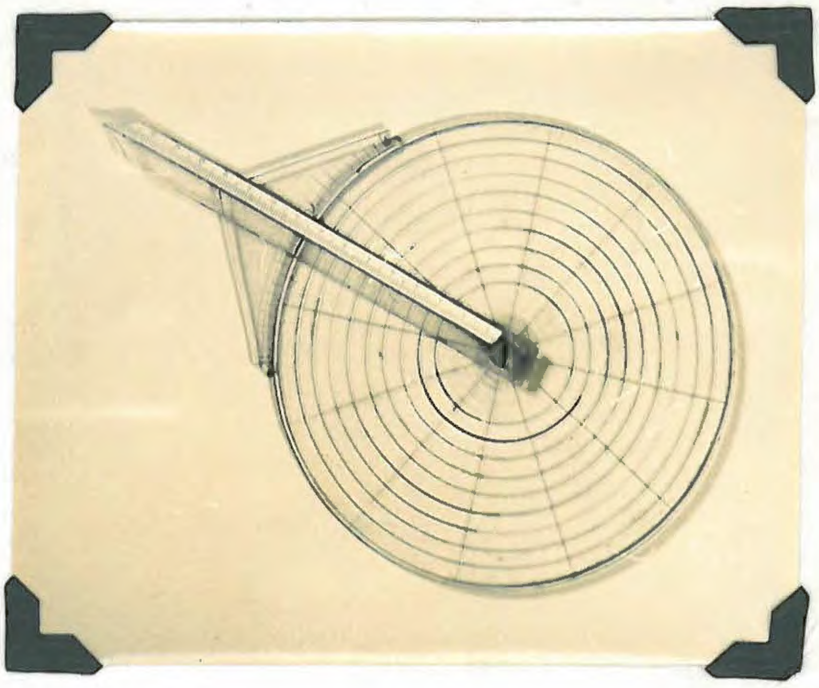

FIGURE 19.

Scatometer.

(b) Method and apparatus.

Smith (1937) found that paper treated with bromocresol green turns from yellow to blue when honeydew falls on it. Using this technique as the basis, the following apparatus was constructed to measure the rate of honeydew excretion by Soft Brown Scale insects.

(1) Scatograph. This consisted of a rotating light aluminium gramophone record 6.5 inches (5.5 cm.) in diameter attached to the hour-hand of a 12-hour alarm clock, or the rotating clock of a thermohygrograph which could be run at different speeds by using 'change-wheels' for weekly or daily records. A disc of paper treated with bromocresol green was fixed to the gramophone record with adhesive tape. The entire apparatus was placed beneath a young potted orange tree with a heavy scale infestation, the time noted, and a thin pencil line drawn on the paper disc at the point directly below the branch with the scale insects being used in the experiment. To prevent the other scales on higher branches from ruining the experiment, a piece of paper was placed below them. (Fig. 18).

(2) Scatometer. This instrument was constructed to measure the rate at which honeydew droplets were excreted and the distance they were ejected. Fig. 19 shows the instrument, which consists of a disc of 1/8th inch (0.31 cm) thick perspex, 6.5 inches in diameter, with a series of concentric rings 6 mm. apart scratched on the surface and blacked in with Indian ink.

When more than one specimen was used, the concentric rings served to separate out the rows of honeydew droplets excreted on the treated paper by individual scale insects. The disc was then divided into 12 segments, each at an angle of 30°. Attached to the centre is a moveable arm, down the centre of which a fine line was drawn, which, when the arm was moved, coincided with the lines of the 12 segments. A piece of white celluloid with 1 mm. divisions was glued down parallel to the line running down down the arm. At the distal end of the arm the structure like an arrow-head fitted closely to the rim of the perspex disc and bore another scale. One half of the total length of this scale was equal to the distance between the extremities of one segment In other words, when the three lines marking two segments were projected on to the arrow-head, and the centre line of the arm was placed above any radius line, the distal division of the arrow-head scale on either side of the arm coincided with the outer lines of two segments. The arrow-head scale contained 12 divisions on either side.

Thus the scatometer could be used to give the times of honey excretion over a twelve-hour period, and an accurate estimate of the exact time was obtained by using the scale on the arrow-head, each small division representing 5 minutes.

To take the readings, the disc of indicator treated paper was placed underneath the scatometer. Then the scatometer was manipulated until it coincided in terms of time with the blue mark of a hoheydew droplet which had fallen at a known time. From this setting the times when the remainder of the drops were ejected could be read off by placing the line on the arm over the droplets and then either adding or substracting the times on the arrow-head scale from the hour (segment lines).

The scatometer could not be used to record the times of excretion on a weekly scatograph. In such cases the paper discs was divided into seven segments with pencil lines.

(c) Experiments and results.

Experiment (1).

In the first experiment a thermohygrograph with weekly change wheels was placed beneath Soft Brown Scale insects on a small orange tree in a room which was maintained at a temperature of about 26°C. at night, but exceeded this temperature during the day. Fig. 20 shows the results over a period of three days. The arrows on the scatograph indicate the tendency for scale to reduce the rate of production, and distance of ejection, of honeydew droplets at about midday. This suggests that at high temperatures, the rate of honeydew excretion is reduced. However, at about 11 p.m. there are also indications of a slight reduction in the excretory rate.

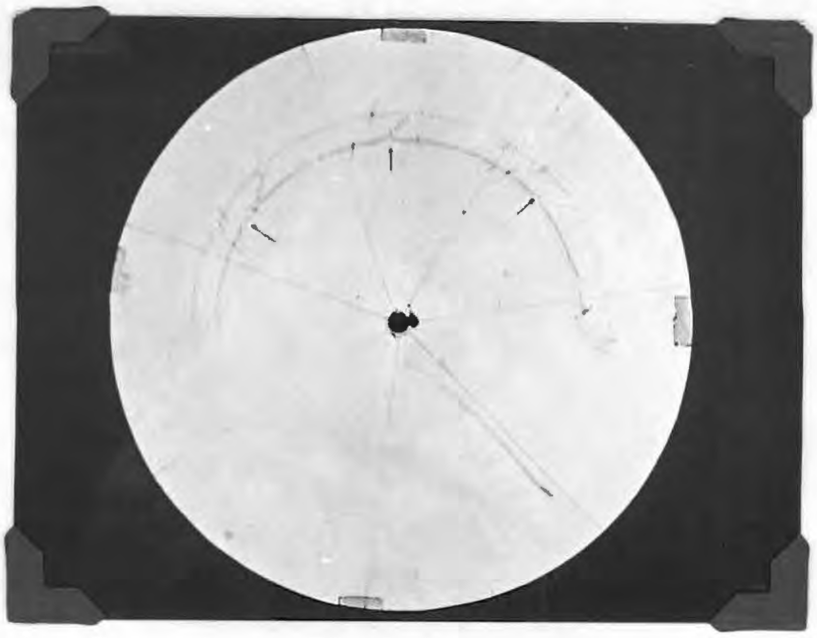

FIGURE 20.

A Scatograph record of honeydew excretion by two scale insects over a period of three days. Each segment represents one day.

Results.

From the two tracings of honeydew droplets on the scatograph (Fig. 19) over a period of three days, the following results were obtained.

TABLE 38.

Day:Specimen	No. drops			Average No. Drops	
	1	2	3	per day.	per hour.
1	41	43	39	40.7	1.71
2	45	39	34	39.3	1.64
Total:	86	82	73	40.0	1.67

Thus at about 26°C. Soft Brown scale excretes on an average over 1.5 drops per hour.

At approximately the same temperature (26°C.) Smith (1937) found that M.persicae produced honeydew at different rates depending on the stage of development and the crowding of individuals. Grouped pregnant females defecated on the average of 1.3 times per hour, while isolated females produced

3.0 drops per hour. Grouped and isolated 4th instar nymphs excreted an average of 1.5 and 3.1 drops per hour, respectively.

The rate of excretion by grouped aphides agrees fairly closely with my observations on Soft Brown Scale (Table 38). However, my experiments are incomplete, and the effects of population density, and age of the scale insects, on the rate of honeydew excretion have not been considered.

