An investigation into the effects of ant control on scale insect populations (Homoptera, Coccoidea) of citrus trees in the Eastern Cape Province, South Africa.

by

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INTRODUCTION.

In order that the citrus industry in South Africa may be commercially developed to the greatest possible extent it is of importance that certain basic ecological problems should be investigated. Until the complex relationships between the host plant, the insect pests and their parasites and predators are known, the results of applications of either chemical or biological control must be largely a matter of chance. A certain amount of rather generalised work in this connection has already been done in South Africa, principally by Carnegie (1955), Smithers (1953) and Whitehead (1948) in the Eastern Cape Province and by Steyn (1954) in the Transvaal. The first three of these workers were content to determine which species of insects occurred in citrus orchards and made some attempts to study the biology of certain predators. Steyn went a little further when he correlated ant activity with scale insect infestations.

Without doubt the most economically important insect pests of citrus are the scale insects (Homoptera: Coccoidea). In South Africa red scale (Aonidiella aurantii (Maskell)) and mussel scale (Lepidosaphes beckii (Newman)) are considered to cause the most damage; while at certain times localised outbreaks of soft brown scale (Coccus hesperidum Linnaeus) may occur (Simmonds 1960).

In most parts of the world in which citrus is grown on a large scale much research has been directed towards the insect pests of this crop. The citrus industry of California is one of the largest and most highly developed in the world and it is therefore not surprising that the main contributions to citrus entomology have come from this region. Indeed, it is apparent that the initiative for research into many problems of citrus entomology has stemmed from work originally done in California. However, though research carried out in one country may be based on Californian work, it does not necessarily follow that the results will be the same in both instances.

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It seems relevant to consider briefly the control methods used against scale insects in California. Fumigation with hydrogen cyanide was the first successful method employed against these pests; but after some 30 years A. aurantii started to become resistant to this chemical (Quayle 1938). Shortly after World War II cyanide fumigation was replaced by the organophosphorous insecticidal sprays, parathion and malathion (Ebeling 1950). Even though these materials gave entirely satisfactory control of all the important species of scale insects, studies were initiated in 1948 on the possibilities of the biological control of these pests (DeBach, Flesohner and Dietrick 1949). These studies were undertaken because it was feared that the scale insects might eventually become resistant to the organophosphorous insecticides.

The pattern of scale insect control in South Africa has followed that of California, but has so far lagged behind in regard to biological control. This can probably be ascribed to the absence of satisfactory evidence that this form of control is economically acceptable. Based on the encouraging results obtained in America, entomologists in this country were fairly certain that some form of biological control could be put into practice; on the other hand the majority of citrus growers remained unconvinced. The present investigation was therefore carried out in an attempt to settle this controversy.

It has been known for a long time that plant-feeding insects such as unarmoured scale insects, aphids and mealybugs which produce the sweet substance known as honeydew are almost invariably attended by large numbers of ants. It is generally accepted that a form of symbiosis exists between ants and honeydew-producing insects. The ants derive a source of food from the association while the unarmoured scale insects, with their low powers of locomotion, are prevented from being drowned by their own excretory products. In South Africa the most usual scale insect

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on citrus trees which is attended by ants for the purposes of obtaining honeydew is C. hesperidum. It should also be noted, however, that citrus trees which are infested with A. aurantii only are often patrolled by ants (Smithers 1954). This species of scale insect does not produce honeydew and as far as is known it does not excrete any substance to which the ants are attracted.

Although early Chinese citrus growers thought that ants were beneficial because they attacked the scale insects, it is now realised that this is quite untrue. In 1945 Flanders showed that when honeydew-producing scale insects are attended by vigorous ant patrols, non-excreting scale insects are nearly always present as well. This type of co-incident infestation brought about as a result of the ant activity suggests that ants may be hindering the natural enemies of the scale insects. That this was indeed true was demonstrated originally by DeBach, Fleschner and Dietrick (1951). There is no evidence to suggest that the ants attack the predators and parasites of scale insects, but by their constant activity they prevent the natural enemies from eating or parasiting the coccids. In view of this it was thought that a form of biological control of scale insects could be carried out by preventing the ants from gaining access to the trees. The greater part of the present investigation has therefore been concerned with a detailed analysis of the population changes of prey, predator and parasite in the presence and in the absence of ants.

Most of the remainder of the work has been taken up by a study of the life history and feeding habits of a new species of coccinellid under controlled conditions, and also the feeding preferences of various other scale insect predators. A preliminary study has also been made of the wind dispersal of crawlers (first instar nymphs) of A. aurantii, L. beckii and C. hesperidum, a field in which surprisingly little work has been done.

I. Methods of ....../4

I. METHODS OF CONTROLLING ANTS AND THE EFFECTS ON COCCIDS AND THEIR NATURAL ENEMIES.

(i) Description of the orchards and the climatic conditions of the area :

The orchards in which this work was carried out were situated on a farm in the Fish River Valley, in the vicinity of Fort Brown in the Eastern Cape Province.

The trees, which were all of the Washington navel orange variety, were between eighteen and twenty years old. However, in spite of being comparatively old, the trees were mostly rather small; this was apparently, in part, due to an almost chronic lack of water.