Experiment (ii). Two scatograph records were made with a 12-hour clock in the open on two consecutive nights in November, 1955, with the view to finding out what effect the changing meteorological conditions had on the excretory rate of the scales. Perhaps this could be correlated with the decrease at night and the morning flush in foraging of A. steingroeveri.

Results

(i) 22.XI.1955. TABLE 39.

	DROPS PER HOUR													
Time	p.m. 10	11	12	a.m. 1	2	3	4	5	6	7	8	9	Totals	Average.
Specimen 1	3	4	3	2	2	3	2	2	3	1	1		26	2.36
2	2	1	1	1	2	0	1	1	1	1	0		11	1.00
3	3	3	2	1	2	2	3	2	3	1	2		24	2.18
Totals:	8	8	6	4	6	5	6	5	7	3	3		61	1.85

(ii) 21.XI.1955 TABLE 40.

	DROPS PER HOUR													
Time	p.m. 10	11	12	a.m. 1	2	3	4	5	6	7	8	9	Totals	Averages
Specimen 1.	2	1	2	1	2	1	1	1	1	1	0		13	1.10
2.	1	1	1	1	0	1	1	1	0	1	0		8	0.73
3.	1	2	1	2	1	1	1	2	1	3	2		17	1.54
4.	0	1	1	1	1	0	1	2	0	1	1		9	0.82
Totals:	4	5	5	5	4	5	4	6	2	6	3		47	1.06

The grand average of the number of drops produced per hour (1.85) from the record made on the 22.XI.1955 (Table 39)was almost the same as that recorded over three days (1.67) in the first experiment. The records made on 21.XI.1955 (Table 40) indicate that the rate of excretion was lower (1.06 drops per hour).

Excretory rates between specimens varied considerably. Some scales excreted almost twice the number of honeydew droplets as others, which may be a reflection of the different stages of development between the scales.

There is no noticeable reduction in the rate of honeydew production at or immediately after midnight. Surprisingly the records show that the scales have a tendency to produce less honeydew in the morning after sunrise.

The distances to which the honeydew is ejected varied considerably: sometimes within the same hour one of two consecutive drops was shot out 5 mm. further than the other, but there was no obvious correlation between the reduction in frequency of excretion and distance of honeydew ejection.

Further investigation is needed on the question of the factors which influence or control the distance to which the honeydew is ejected. Some specimens maintained a fairly constant ejection range of 2 mm. on either side of the mean distance, and there were no sudden changes in the ejection distance. Other Soft Brown Scales shot out their honeydew in a more erratic manner, as described above.

No temperature and humidity records were made of the conditions prevailing in 21.XI.1955 and 22.XI.1955, when the two scatograph records were obtained. Thus the honeydew production over these two periods cannot be correlated with climatic conditions.

<u>Experiment (iii)</u>. A third experiment designed to assess the effects of low air temperatures on honeydew excretory rate of the scales was made in a cold-storage room where the temperature remained almost constant at 7°C. and never exceeded 8°C.

Relative humidity remained fairly constant at about 70%.

The orange tree bearing the scales was introduced into t cold-storage room 24 hours before the scatograph records were started. Light intensity was kept at a very low level with an orange-red photographer's safety-light.

The experiment ran for 24 hours from noon on 2.XII.1956 until midday on 22.XII.1956, the results of which appear in Table 41.

TABLE 41.

DROPS PER 2 HOURS.

Time	Noon p.m. 12	2	4	6	8	10	12	2	4	6	8	10	Noon 12		Total	Av.
Specimen															Total	Av.
1.		0	1	1	1	1	2	1	1	1	1	0	0		10	.416
2.		1	1	1	1	1	1	1	1	1	0	1	1		11	.458
3.		1	0	0	1	0	0	1	0	1	0	0	1		5	.208
4.		0	1	0	1	1	0	1	0	1	0	1	0		6	.250
Totals:		2	3	4	4	3	3	4	2	4	1	2	2		32	0.333

At 7°C. the scales excrete honeydew at a much reduced rate than at higher temperatures. The average rate of excretion for the four specimens was 0.333 drops per two hours, or approximately one drop every ~~three~~ six hours. Once again some scales produced approximately twice as many drops in the same time and condition as others.

The validity of these results is questionable. Under natural conditions the scales would not have been subjected to such low temperatures for such a long duration of time. This long exposure to a temperature of 7°C. may have seriously affected the physiology of the scales. Furthermore, the absence of sunlight and the low temperature may have changed the physiology of the orange tree to such an extent that the feeding of scale insects was affected.

It is remarkable that the scales did produce honeydew under the unnatural and harsh conditions in the storage room.

(d) Conclusion.

It is reasonable to suggest that under natural conditions in orchards, the scale continues to produce honeydew at night even in cold weather, and the foraging rhythm of the ants is no correlated with the rate of production of honeydew. The resul of the '*ad. lib.*' feeding experiments lend further weight to this suggestion. Broadbent (1951) found that aphides fed and excreted during the day and at night, and also that the rate of excretion was influenced by temperature and wind. The aphides excreted more frequently at high temperatures on windless days.

It is regrettable that it was not possible to carry out any further work on honeydew excretion, especially in the field. In the only field experiment attempted, it was found that the indicator soon lost its efficacy on exposure to direct sunlight.

V. THERMOKINETICS AND FORAGING OF CREMATOGASTER OPACICEPS MAYR UNDER CONTROLLED CONDITIONS.

(a) Introduction.

Many different environmental factors have been regarded as directly affecting the foraging behaviour of different species of ants. It would be wrong to discount some factors in preference to others. Various authors mentioned above (p. 95) including Steyn (1954a), together with my observations on A. steingroeveri, have shown that numerous factors may be strongly correlated, either positively or negatively, with foraging rhythms of different ant species. The results are unsatisfying as Steyn says,

> "..... It was not always possible to distinguish or separate the effect of one of these three climatic factors (temperature, relative humidity and light intensity) from the other factors."

I, therefore, decided to examine the effects in laboratory conditions of a limited number of climatic factors on Crematogaster opaciceps Mayr, an arboreal ant which constructs carton nests in thick bush.

Carton nests are easily handled. It is not necessary to dig up and build artificial nests to house ants, as would be the case for soil inhabiting species. Most important of all, by experimenting with tree-inhabiting ants, some of the factors are eliminated immediately, especially soil temperatures and evaporation rates.

C. opaciceps Mayr is dark black in colour, which suggests that it is dependent on absorption of solar radiation to a certain extent for its body warmth (Kalmus, 1941; Gunn, 1942). However, its reactions, shown by its speed of walking and foraging intensity, to two environmental factors only, (1) air temperature, and (2) relative humidity, were considered. All other factors, except barometric pressure, were eliminated, or kept constant.

(b) Procedure.

The following procedure was adopted for the investigation A nest of C.opaciceps was housed within a constant temperature chamber which was constructed for the experiments. Then the ants were subjected to a range of temperatures at alternatively the highest and lowest humidities obtainable within the apparatus at each temperature.

A conditioning period of over 5 hours was allowed in which the ants became accustomed to each change in temperature and humidity. Then the average time for twenty ants to travel 10 cm. was determined. Also the number of ants passing to and fro from a food source for a period of 2 minutes was recorded.

From the responses of the ants to the various combinations of different temperatures and humidities, the effects of these two agents on and thermokinetics and foraging activity of the ants were determined from statistical and graphic analysis of the results.

(c) Apparatus.

(1) Box. I constructed a 'climate' box 80 cm. high by 96 cm. long, and 35 cm. wide, of 2 cm. thick flooring board. It had on two sides double windows of perspex (Figs. 21, 22.) The entire box was painted white and made as air-tight as possible to lag it against the air temperatures and humidities prevailing outside.

2. Heating; and heat regulation. Within the box a small electric fan assured good air circulation. Immediately in front of the fan stood a heating apparatus consisting of a ladder of resistance wire (0.25 Ohms). The sensitive element of a thermo-regulator was placed next to the heater (Fig. 23). The thermo-regulator contained the following parts: a sensitive element consisting of a series of vertical hairpin bends of copper piping, (9.5 mm. in diameter) 46 cm. long, which was joined by very thin metal piping (about 2 mm. in diameter, from a motor car oil pressure indicator) to the arm of a glass U-tube containing clean mercury. The metal pipes were filled with

FIGURE 21.

Front view of climate box; showing clamped doors, with observation window above the right hand door. Dew-point apparatus is situated above the box into which it leads by connecting rubber tubing. Suction syringe of dew point apparatus on left hand side. Bulb of freezing pump on the right hand side.

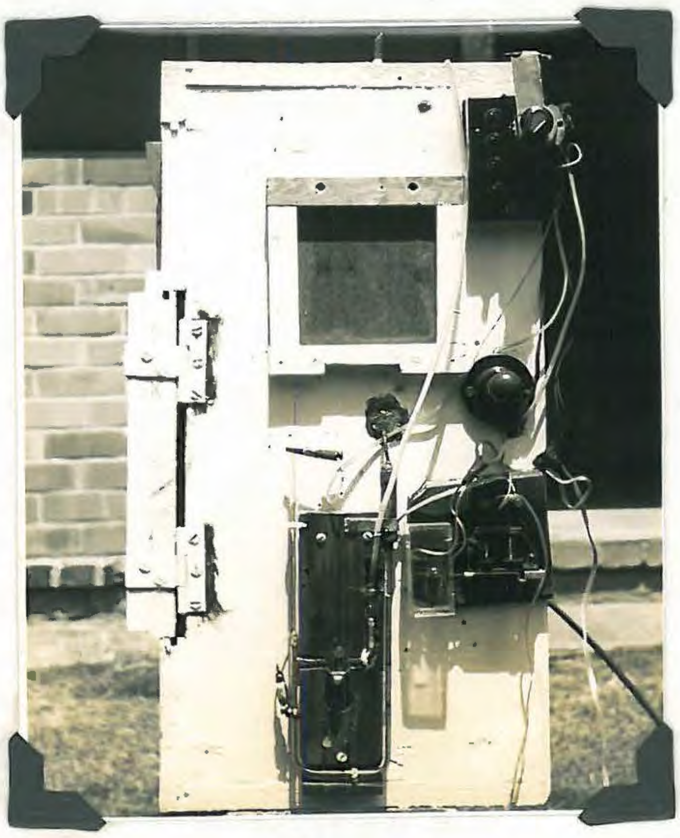

FIGURE 22.

Side view of climate box; showing control board and variable resistance, pilot light, relay, mercury-filled U-tube of the thermoregulator, and covered observation window.

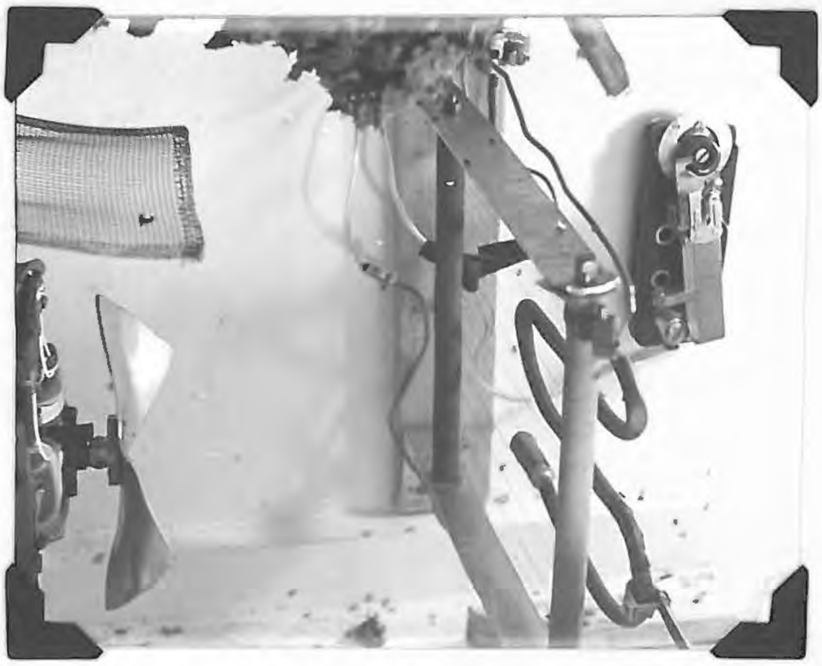

FIGURE 23.

Details of layout within climate box; showing bottom of ant nest, protective gauze, fan, harp of resistance wire of heating element, sensitive element of thermoregulator consisting of 'S'-bends of toluene-filled copper tubing, and safety thermostat.

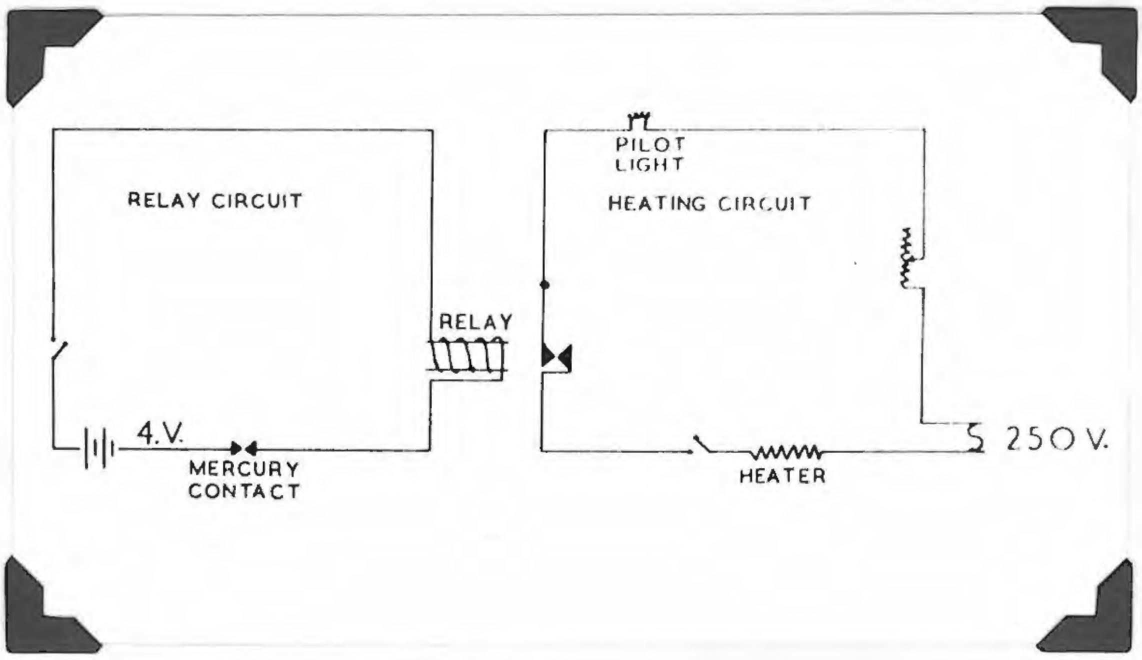

FIGURE 24.

Details of heating and relay circuits.

toluene (which has a high coefficient of expansion). Heating caused the toluene to expand and move the mercury column up the fine capillary tubing (0.5 mm. diameter) of the other arm.

A piece of fine stainless steel wire was inserted down the capillary tube, and this formed the one contact in a relay circuit with the mercury column. Another lead to the mercury was made through a piece of platinum wire inserted into the lower portion of the U-tube. The relay was constructed from a door-bell. Two 2-volt accumulators supplied current to the circuit.

The relay controlled the contacts of the heating circuit in such a way that when the relay circuit was completed the heating circuit was broken,and vice versa. This meant that when the temperature within the box reached a certain point, the expansion of toluene caused the mercury-wire contact to be made, completing the relay circuit, which broke the heating circuit. This prevented further heating. On cooling, the toluene contracted and the mercury column dropped, breaking the relay circuit and completing the heating circuit. (See Fig. 24).

A well of mercury was joined to the capillary arm by a glass tube in which a tap was inserted. Coarse adjustments to the height of the mercury column in the capillary tubing were made, either by simply opening the tap or by sucking a polythene tube attached to the well. (Fig. 22). Then the tap was closed. The method employed depended on the relative heights of the two columns of mercury, and whether a high or low temperature was required. The fine adjustment was obtained by moving the steel wire up or down the capillary tube. By combining the two adjustments, the desired temperatures were obtained. Once the thermoregulator was set, temperature variation within the box did not exceed ± 0.15°C.