These particular orchards were admirably suited to the type of investigation described below, since the trees had never been sprayed with organophosphorous materials and were last fumigated four years before the present work was begun. Even then, the fumigation had consisted of only treating occasional heavily scale-infested trees. As a result of this the natural enemies of the scale insects had had a chance to breed up to quite high levels. As will be shown later, the parsites and predators were prevented from breeding up to even higher population levels by the presence of ants on the trees. Even though natural enemy populations were fairly well developed, there were still quite considerable populations of the scale insects A. aurantii and C. hesperidum.

The climate in this region is rather harsh, having high summer temperatures and an average annual rainfall of about 380 millimetres, (Dyer 1937). The surrounding countryside, as a result of this low rainfall, supports a sparse, scrub-like vegetation to which Dyer has given the name Karroid. A discussion of the prevailing climatic conditions in the Fish River Valley region is important, especially as it has a bearing on the effectiveness of scale insect parasites. Mention will also be made of the similarity of these climatic conditions to those

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prevailing in the citrus growing regions of inland southern California.

Unfortunately there is no meteorological station at Fort Brown. However, the owner of the farm did record the rainfall and made some temperature records. The field work on this investigation was started in 1959 and the farmer's rainfall measurements for that year gave a total of 412 millimetres and 45 rain days. The shade temperature was only recorded if it exceeded 35°C. and during 1959 there were 23 such days. On 19 days the temperature exceeded 38°C. and the highest recorded temperature was 41°C. Similar records were only made for the first three months of 1960, since shortly afterwards the farm changed ownership. For these three months the total rainfall was 91 millimetres falling on 18 days. On nine days the temperature rose to above 38°C. and the maximum temperature was 45.5°C.

In order to get more information on the sort of temperatures experienced in the orchards a maximum and minimum thermometer was suspended inside one of the experimental trees during the summer of 1960-61. This was read on the first day of each month and in this way a record of the highest maximum and the lowest minimum temperature was obtained for each of several months.

Through the kindness of Dr. P. DeBach of the University of California Citrus Experiment Station I was able to obtain detailed meteorological records of the Riverside area, covering the years 1955 to 1960 inclusive. These records show that there is a striking similarity between the weather in the citrus growing region of inland southern California and that in the Fish River Valley. The main climatic difference between the two area is that southern California has the Mediterranean region characteristic of winter rainfall; while in the Fish River Valley small amounts of rain can be expected in every month.

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In Table 1, below, the highest maximum and the lowest minimum temperatures for seven months in the Fish River Valley and the six-year means of the same temperatures in inland southern California are given. The months and figures in brackets are those pertaining to the latter region.

TABLE 1.

Month.	Highest max. temp. in degrees Celsius.	Lowest min. temp. in degrees Celsius.
Sept. (March)	37 (30)	2 (2)
Oct. (April)	38 (34)	8 (3)
Nov. (May)	42 (36)	8 (4)
Dec. (June)	40 (39)	9 (9)
Jan. (July)	41 (42)	10 (12)
Feb. (Aug.)	41 (41)	12 (12)
March (Sept.)	37 (41)	6 (11)

(ii) Ant control :

There were two species of ants obtaining honeydew from C. hesperidum in the orchards. One of these, Anoplolepis steingroeveri Forel, was much more abundant than the other species, Pheidole megacephala Fabricius. The biology of these two species of ants was studied by Myers (1957) in the same orchards in which the present investigation was conducted. Since the dominant ant species, A. steingroeveri, prefers to nest in compacted, well insolated earth, Myers advocated that mulches should be used in the orchards as a means of ant control. However, since mulching is not a general citricultural practice it seems unlikely that citrus farmers could be persuaded to adopt this method. In addition, there is little evidence that mulching would effectively suppress A. steingroeveri activity.

Since Stofberg (1954) has shown that P. megacephala can be satisfactorily controlled by spraying the trunks of the trees with either dieldrin or chlordane, I have made no attempt to control this ant. However, it seems undesirable to apply insecticides to

tree ..../7

tree trunks since the deposits may be harmful to certain coccinellids pupating on this part of the tree.

In experiments to control A. steingroeveri six insecticides were used at various rates and methods of application.

Aldrin (1, 2, 3, 4, 10, 10-hexachloro-1, 4, 4a, 5, 8, 8a-hexahydro-endo-1, 4-exo-5, 8-dimethanonaphthalene) was considered to be a worthwhile insecticide to try against ants since it has been previously used to control various soil inhabiting insects such as elaterid and scarabaeid larvae, (Brown 1951). In addition, Gannon and Bigger (1958) have shown that aldrin is epoxidised to dieldrin in the soil and such a conversion may be assumed to be advantageous, since dieldrin is not only toxic to insects but also has a longer residual effect than aldrin. Also, aldrin is much less toxic to scale insect parasites and predators than, for instance, either DDT or parathion, (Bartlett 1953). Thus if a coccinellid became dislodged from the tree and fell onto the aldrin-treated ground it would stand a good chance of survival. However, after the aldrin treatments had been applied, a paper was published by Mulla (1960) which showed that when aldrin was sprayed onto the soil surface it lost 60% of its toxicity to eggs of the eye gnat, Hippelates collusor (Townsend), after only 72 hours. Also on the debit side is the fact that aldrin is fairly toxic to mammals: the oral L.D.50 value to rats being 67 milligrams of insecticide per kilogram body weight (Metcalf 1955).