The entire apparatus was housed in a cold-storage room in which the temperature never fell below 7°C., or rose above 10°C; fluctuations in room temperatures were due to only the number of times the door was opened. Heat created by the fan motor and the neon lamp within the climate box prevented the temperature being lowered below 10.7°C. The ants were subjected to a series of temperatures ranging from 10.7°C. to 30.0°C., the latter being the highest which the ants normally meet in the veld.

As a precautionary measure, a bimetallic thermoregulator was included in the heating circuit inside the box and adjusted to break the circuit at 31.0°C. (Fig. 23). In this way the hazard of fire resulting from relay failure was avoided.

The ants moved on a perspex runway. The air temperature around this was determined by placing two thermometers pointing in opposite directions on either side of the runway (Fig. 25). After calibration against a standard thermometer, the thermometers showed that the same temperatures prevailed along the entire length of the runway.

(3) Humidity. Air humidity within the apparatus was kept either high or low. For low humidities a plastic dish containing saturated salt solution of lithium chloride was placed in front of the fan. High humidities were created in the same manner, except that the lithium chloride solution was replaced with water only. To assist evaporation of moisture from the dish, cotton-wool was placed into the water in such a way that a large portion of damp cotton-wool was held above the water surface and exposed to the effects of the air being blown over it. No attempt was made to improve the efficiency of water vapour absorption by the lithium chloride solution.

Air humidity was recorded with an Edney paper hygrometer inside the box, and a dew-point apparatus which could be detached from the box. A tube leading into the box from the dew-point apparatus was stoppered with a glass tap. The dew-point apparatus was kept in another room, and only brought into the cold-storage room when samples of air were taken from the climate box. Sampling consisted of sucking air into the dew-point apparatus with a rubber bulb and then a sample of air was trapped by closing a glass tap on either side of the apparatus (Fig. 21). To ensure that only the air from within the box was sampled, the bulb was squeezed on an average of twenty times;

then relative humidity was calculated from tables according to Buxton (1931).

(4) Illumination and wind. Illumination was kept constant throughout the experiments. A neon lamp inside the climate box provided just sufficient light for the ants, and the figures on the thermometers and Edney hygrometer, to be seen. This pale orange-coloured light resembled that of a photographic dark-room, and gave about the same intensity of illumination. Furthermore, the neon lamp generated much less heat than an incandescent lamp of equal wattage. By this means the climate box could be run at a fairly low temperature. The light source in the cold-storage room consisted of two red dark-room incandescent bulbs.

The air current created by the fan did not pass directly over the ants, and was kept at a constant speed throughout the experiments. No observable ill-effects on the ants were caused by the draught. Because the efficiency of the thermoregulator was dependent on the air current, no experiments could be undertaken to gauge the effects of wind on the ants. Furthermore, when the fan was not running, a vertical temperature gradient developed in the climate box.

Thus the effects, if any, of variations in the dim light and slight wind on the ants were negligible; temperature and relative humidity were the only variables. The behaviour of the ants is to be considered as a response to these two agents.

(5) Nest and food. The carton nest was situated immediately above the fan. A piece of mosquito gauzing was placed below the nest to prevent ants from falling into the fan. A length of perspex 0.3 cm. thick, 1.3 cm. wide and 40 cm. long joined the nest to a food source on the opposite side of the box. The food source, a sugar solution in two small glass dishes, was housed in a plastic box with a small entrance hole. This helped to prevent the sugar solution from altering the humidity within the constant temperature chamber.

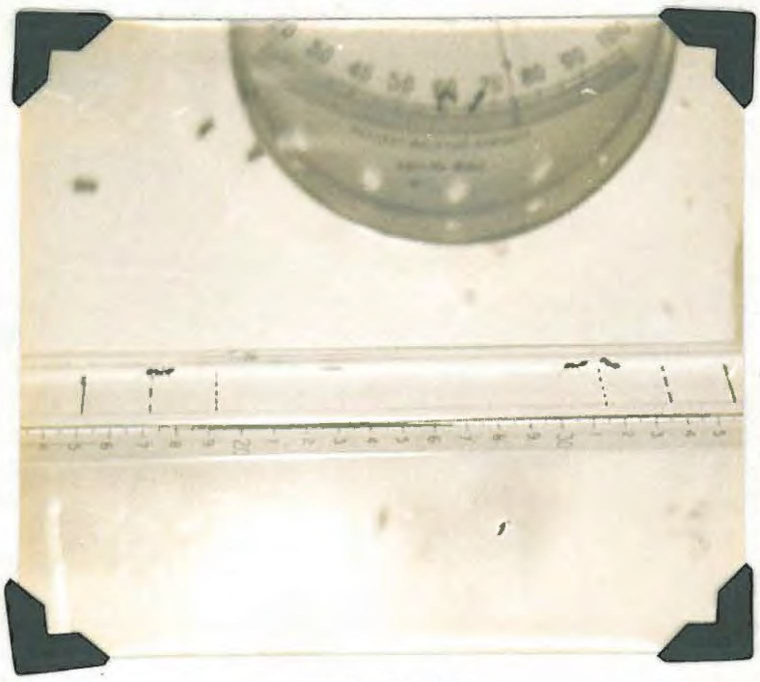

FIGURE 25.

Ants walking on perspex runway with thermometers on either side of it. A 10 cm. distance is shown by the complete cross lines. Additional distances are represented by dashed or dotted lines on either side of the complete lines. Edney hygrometer is situated in the background.

6. Runway and timing. The horizontal runway leading from the nest to the food was divided into three lengths of 10 cm. each by lines drawn across it with Indian ink. Two further lines 1 cm. apart were drawn across the runway on either side of each main line (Fig. 25). These subsidiary lines provided an additional twelve 10 cm. distances over which the ants could be timed, and speeded up the rate at which observations were made. The ants were timed over the 10 cm. distance with a summation stop-watch, and the speeds of those ants which suffered least interference from other ants were recorded. While the ants were not moving, and had paused to investigate other ants, the time lost in stopping was not included in the final result.

For each set of temperature and humidity the times taken for 20 ants to cover 10 cm. was recorded; the mean speed in cm./sec. (m), standard error of the mean (S.E.), and the difference between the means, the significance of which is expressed in terms of P, were calculated.

7. Conditioning; and air temperature humidity variation.

After each temperature change, a period of at least five hours was allowed to elapse in which the ants became conditioned before further observations were made. Table 42 below shows that conditioning is almost complete after two hours.

TABLE 42.

Time	Temp. °C.	R.H. (Edney)	m and S.E. (cm./sec.)	t	P	N.	
						To	From
5 p.m. set to	30.0	(from 20°C. and 93% R.H.)					
5.38 p.m.	30.0	85.5	3.28 ± 0.16	0:5108	>0.10	83	75
7 p.m.	30.0	86.0	3.39 ± 0.13	0.0138	>0.10	-	-
11 p.m.	30.0	88.0	3.36 ± 0.14			85	78

Where 'N' is the number of ants going to and from food in 2 mins.

Three temperatures (10.7°C., 20.0°C., and 30.0°C.) were used in the course of the investigation. Once the humidity within the climate box was set, either high or low, the air temperature was varied through the levels indicated above, and

TABLE 43.

Comparison of locomotory speeds of ants going to and from food.

Direction	Temp. °C.	%R.H.	m and S.E. (cm./sec.)	t	P
To Food 1	20.0	53.0	1.74 ± 0.06	0.827	>0.10
From Food 2	"	"	1.65 ± 0.07		
To " 3	16.4	86.25	1.60 ± 0.04	-	>0.10
From " 4	"	"	1.60 ± 0.04		
To " 5	30.4	21.5	3.50 ± 0.16	0.302	>0.10
From " 6	"	"	3.70 ± 0.12		
To " 7	31.1	37.0	3.76 ± 0.14	0.719	>0.10
From " 8	"	"	3.62 ± 0.13		
To " 9	19.2	52.0	2.10 ± 0.07	0.442	>0.10
From " 10	"	"	2.06 ± 0.05		

TABLE 44.

Main results showing the effects of different temperatures and relative humidities on the locomotory speed and foraging intensity of *C. opaciceps*.