Aldrin was used in three trials, the first at a 5% strength and the other two at 0.5%. The experimental plots consisted of eight trees each, of which two were left untreated and served as controls. The layout of the treated and untreated trees, for the first two experiments, is shown in Figure 1; that of the last experiment is given in Figure 2.

The insecticide was used in the form of a 40% wettable powder and in the first trial it was sprayed onto the ground beneath the skirts of the trees at a rate of 0.11 kilograms of active ingredient per tree. This is a very high rate of application and at the present price of aldrin is completely uneconomical. The experiment was started on 16th February 1960 and the results of this trial are shown in Table 2. In this, and in the following Tables, the 'ant count' refers to the number of ants ascending the trunk over a period of two minutes. An ant count of less than ten indicates that there is no organised patrol. The numbers at the head of the ant counts columns refer to Figure 1.

TABLE 2.

Effect of 5% aldrin on Anoplolepis steingroeveri, applied in the form of a suspension of the wettable powder.

Weeks since experiment started.	Ant counts on:- Treated trees.						Untreated trees.	
	1	3	4	5	6	8	2	7
0	48	42	26	54	26	23	50	46
5	0	0	0	0	0	0	38	27
13	0	0	0	50	0	0	50	31
28	0	0	0	55	0	0	63	39
37	0	0	0	21	0	0	34	35
46	0	0	0	26	0	0	64	54
54	0	0	0	70	0	0	73	61

As can be seen from the above Table there has been almost complete control of A. steingroeveri for more than one year. Tree 5 is one the edge of the orchard and the re-infestation, which occurred between five and ten weeks after the start, came from a nest situated well outside the orchard.

In the second aldrin trial the method of application was the same but the amount of insecticide used was one tenth that of the first trial. The rate of application was therefore 0.01 kilograms of active ingredient per tree. The results of this experiment, which was started on 10th April 1960, are shown in Table 3.

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TABLE 3.

Effect of 0.5% aldrin on Anoplolepis steingroeveri, applied in the form of a suspension of the wettable powder.

Weeks since experiment started.	Ant counts on :-							
	Treated trees.						Untreated trees.	
	1	3	4	5	6	8	2	7
★ 0	P	P	P	P	P	P	P	P
6	23	0	0	53	0	0	10	26
21	40	2	3	25	0	0	11	13
29	23	4	11	30	4	3	19	29
38	42	0	12	44	0	2	30	40
46	33	3	13	49	5	0	43	53

★ Initial ant counts could not be done, since I did not have a watch;

P = ants present on the tree.

It is noticeable that the two trees which very rapidly became re-infested with ants are both on the edge of the orchard. Tree 1 became re-infested between two and a half and six weeks after the start; while ants began to appear on tree 5 after only two and a half weeks.

A year after the above trials had been started a further ant control experiment was initiated, this time using aldrin wettable powder mixed with orchard soil and broadcast under the trees. This method of application was tried because it was felt that a more satisfactory control of ants might be achieved and was prompted by the fact that Whitehead (1957) had shown that dieldrin applied in this way gave good control of the Argentine ant Iridomyrmex humilis (Mayr) in vineyards. Whitehead also showed that dieldrin mixed with soil was much easier to apply, on a large scale, than the same insecticide in the form of a spray. In the present experiment the ground under each tree was treated with 25 grams of the 40% wettable powder thoroughly mixed with about 6,000 cubic centimetres of orchard soil to give a rate of application of 0.01 kilograms of active ingredient per tree. The results of this experiment, which