Humidity agent.	Temp. °C.	% R.H. (Dew Pt.)	%R.H. (Edney)	m and S.E. (cm./sec.)	t	P	N.	
							To	From
$LiCl_2$	10.7	56.59	41.25	0.435 ±0.021	1.71	>0.05	3	2
H_2O	10.7	98.16	96.25	0.499 ±0.023			2	3
$LiCl_2$	20.0	41.42	45.0	1.84 ±0.052	0.19	>0.10	34	17
H_2O	20.0	70.30	93.25	1.86 ±0.071			30	29
$LiCl_2$	30.0	29.88	38.0	2.83 ±0.079	3.49	<0.01	49	43
H_2O	30.0	43.49	88.0	3.36 ±0.135			85	78

Where N is the numbers of ants going to and from food in 2 minutes.

at the end of the five-hour conditioning period the effects of the particular conditions on the ants were recorded. These included the speed of movement and the intensity of activity as reflected by the number of ants passing to and from the food source at a point on the runway in two minutes. Only those ants going to the food were timed, as their trailing was less erratic than those returning. Furthermore, it was thought unwise to introduce an additional complication of fully fed and hungry ants. However, the same colony was used in some preliminary experiments in the open under shade. In these experiments ten ants were timed going both to and from the food over a distance of 10 cm.

Table 43 shows that there is no significant difference in the speed of walking of ants going to and from food. This suggests that the condition of the crop does not influence the rate of movement of these ants.

(d) Results. These are summarised in Table 44.

The obvious discrepancies between the relative humidity derived from the dew-point apparatus and that registered by the Edney hygrometer were found to be largely due to condensation of moisture within the long rubber tubing connecting the dew-point apparatus to the climate box. Subsequent experiments using alternately long and short lengths of rubber tubing show a difference of 6% relative humidity, indicating that at the same humidity and temperature more condensation took place in the long tube. It was not possible to measure the amount of condensation occurring in the short rubber tube, or in the glass tap in which moisture was seen collecting.

It is noticeable that the humidities obtained from the dew-point and Edney apparatus are similar below 20°C., when the chilling of the rubber tubing does not markedly influence condensation. Thus, because of the inaccuracy of the dew-point method, the relative humidities registered by the Edney hygrometer are to be considered the more valid.

From Table 44 the following conclusions may be drawn:-

(i) Up to 20.0°C. the speed of C.opaciceps Mayr is directly correlated with temperature, and humidity has no effect; but

(ii) at 30.0°C. the rate of movement and the foraging intensity at the high humidity are increased above those at a low humidity.

Fig. 45 shows the relationship between temperature and speed of walking. There is an almost perfect linear relationship between the three temperatures at high humidities, while at 10.7°C. and 20.0°C. at low humidities there is close agreement with these points. At 30.0°C. at a low humidity, however, there is a distinct relative reduction in speed.

It is of interest to note that at 30°C. at the high humidity, large numbers of alates issued from the nest. These conditions resemble those under which the alates are given off under natural conditions. It is not thought that the presence of the alates affected the foraging intensity of the ants.

Regrettably, the effects of other factors on the ants could not be investigated through the lack of time. The effects of the following agents would make a worthwhile study:-

(a) radiant heat;

(b) temperature of the substratum on which the ants move;

(c) light intensity; all of which would contribute much to the interpretation of some aspects of ant behaviour.

(e) Discussion. My general observations agree with those made by Pratt (1925) on Crematogaster lineolata Say. C.opaciceps Mayr is much given to walking along a sinuous trail even on smooth surfaces, and it 'collides' with or investigates other ants, all of which makes timing very difficult. It tends to move in waves, or bunches, along the trail. Bunching is more evident at high temperatures. There is no apparent correlation of any size with speed of movement.

The effect of bunching was investigated, since the variations in number of ants crossing a point at different time

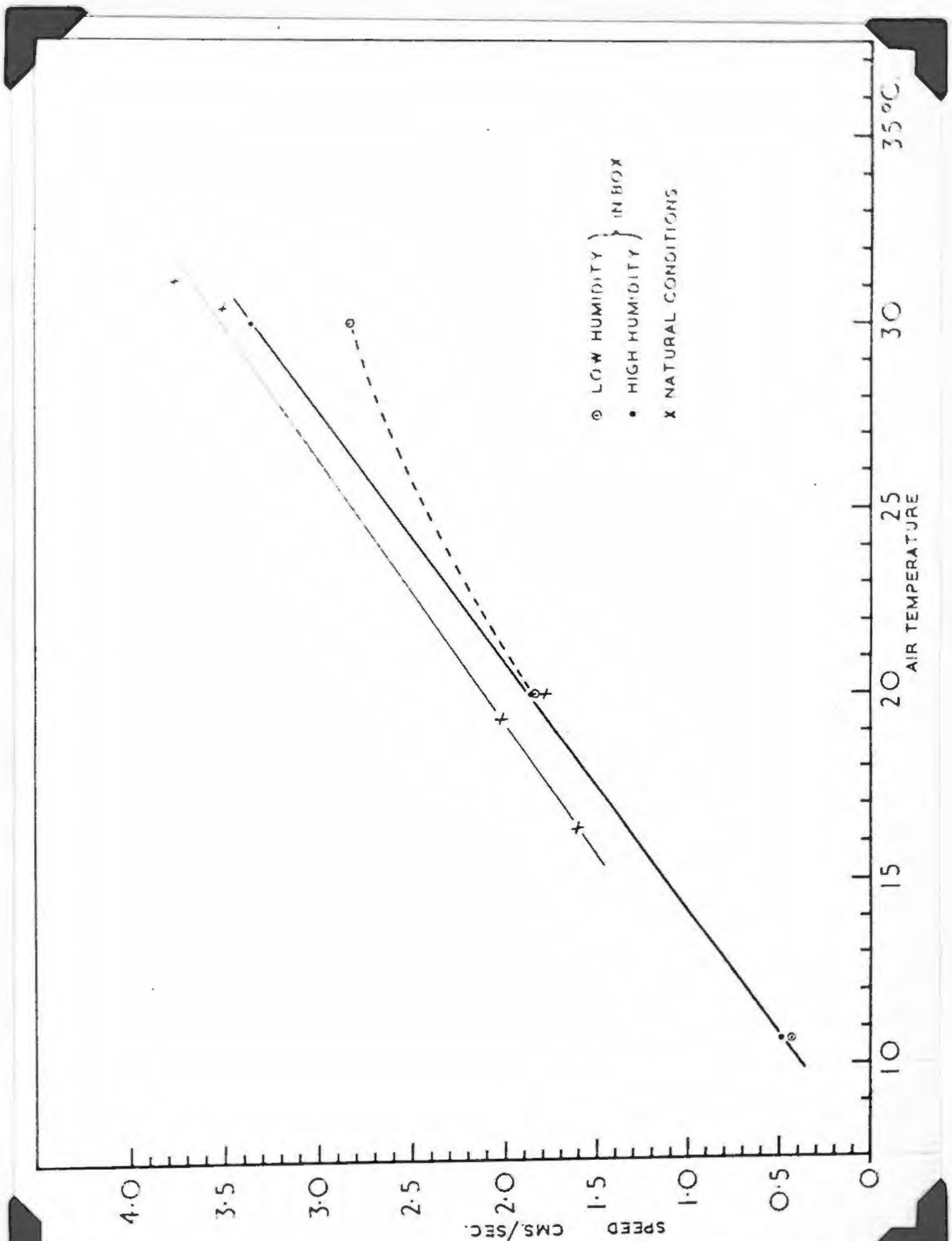

FIGURE 26.

Graph showing the correlation of speed of ant movement with air temperature at high and low humidities. within the climate box, from data in Table 44. Data taken from Table 43 are also included.

intervals may substantially invalidate the 2-minute quantitative counts of activity.

The numbers of ants passing to and from the food source at 1 minute intervals for 10 consecutive minutes at 20°C and 93% relative humidity were counted. The ants were conditioned for 6.5 hours;

Results:-

Direction	m and S.E.	
To food	16.4 - 1.06	) x 2 for) 2 minutes.
From food	14.8 - 0.91	)

Where m = mean number of ants, and
S.E. = standard error.

These results show a S.E. of - 2 ants per 2 minutes, which means that the wave effect or bunching would not have altered the results significantly.