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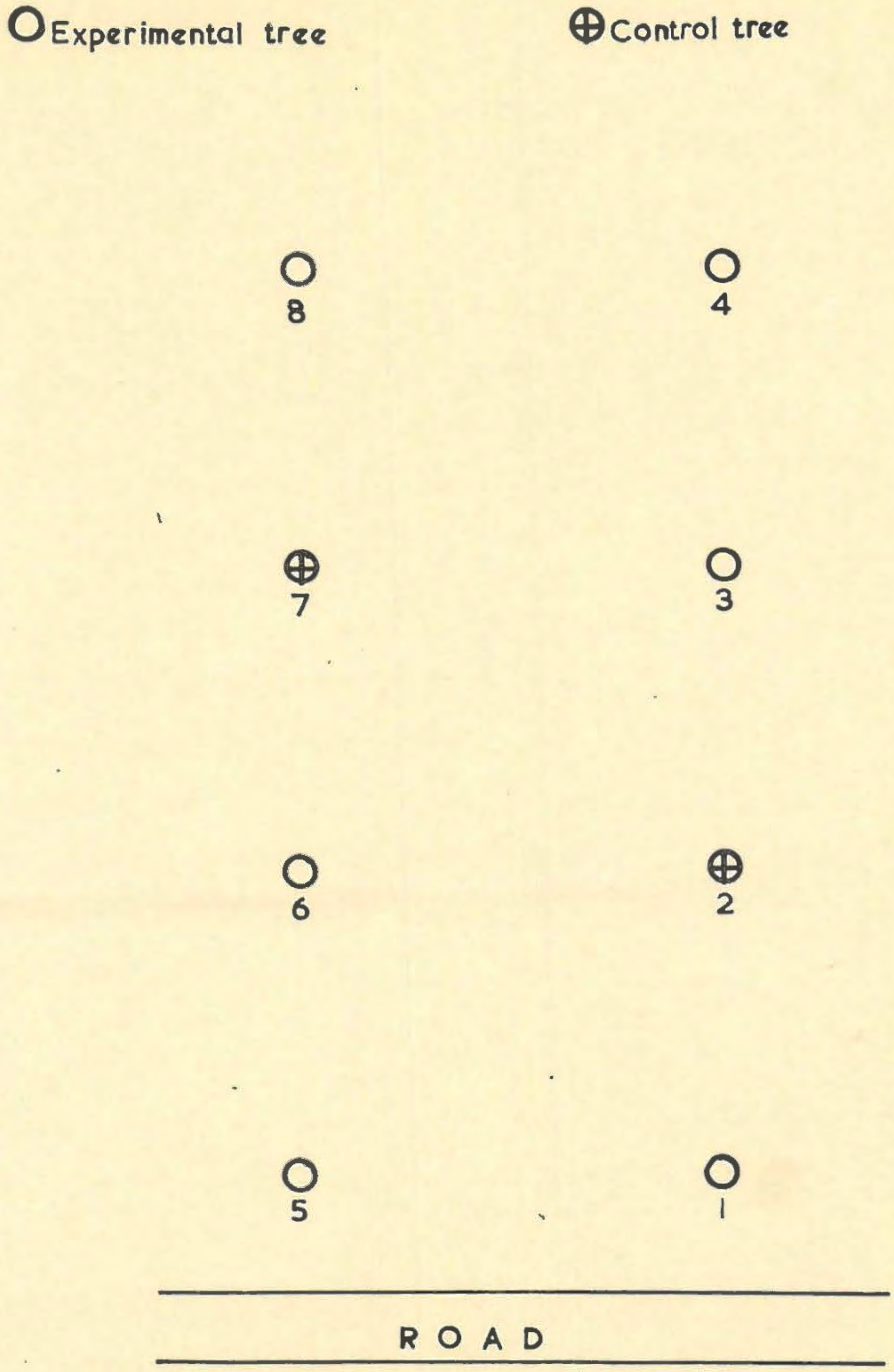

1 Layout of trees for ant control trials:
5% and 0.5% aldrin (powder mixed with water);
5% and 0.5% dieldrin (powder mixed with water).

was started on 18th April 1961, are given in Table 4 while the layout of the trees is shown in Figure 2.

TABLE 4.

Effect of 0.5% aldrin on Anoplolepis steingroeveri, applied in the form of wettable powder mixed with soil.

Weeks since experiment started.	Ant counts on:-							
	Treated trees						Untreated trees	
	1	2	3	4	6	7	5	8
0	41	22	30	20	31	38	35	25
3	0	0	0	0	0	0	30	28
7	0	0	15	0	6	5	28	24
17	0	3	20	1	4	6	30	29

Comparing Tables 3 and 4 it appears that there is little to choose between the two methods of application of aldrin. Once again it is apparent that trees at the edge of the orchard are liable to become re-infested before the others. The results of these three aldrin experiments would seem to indicate that it is not a very satisfactory insecticide to use against A. steingroeveri.

Dieldrin (1, 2, 3, 4, 10, 10-hexachloro-6, 7-epoxy-1, 4, 4a, 5, 6, 7, 8, 8a-octahydro-endo-1, 4-oxo-5, 8-dimethanonaphthalene) was the second insecticide to be used against A. steingroeveri. It is somewhat more expensive than aldrin since the latter is an intermediate compound in the synthesis of dieldrin. Dieldrin is slightly more toxic than aldrin to beneficial citrus insects, but even so it is very much less toxic than the organophosphorous insecticides (Bartlett 1953). It is slightly less toxic to the rat than aldrin, the oral L.D.50 value being 87 milligrams of insecticide per kilogram body weight (Metcalf 1955).