Pratt also found that the rate of movement of C.lineolata Say has a marked positive correlation with air temperature in the open. Although he noted the presence or absence of clouds, he does not fully relate the effect of cloudiness to the speed of ant movement. He mentions once a sudden reduction in the rate of activity when a cloud shaded the trail, but neglects to take into consideration the effects of solar radiation on the ants. Furthermore, the runway temperature, which he does not record, may have had an effect on the rate of activity. In the climate box the runway temperature could not have been in excess of that of the air, and furthermore, the heating element was designed not to glow and give off radiant heat. Thus C.opaciceps Mayr, in the experiments described above, was not affected by radiant heat, or the heat of the runway, and was subjected to the effects of air temperature only.

Fig. 26 shows the graphical comparison between the data in Tables 43 and 44. It is obvious that the ants from the same nest moved at a greater speed at the same temperature in the open under shade than in the climate box (only the speeds of the ants

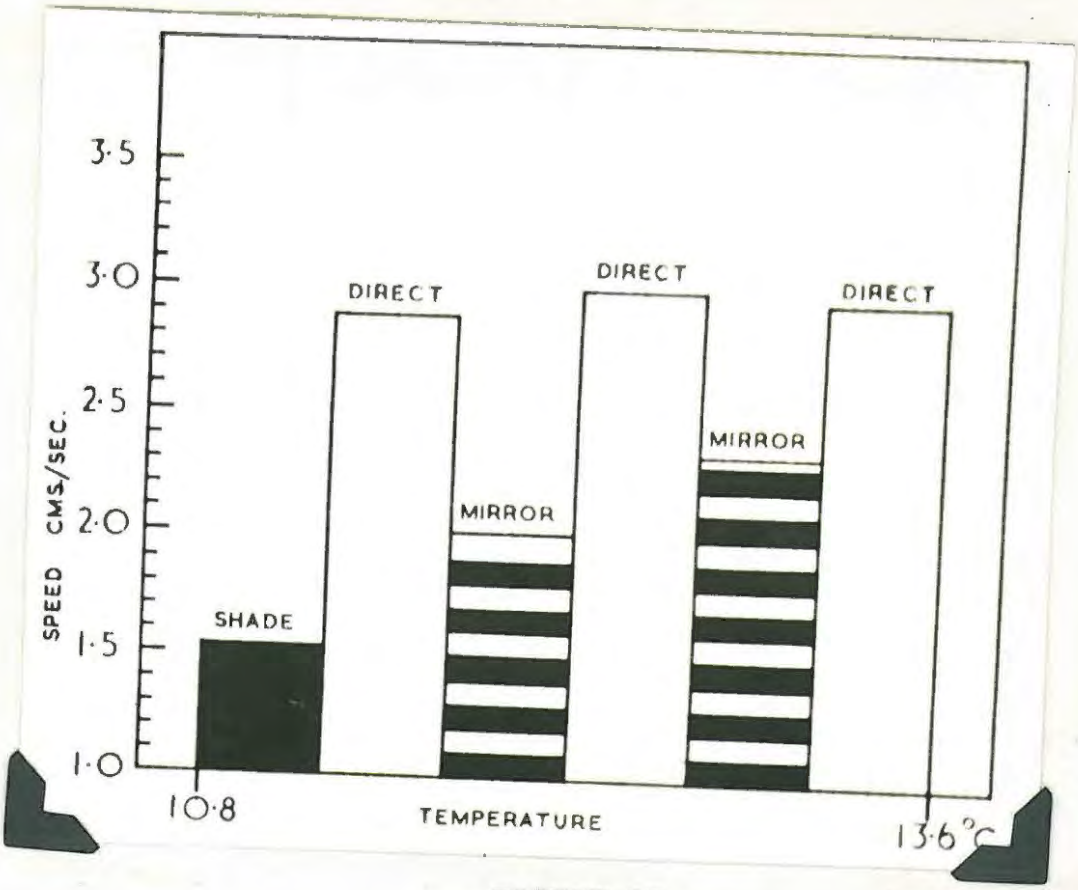

FIGURE 27.

The effect of complete shade followed by periods of exposure to direct sunlight, and then shade with reflected sunlight on locomotory speed.

TABLE 45.

	N.	m & S.E. cm/sec.	t	P
Shade 1	20	1.53 ± 0.076	12.94	< 0.01***
Direct 2	20	2.89 ± 0.073	9.63	< 0.01***
Shade 3	20	2.06 ± 0.047	10.44	< 0.01***
Direct 4	20	3.02 ± 0.079	5.43	< 0.01***
Shade 5	10	2.35 ± 0.076	4.33	< 0.01***
Direct 6	10	2.97 ± 0.122		
Shade 1	20	1.53 ± 0.076	5.87	< 0.01***
3	20	2.06 ± 0.047	3.41	< 0.01***
5	10	2.35 ± 0.076		
Direct 2	20	2.89 ± 0.073	1.142	> 0.1
4	20	3.02 ± 0.079	0.032	> 0.1
6	10	2.97 ± 0.122		

Note: N = number of observations

going to food are extracted from Table 43). Hence, when the ants do not receive direct sunlight they either derive additional heat from diffuse solar radiation (Kelly <u>et alia</u>, 1954), or respond to optical stimulation, which produces an increase in velocity of locomotion.

The effect of sunlight, in terms of solar radiation of heat and intensity of illumination, on the speed of ant movement was investigated in the open.

Ants walking over a horizontal runway were timed over a distance of 10 cm. in the early morning soon after sunrise when the first rays of sunlight struck the runway. In the first four observations twenty specimens were timed, while in the last two observations only ten ants were timed.

During the first observation the ants were completely shaded from the sun, while in counts 2, 4 and 6 they received direct sunlight. For the 3rd and 5th observations the runway was shaded from direct sunlight, but was illuminated with reflected light from a large mirror, 1.5 feet by 2.0 feet (46 cm. by 61 cm.) in size, placed a yard from the runway. No difference in the intensity of illumination could be detected with an exposure meter between the direct sunlight and that reflected by the mirror.

From Fig. 27 and the calculation (Table 45) there is a significant difference in the speed of walking of the ants between the consecutive periods when they are subjected to (1) direct sunlight; (2) complete shade; and (3) both shade and reflected sunlight. Within the limits of the apparatus, these results suggest that radiant heat and not the intensity of illumination causes a marked increase (over and above that of air temperature) in their locomotory speed.

It will be noted that the increase in speed between the the time when the ants were completely shaded and on the two occasions when they received reflected light from the mirror is correlated with the increase of air temperature during the course of the experiment (10.8 to 13.6°C.). It is noticeable (Fig. 27) that the speed of ant movement in direct sunlight is apperently not affected by the increase in air temperature. In point of fact, a decrease in speed was recorded in the last observation. This reduction may be attributable to fewer specimens (10) being taken in the sample.

By using the straight line graph in Fig. 26 as the basis for the interpretation of the data obtained from the mirror experiment (Table 45) for the speed of ant movement in direct sunlight, the following results read from the graph emphasize the effect of solar radiation on the thermokinetics of <u>C.opaciceps</u> It is assumed that the air temperature in the open never exceeded 14°C. during the course of the investigation. The highest temperature actually recorded was 13.6°C.

<u>TABLE 46</u>.

Speed in direct sunlight cm./sec. m. and S.E.	Temperature from graph °C.	Less air temperature (14.0°C.)
2.89 ± 0.073	26.75	12.75
3.02 ± 0.079	27.65	13.65
2.97 ± 0.122	27.25	13.25
	Average =	13.2

Thus the average heat derived by the ants from solar radiation was equivalent to an increase in air temperature of 13.2°C. This amount represents almost 50 per cent of the heat affecting the ants. It is not thought that the runway temperature marred the effects of radiant heat on the ants, since the runway was made of light coloured wood and was only exposed to direct sunlight during the brief periods of observation.

The experiments with <u>C.opaciceps</u> suggest that for this species under controlled conditions, it is only at high temperatures when low humidity affects their speed of movement and foraging intensity. The mirror experiment provided limited evidence of the effect of radiant heat on the thermokinetics of this ant. Unfortunately some factors were not sufficiently controlled for overmuch stress to be placed on these other noteworthy results.