Dieldrin has become one of the standard household ant eradicants and, as previously mentioned, it is effective against P. megacephala. In addition, Dürr (1955) has shown that at a concentration of 0.5% it can control the Argentine ant, I. humilis,

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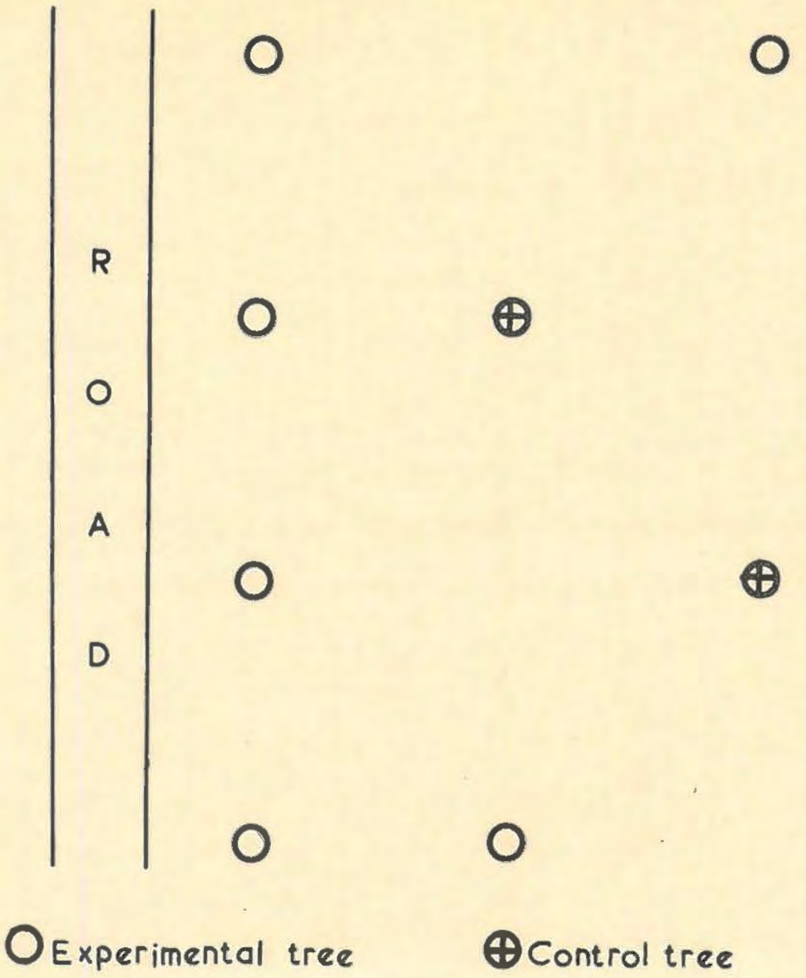
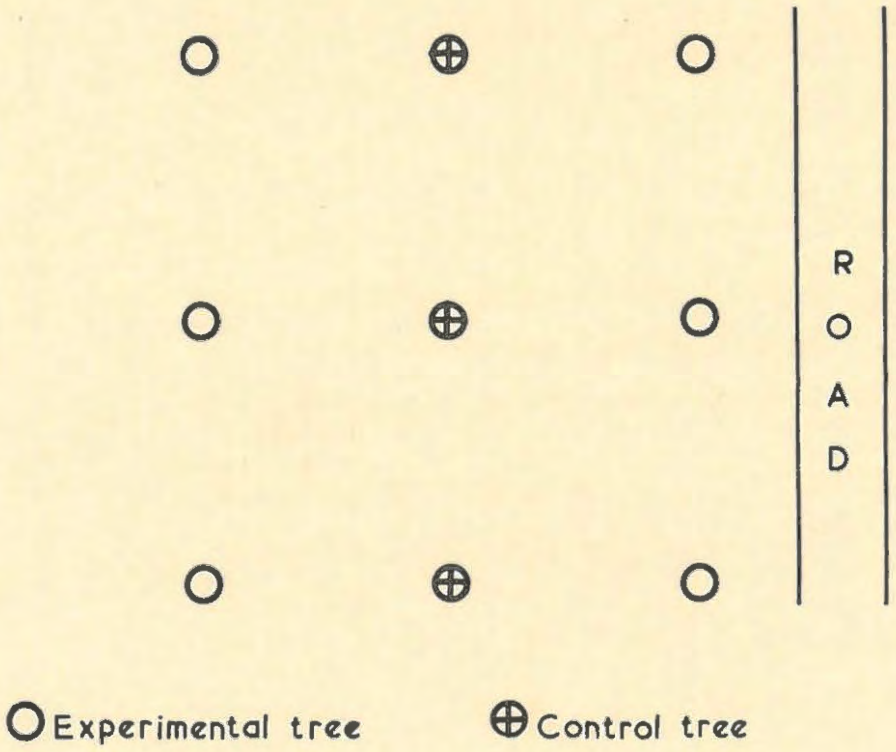


2 Layout of trees for ant control trial: 0.5% aldrin (powder mixed with sand).



3 Layout of trees for ant control trial: 0.5% dieldrin (powder mixed with sand).

in vineyards in South Africa for at least fourteen and a half months. Finally, Way (1953) working in Zanzibar has shown that 2% dieldrin is effective in controlling Anoplolepis custodiens Smith for a period of about two and a half months. He also showed that 2% DDT had virtually no effect on this ant.

As in the aldrin experiments, dieldrin was used at two strengths: 5% and 0.5%. The layout of the trees in the first two experiments is shown in Figure 1. In the first experiment 50% wettable powder is mixed with water and sprayed onto the ground under the trees. The results of this trial are shown in Table 5; the experiment was started on 16th February 1960.

TABLE 5.