(f) Conclusion. These results do not assist in the interpretation of the foraging behaviour of *A.steingroeveri* in orchards. Contrary to the findings with *C.opaciceps*, the activity of *A.steingroeveri* is curtailed by high humidities, especially at low temperatures near the temperature threshold, whereas no significant differences were recorded in the foraging intensity of the former species at high or low humidities at a low temperature.

The possibility exists that a difference may have become apparent at near freezing-point temperatures, but these temperatures could not be obtained in the climate box. By and large, it is to be expected that two ant species from different habitats would not have the same reactions to similar environmental conditions.

C. SUMMARY.

(1) A survey of the distribution of different ant species in citrus orchards was undertaken in the Sundays River Valley and the Fish River Valley in the Eastern Cape Province.

(2) (a) In the S.R.V. A.custodiens was the dominant ant, and only on a few farms were A.steingroeveri and P.megacephala found.

(b) In the F.R.V. there was an anomalous situation where, with the exception of one orchard, A.steingroeveri and A.custodiens occurred on separate farms to the exclusion of the other species.

In the orchards inhabited by A.custodiens few other species were tolerated by this ant, whereas A.steingroeveri tolerated several species, most of which were not honeydew foragers. P.megacephala occupied more territory than A.steingroeveri in the orchards studied on the farm 'Dunbar', but the trees in its territory were mostly scale-free and supported weak colonies of P.megacephala.

(3) The occurrence and territorial relationships of the three most widely distributed species - A.custodiens, A.steingroeveri and P.megacephala - has been ascribed to behavioural characteristics, brood rearing requirements, and the effects of farming practices.

(a) Both Anoplolepis species require well insolated, undisturbed soil in which to develop their brood.

(b) A.custodiens is able to nest in irrigated soil but prefers flood-free soil when it is available. On the other hand, A.steingroeveri is restricted to nesting in flood-free ground, and is only able to penetrate terraced orchards.

(c) P.megacephala appears to be able to survive in a wide variety of habitats, and is found in those portions of orchards not sought after by Anoplolepis ants.

(d) The distribution of all three species could not be attributed to different soil types in the areas investigated.

(e) Availability of food did not restrict ant territory. The loss of the honeydew supply through the fumigation of Soft

Brown Scale insects markedly reduced the foraging intensity of A.steingroeveri, but not its territory.

(f) Very little warfare occurred between A.custodiens and A.steingroeveri; the distribution of these ants was largely determined by the conditions within orchards. In warfare between A.steingroeveri and P.megacephala the former species usually obtained from the latter the territory it required.

(g) In all, interspecific territorial relationships were governed by one or other species being affected by farming operations. Although there was seasonal variation in the territory of different species there is nothing to suggest that any one of these species was able to exploit seasonal incapacitance of another.

(h) On the basis of these findings a method of ant control is suggested, which involves mulching of orchards to render them unsuitable for brood rearing.

(4) The biology and foraging behaviour of A.steingroeveri was investigated. In many respects it is similar to A.custodiens.

(a) A.steingroeveri is most active in summer and least active in winter. It has two distinct foraging patterns. In summer there is continuous foraging throughout the day and night, while in winter there is discontinuous foraging when there is no activity for part of the night.

(b) Foraging activity is governed initially by a temperature threshold at about 10°C., above which it is suppressed by high humidities.

(c) While the continuous foraging pattern prevailed in summer, it was found that the ants were active at temperatures at which they ceased foraging in winter. The explanation for this was attributed to the ants being stimulated by larvae which are most numerous at that time.

(d) Overcast skies in the early winter mornings, and strong winds retarded ant activity.

(e) The possibility of there being a diurnal honeydew flow and its affecting ant foraging was investigated both in the field and the laboratory. It was found that this factor did not account for the diurnal foraging of A.steingroeveri in winter, and confirmed the existence of the temperature threshold.

(5) The reactions of the Cocktail ant, C.opaciceps, to temperature and humidity in controlled conditions were examined. its thermokinetics and foraging activity were not affected by humidity at and below 20°C., but at 30°C. there was a distinct drop in its speed of movement and foraging intensity at a low humidity as opposed to the results obtained with a high humidity. This result is contradictory to that found for A.steingroeveri, whose activity is restricted by high humidities, which is due to the ants originating from different environments.

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('X' denotes references not seen)

E. APPENDICES.

I. ANT SIZE:

(a) Introduction.

Brian and Brian (1951) produced under controlled conditions large ants (macrogyna forms) by subjecting larvae to high temperatures and including a large proportion of sugar in their diet. They therefore concluded that these two factors accounted for the variation in ant size which they found under natural conditions between colonies receiving different amounts of insolation. Where the insolation was great, more aphids were present and the larvae accordingly had more carbohydrate in their diet. Where insolation was of a low level, few aphids were found and the ants of such environments were mainly carnivorous.

From both their field observations and laboratory experiments Brian and Brian decided that a certain temperature was necessary for the normal development of larvae. Thereafter ant size was determined largely by the amount of sugar they received, over and above proteinaceous food obtained from insect prey.

On the basis of these findings , and also because Steyn (1954) had observed that queen ants (*A. custodiens*) from orchards were smaller than those in veld colonies, I decided to investigate the possibility of there being a size different between ants occurring in orchards and the neighbouring veld.

(b) Methods.

Anoplolepis ants were selected for the investigation as they were the most readily available. In Soft Brown Scale infested orchards the ants receive a large amount of carbohydrate (honeydew in addition to other insects in the 'honeydew complex', in their diet; whereas ants in the veld feed mainly, and sometimes exclusively, on the flesh of their prey.

Anoplolepis nests occur in different microenvironments within and immediately around orchards (see p. 20) and are heated to varying degrees, ranging from total exposure to the sun of the extra-orchard mother nests to complete shading of nests beneath trees. Owing to the possible instability of the populations of individual nests through the free acceptance, and intervisiting, of individuals between different nests, no reliance may be placed on samples taken from inside the orchard. Thus the effect of shade, if any, could not be investigated. It was only possible to compare the effects of the two types of diet by taking samples of ants from extra-orchard mother nests and veld nests. Both of these types of nests received, to all intents and purposes, the same amount of insolation, but their food contained more and less carbohydrates, respectively.

Nests in the two environments were dug up and the adult ants preserved in alcohol. A random sample of over 200 ants was drawn from the material collected from each nest, then each ant was decapitated and the width of its head measured with a calibrated eyepiece micrometer. Each micrometer division represented 0.1428 mm. The results of these measurements were grouped into micrometer divisions. Thus 6 > 7 indicates that in this micrometer grouping, ants with headwidths less than seven, but greater than, and including, six micrometer divisions fell into this group.

(c) Results.

The results of the comparison of samples of *A. steingroeveri* ants from nests in the two environments may be seen in Fig. 11 and Table 1 below.

TABLE 1.

Micrometer Grouping	Veld nest no. specimens	%	Orchard nest no. specimens	%
4				
5	9	21	6	1.7
6	126	29.6	123	35.1
7	80	18.7	100	28.6
8	49	11.5	35	10.0
9	29	6.8	25	7.1
10	25	5.9	19	5.4
11	28	6.6	12	3.4
12	15	3.5	9	2.6
13	30	7.0	10	2.9
14	20	4.7	7	2.0
15	12	2.8	4	1.1
16	3	0.7	0	0.0
Totals	426	99.9	350	99.9

When the samples were compared statistically, it was found that they were significantly different ($P = < .01$), showing that diet did apparently affect the size of the ants. Fig. 11 and Table 1 show that there is a tendency for more larger ants to be produced in veld nests than in orchards, while proportionately more smaller ants were found in the latter than in the former.

Although these results are contrary to Brian and Brian's findings, they are not unexpected. It has been shown (p. 54) that most honeydew foraging is done by minor workers in orchards, and one would expect the evolutionary trend to work in that direction. On the other hand in veld nests the trend would be towards producing soldiers which are more useful in capturing and subduing large insects and other prey.

A set of samples of A.custodiens ants were taken from another farm - 'Brandeston'. On this occasion two samples were taken from veld nests, and one from within the orchard. An orchard nest was used in this instance because the orchard was highly insolated (see Fig. 7), and there were few extra-orchard mother nests, which were usually shaded to a certain extent. The results appear in Table 2 below.

TABLE 2.