Effect of 5% dieldrin on Anoplolepis steingroeveri, applied in the form of a suspension of the wettable powder.

Weeks since experiment started.	Ant counts on:-							
	Treated trees.						Untreated trees.	
	1	3	4	5	6	8	2	7
0	39	76	26	13	20	38	40	30
5	0	0	0	0	0	0	36	18
13	0	0	0	0	0	0	23	9
28	0	0	0	0	0	0	27	12
37	0	0	0	0	0	0	35	15
46	0	0	0	0	0	0	43	21
54	0	0	0	0	0	0	72	40

These results show that A. steingroeveri was completely controlled for more than a year by 5% dieldrin. However, with the present high price of dieldrin such a rate of application is uneconomic.

In the second dieldrin trial the method and rate of application was the same as that of the second aldrin trial. The experiment was started on 10th April 1960 and the results are shown in Table 6.

Table 6 ..../12

TABLE 6.

Effect of 0.5% dieldrin on Anoplolepis steingroeveri, applied in the form of a suspension of the wettable powder.

Weeks since experiment started.	Ant counts on :-							
	Treated trees.						Untreated trees.	
	1	3	4	5	6	8	2	7
✯ 0	P	P	P	P	P	P	P	P
6	6	0	0	22	0	0	51	30
21	22	0	0	36	0	0	31	25
29	24	0	0	34	5	0	50	24
38	25	0	0	31	0	0	62	21
46	46	0	0	69	0	0	37	50

✯ Initial counts could not be done since I did not have a watch;

P = ants present on the tree.

As in the 0.5% aldrin trial, the two trees on the outside row of the orchard soon became re-infested by ants from outside the orchard.

A third dieldrin experiment was started a year later, the wettable powder being mixed with soil and broadcast underneath the trees. The amount of insecticide used gave a rate of application of 0.01 kilograms of active ingredient per tree. This experiment was started on 18th April 1961 and the results are shown in Table 7; the layout of the trees is given in Figure 3.

TABLE 7.

Effect of 0.5% dieldrin on Anoplolepis steingroeveri, applied in the form of wettable powder mixed with soil.

Weeks since experiment started.	Ant counts on :-								
	Treated trees.						Untreated trees.		
	1	2	3	7	8	9	4	5	6
0	31	35	59	24	58	24	20	96	28
3	0	0	0	0	0	0	24	91	51
7	0	0	4	0	2	11	37	117	36
17	0	0	2	0	5	10	30	44	25

Comparison of Tables 6 and 7 shows that there is little difference between the effectiveness of dieldrin either applied as a spray or mixed with soil.

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The ease with which ants living outside the skirt area can re-infest a tree in a comparatively short time after application of the insecticide can probably be explained by the work of Barlow and Hadaway (1955, 1958). Initially they showed that DDT was adsorbed, in the vapour phase, more rapidly by some soils than others. It appeared that lateritic soils, which have a reddish-brown colour and a high iron content, are the most active. Later Barlow and Hadaway were able to show that when dieldrin in the form of a wettable powder was sprayed onto such soils it was quite rapidly adsorbed. Two hours after spraying at a dosage of 100 mgm/sq. ft. there was a 100% kill of Aëdes aegypti (Linnaeus) in a quarter of a minute; but 19 days later there was only a 53% kill of A. aegypti after 64 minutes. These authors also demonstrated that after 48 weeks the adsorbed dieldrin within the soil had not been decomposed in any way.

The orchard soil involved in the present investigations possessed a reddish colour which suggested that it might be described as lateritic. Soil samples were therefore tested for the presence of iron using the thiocyanate method of Snell and Snell (1949) and they gave a strong positive reaction to this element.

It therefore seems probable that the failure of both aldrin and dieldrin to prevent extra-orchard ants from gaining access to the treated trees was due to the insecticides being removed from the soil surface by adsorption. It would also explain why none of the re-infested trees were patrolled by ants from within the skirt area, since the adsorbed insecticide would prevent ants from making nests in this region. In ten of the twelve control trees (from all aldrin and dieldrin trials) the ants' nests were situated close to the base of the trunk.

The results of these experiments show that dieldrin is quite a satisfactory insecticide for controlling A. steingroeveri. The problem of avoiding re-infestation by extra-orchard ants could probably be overcome by extending the insecticide treatments to a

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short distance outside the orchard.

Telodrin (1, 3, 4, 5, 6, 7, 8, 8-octachloro-3a, 4, 7, 7a-tetrahydro-4, 7-methanonaphthalan) is the name given to a recently developed insecticide. It was formerly known as W.L. 1650 and it was under this code name that a sample was given to me for ant control trials.

The following information concerning Telodrin, together with the chemical name given above, was supplied by the Shell Chemical Company of Africa (personal communication). Telodrin is chemically related to other chlorinated hydrocarbons such as aldrin and dieldrin. It is highly toxic to mammals, the oral L.D. 50 value to rats of the 15% emulsifiable concentrate was found to be 6 milligrams of insecticide per kilogram body weight. The corresponding dermal L.D. 50 value was 5-10 milligrams per kilogram. These figures show that Telodrin should be handled with extreme care during ant control operations.