Micrometer groupings.	Veld nests				Orchard nest.	
	'A'	%	'B'	%		%
4						
5	0	0.0	0	0.0	3	1.5
6	28	11.2	32	12.8	38	19.0
7	38	15.2	59	23.6	46	23.0
8	36	14.4	42	16.8	29	14.5
9	44	17.6	37	14.8	26	13.0
10	34	13.6	29	11.6	27	13.5
11	41	16.4	26	10.4	15	7.5
12	21	8.4	17	6.8	8	4.0
13	7	2.8	7	2.8	6	3.0
14	1	0.4	1	0.4	2	1.0
Totals:	250	100.0	250	100.0	200	100.0

Statistical analyses of the results were:-

(1) There was no significant difference between the samples taken from veld nests 'A' and 'B' ($P = > 0.1$).

This shows that the samples taken from veld nests contained more or less the same number of specimens in each micrometer group. Furthermore, it would appear to justify the sampling method.

(2) Veld nest 'A' and the orchard nest were significantly different ($P = <.01$).

As the figures in Table 2 show, there are proportionately more soldiers (Major subcaste) present in veld sample 'A' than in the orchard sample which contained more workers (minor subcaste). This substantiates the results obtained with *A.steingroeveri.*

(3) Veld nest 'B' and the orchard nest were not significantly different ($P = >.1$).

This result is enigmatical, for although the two veld samples, 'A' and 'B', were not significantly different, sample 'A' was significantly different to the orchard sample, while veld sample 'B' was not. This is because the two veld samples were almost significantly different ($\chi^2 = 10.05$ with 7 degrees of freedom; χ^2 at the 10% level = 12.0), and when they are compared with another set of figures, the orchard sample, the difference becomes more apparent.

(d) *Discussion*.

Both of the *Anoplolepis* species mentioned above have a continuous caste system, and although three separate worker subcastes have been ascribed to them (Arnold, 1922), there are always intermediate forms or intercastes. This type of 'polymorphism' exhibited by *Anoplolepis* ants is called 'incipient triphasic allometry' by Wilson (1953). By that he means the differention of the original monomorphic stock into three separate and distinct castes is incomplete, and no true worker sub-castes can be recognised on an allometric basis. Thus one cannot recognise increases in size within any sub-caste. For this reason the choice of *Anoplolepis* species for this work was unfortunate. The effects of diet could only be measured by the relative numbers of the different sub-castes occurring in the samples. *Pheidole megacephala*, with its two distinct sub-castes, would have been a more suitable species with which to make the investigation.

It would appear that an increase in size for honeydew foraging would be of no significance to both the Anoplolepis species. However, an increase in size of Pheidole workers may occur without reducing their ability to forage honeydew, since they are considerably smaller than Anoplolepis minor workers. It may even improve their foraging ability.

There are a number of variables which must be taken into account before a study of this nature can have any value.

When one is using Anoplolepis ants it is necessary that one should ensure that the samples obtained are not affected by a portion of the population being absent from the nests. To prevent this error, samples were taken either early on winter mornings before the ants became active and started foraging, or the nest entrances were blocked up late at night and the colony dug up the following morning. This will not be necessary with Pheidole, unless one is considering the ratio of workers to soldiers, in addition to sub-caste size.

The average length of life of worker ants must be determined This allows one to estimate the percentage of the population being sampled which has developed under known conditions. The amounts of insolation and honeydew received by individual colonies must be known. Both the insolation and honeydew may vary,as the vegetation covering the soil may be removed or extended, and applications of insecticides against Soft Brown Scale will reduce the output of honeydew. Colony age is another factor which influences not only caste structure, but also the size of individuals within sub-castes (Bodenheimer, 1937). Thus comparisons must be made between colonies of approximately the same age.

For a successful field study of the problem of ant size, a small species with a discontinuous caste system in which there are no intercastes must be used, together with detailed knowledge of the diet and insolation received by each colony.

Since these conditions were not fulfilled, in that Anoplolepis ants were unsuitable; the average length of life of worker ants was not determined, and as there was no complete history of the conditions under which the different colonies lived, the investigation was brought to a halt. There was not sufficient time to carry out a similar investigation with Pheidole megacephala.

To complete the field investigation an attempt was made to maintain six separate colonies of A.custodiens in the laboratory. The colonies were given the same amount of heat; two of which fed only on honey solution, another two had a diet of meat only, while the last pair received a mixed diet of meat and honey solution.

It was found that this species of ant is very difficult to culture in the laboratory. Several of the colonies died. It was also difficult to confine the ants to isolate the colonies from each other. Thus one often found the ants crossing from one colony to another over a barrier of 'Tangle-foot', and mixing with individuals of other colonies. Because of these difficulties, work on this aspect of the investigation was suspended.

(e) Summary.

The effect of honeydew diet on orchard ants has been investigated by comparing the size of orchard ants with those from veld colonies.

The results suggest that orchard colonies of A.steingroeveri have a tendency to produce more minor workers than veld nests. Similar results were obtained with A.custodiens, but not in every case. The production of more minor workers is interpreted as being an adaptation by orchard ants to honeydew foraging. Steyn's (1954a) observation that the queens of orchard nests are smaller than those found in veld nests cannot be interpreted on that basis

(f) References.

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II. ANT CONTROL.

An Experiment Designed to Test the Efficacy of Dieldrex 15 Emulsion against the Pugnacious Ant. (*Anoplolepis custodiens*.)

By C.A. Lombard, B.Sc. (Agric.) and N.J. Myers,
B.Sc. (Hon.)

1. Object: To test the efficacy of Dieldrex 15 for the control of the Pugnacious ant in citrus orchards.

2. Site: An orchard of Brandeston Farm on the Fish River owned by Mr. M. Malcomess was selected for the following reasons:-

- (a) The trees of the orchard are high-skirted as a result of the introduction of sheep. This restricts the avenues of ingress for the ants to the tree-trunks, and application of the insecticide is thereby facilitated.
- (b) The orchard has an extremely dense ant population.
- (c) The trees are infested with Soft Brown Scale (*Coccus hesperidum*).

3. Date of Application: 14th September, 1955.

4. Experimental design: Randomised 2 tree plots replicated 4 times for each of the 5 treatments.

5. Treatments: The insecticide was applied at the following levels at a rate of about ½ a gallon per tree:-

(1) 1:10 1845 mls.
(2) 1:12 1535 mls. of Dieldrex 15 emulsion and
(3) 1:15 1250 mls. made up to 4 gallons
(4) 1:27 680 mls. solution.
(5) Controls; no insecticide applied.

6. Method of Application: The solution for each treatment was thoroughly sprayed onto the tree-trunks to a height of approximately 2 feet from the ground, and onto the soil in a 3 feet diameter circle around the base of the trunk.

7. Results. It was decided to record the effects of the insecticide after the first 12 days and at monthly intervals

thereafter.

(a) <u>12 days</u> after the start of the trials all treatments showed effective control against the ants, while control trees remained ant infested.

(b) <u>30 days</u> after treatment the results were as follows:-

(= ants present; - = ants absent)

Replication Plots		A	B	C	D
Treatment	1.	--	--	++	--
	2.	-+	-+	++	--
	3.	++	--	--	--
	4.	++	++	+-	--
Controls	5.	++	++	++	++

As the above table shows, the effectiveness of this insecticide was falling off after one month.

(c) <u>44 days</u> after treatment it was disappointing to observe that only Plot 1A was free from ants. Some measure of control was being exercised by treatments 1 and 2, there being fewer ants on the tree trunks of all 4 replicates, whereas the number of ants in treatment Plots 3 and 5 had increased, almost corresponding in number to that of the control trees.

8. <u>Conclusions.</u> It is clear from the results quoted above that Dieldrex 15 is effective against the Pugnacious Ant, but that the time over which effective control can be obtained by the present method of application is too short to allow the procedure to be used economically.

The exact factors responsible for this very poor residual effect have not been investigated. It could be that the prolong drought conditions recently experienced in the Albany district have been responsible. In practical terms, however, the point i unimportant, as the method is clearly unsatisfactory.

The possibility remains that other methods of application can be developed which, rather than attempting to protect the trees from the ants, directly attack the ants upon the soil. This would appear to be the most profitable line of investigation in the future to this area.