In experiments to control A. steingroeveri the insecticide was used in the form of a 15% emulsifiable concentrate. The method of application was the same as that of the third aldrin and dieldrin trials. In this instance the ground under each tree was treated with 82 millilitres of insecticide mixed with about 6,000 cubic centimetres of orchard soil. The layout of the four treated and the two untreated trees is shown in Figure 4. The treatments were laid down on 1st September, 1960, and the results of this experiment are shown in Table 8.

TABLE 8 ..../15

TABLE 8.

Effect of 0.5% Telodrin on Anoplolepis steingroeveri.

Weeks since experiment started.	Ant counts on :-					
	Treated trees.				Untreated trees.	
	2	3	5	6	1	4
0	36	55	60	20	44	74
5	0	0	0	0	68	22
9	0	0	0	0	43	12
18	0	0	0	0	85	18
26	0	0	0	0	67	31
30	0	0	0	0	80	79

Reference to Figure 4 shows that the experimental trees 2 and 3 were in the outside row of the orchard and yet after seven months there was no re-infestation of these trees by extra-orchard ants. It therefore appears that 0.5% Telodrin is even more effective than dieldrin, at the same strength, for controlling A. steingroeveri.

Thiodan (6, 7, 8, 9, 10, 10-hexachloro-1, 5, 5a, 6, 9, 9a-hexahydro-6, 9-methano-2, 4, 3-benzodioxathiepin-3-oxide) was another insecticide used in an attempt to control A. steingroeveri. The main reason for using this insecticide was that it had only recently been developed and a survey of the literature up to the end of 1960 showed that it had not yet been used against any species of ant. Lindquist and Dahm (1957) described Thiodan as an heterocyclic sulphur-containing experimental insecticide. These authors showed that it was slightly more toxic to non-resistant house flies, Musca domestica L., than DDT. The oral L.D. 50 value for rats was found to be between 40 and 50 milligrams of active ingredient per kilogram body weight. This makes it somewhat more toxic to rats than aldrin.

The insecticide was tried at one strength only, 0.5%. The experimental plot consisted of five trees, of which one was left untreated and served as a control. The arrangement of these trees is shown in Figure 5. A wettable powder containing 35% Thiodan was

used ..../16

used for the experiment; it was applied by mixing the insecticide with orchard soil as described above. The rate of application was 0.01 kilograms of active ingredient per tree.

The results of this experiment, which was commenced on 5th October, 1960, are shown in Table 9.

TABLE 9.

Effect of 0.5% Thiodan on Anoplolepis steingroeveri.

Weeks since experiment started.	Ant counts on :-				
	Treated trees.				Untreated trees.
	1	2	3	5	4
0	32	44	37	51	44
4	27	5	26	18	32
8	30	10	20	11	28

No further observations were made after eight weeks since it was apparent that Thiodan, at least at a strength of 0.5%, was ineffective in controlling A. steingroeveri.

Chlordane (1, 2, 4, 5, 6, 7, 8, 8-octachloro-2, 3, 3a, 4, 7, 7a-hexahydro-4, 7-methanoindene) is another highly chlorinated hydrocarbon insecticide which can be grouped chemically with aldrin, dieldrin and Telodrin. In view of this it might be expected to give satisfactory control of A. steingroeveri. Chlordane has, in fact, been quite extensively and successfully used to control many species of ants (Dürr 1955, Gerhardt 1953, Stofberg 1954, Young 1958). It is a comparatively safe insecticide from the point of view of mammalian toxicity; the oral L.D. 50 value for rats is 523 milligrams of active ingredient per kilogram body weight (Metcalf 1955).

In the following ant control trial, chlordane was used in the form of a 45% emulsifiable concentrate of which 25 millilitres was used for each tree. The insecticide was applied by first mixing it with orchard soil. The layout of the trees was the same as that for the Thiodan experiment (Figure 5). The results of this experiment, which was started on 1st February, 1961, are shown in

Table 10 ..../17

TABLE 10.

Effect of 0.5% chlordane on Anoplolepis steingroeveri.

Weeks since experiment started.	Ant counts on :-				
	Treated trees.				Untreated trees.
	1	2	3	5	4
0	47	12	42	13	35
4	40	0	21	0	36
8	48	0	22	0	74

Observations on ant activity were discontinued after eight weeks since it was apparent that 0.5% chlordane was exerting little effect on the ants. The ants on tree 1 were coming from a nest near the base of the trunk while those on tree 3 were from an extra-orchard nest.

Sevin (1-naphthyl-N-methyl carbamate) has, as far as I know, not been used to any extent as a soil insecticide. It appears to have been mainly employed as a spray against phytophagous insects; while it has also been used to control certain veterinary pests. Its toxicity to mammals is very low, the oral L.D. 50 value for rats being 2,000 milligrams of active ingredient per kilogram body weight (Eldefrawi, Miskus and Sutcher 1960).

I have used Sevin, at the 0.5% level, in a simple trial against A. steingroeveri. The insecticide was formulated as a 50% wettable powder and it was applied to the ground under two trees only, mixed with orchard soil. The ant counts before the Sevin was applied were 51 and 74. When the two trees were examined four weeks later, large numbers of dead ants were found in the skirt area. However, the respective ant counts were 54 and 8. This indicates that while Sevin is initially toxic to A. steingroeveri, its residual action is negligible. For this reason no further trials were carried out with this insecticide.

In conclusion, it appears that Telodrin is the most promising insecticide for use against A. steingroeveri. On the

other ..../18

other hand, dieldrin, while not so effective, is considerably less toxic to mammals. This factor may be important if unskilled labourers are employed in the mixing and application of the insecticides.

(iii) Changes in the coccid population as a result of ant control :

In order to assess the changes in population level of the coccids over a period of time it is necessary to use a sampling method. This method must be reliable enough to give a good estimate of the population but at the same time it should not be so complicated as to limit the number of trees available for sampling. There are three units which can be used to sample the coccids: fruit, twigs or leaves. Counting the number of scale insects on fruit appears to be the most common method used to assess the efficacy of an insecticidal spray treatment. However, this unit was considered to be impracticable for the present study since fruits are not available all the year round. Short lengths of twig are also often used in population studies but they suffer from the disadvantage that the high degree of curvature of the surface makes examination and counting of the coccids an unnecessarily tedious process. In the present work leaves have been used as the sampling unit since they are easy to transport and their flat surfaces enable counting to be accomplished easily and rapidly. Ebeling (1950) has shown that whichever sampling unit is used, at least 40 such units must be taken from each tree in order to get a reasonably representative sample of the population. A preliminary survey of the trees showed that A. aurantii is more or less evenly distributed over each tree, although there are slightly fewer coccids on the western quadrant than on the other three sides. Nevertheless it was considered that this difference was too small to invalidate a random sampling procedure.

The procedure adopted in taking leaf samples was as follows. Each tree was divided into eight equal sectors and from each sector six leaves were picked. Two of these leaves were taken at a height of about seven feet, two at four feet and two at two feet above the ground. In this way a total of 48 leaves were taken from each tree. The leaves were picked at random from each of the three levels, except that flush leaves were avoided. This is because such leaves are too recently formed to have acquired a coccid population.

A group of trees in each of two different orchards were used to study the effects of ant control on the coccid fauna. The two groups of trees were about a quarter of a mile apart, but were of about the same age and size. In one orchard six trees were under observation, while in the other there were five trees. In each group of trees one was left untreated and served as a control. The ground beneath the remaining nine trees was sprayed about once every two months with a 5% suspension of aldrin in order to ensure that no ants had access to the trees.

Starting in May 1959 and continuing up to September 1960, leaf samples were collected once a month from all eleven trees; while from November 1960 to May 1961 leaves were collected once every three months. The leaf samples were brought back to the laboratory in polythene bags where all the coccids on each leaf were carefully examined under a microscope and their condition (alive, parasitised, etc.) recorded. For the first eight months of the survey the following simple groupings were used. A. aurantii : healthy, parasitised, dorsal armour partly eaten by a predator, dead from undetermined causes; C. hesperidum : healthy, parasitised, eaten by a predator or a parasite, dead from unknown causes.

All living individuals from late first instar nymphs to mature males and females, together with empty scales from which males had emerged were included in the 'healthy' category. Under the heading 'parasitised' were included both coccids which were parasitised at the time of examination and also those from which a parasite had already emerged. Individuals grouped into the third

category ..../20

category of C. hesperidum were those which had been completely sucked dry. As a result of laboratory observations it was at first thought that the flattened appearance of these coccids was entirely due to attacks by larvae of the coccinellid Exochomus flavipes Thunberg. However, subsequent study of the literature indicated that the adult female parasite, Metaphycus helvolus Compere, produces the same effect in the 'soft' scale insect Saissetia oleae (Bernard) as a result of its host feeding activities (DeBach 1943). Athough small numbers of M. helvolus were reared from C. hesperidum I have never observed these parasites host-feeding on this coccid in the laboratory. But even if host-feeding does take place in the field it seems to me much more likely that most of these flattened individuals of C. hesperidum are the result of feeding by larvae of E. flavipes rather than by the attacks of adult parasites; especially since even the first instar coccinellid larvae are many times larger than the parasites. Any dead coccid which could not be put readily into either the second or the third category was included under the last heading.

Although it must be admitted that the above categories are too generalised to give a very clear picture of the events occurring as a result of ant control, it was found to be impossible to subdivide the headings when so many coccids had to be examined. In the first month of the survey over 22,000 scale insects were examined and recorded. But as time passed the numbers of scale insect on the ant-free trees declined and, starting in March 1960, the number of categories for each coccid was increased. These new categories were as follows. A. aurantii : live female, live mature male, empty dorsal armour from which a male had emerged, all other living coccids, parasitised coccid, coccid from which a parasite had already emerged, dorsal armour chewed by a predator, coccid sucked dry, dead mature female, residual mortality. C. hesperidum : live mature female, parasitised female, female with parasite emergence hole, sucked and flattened female, residual mortality.

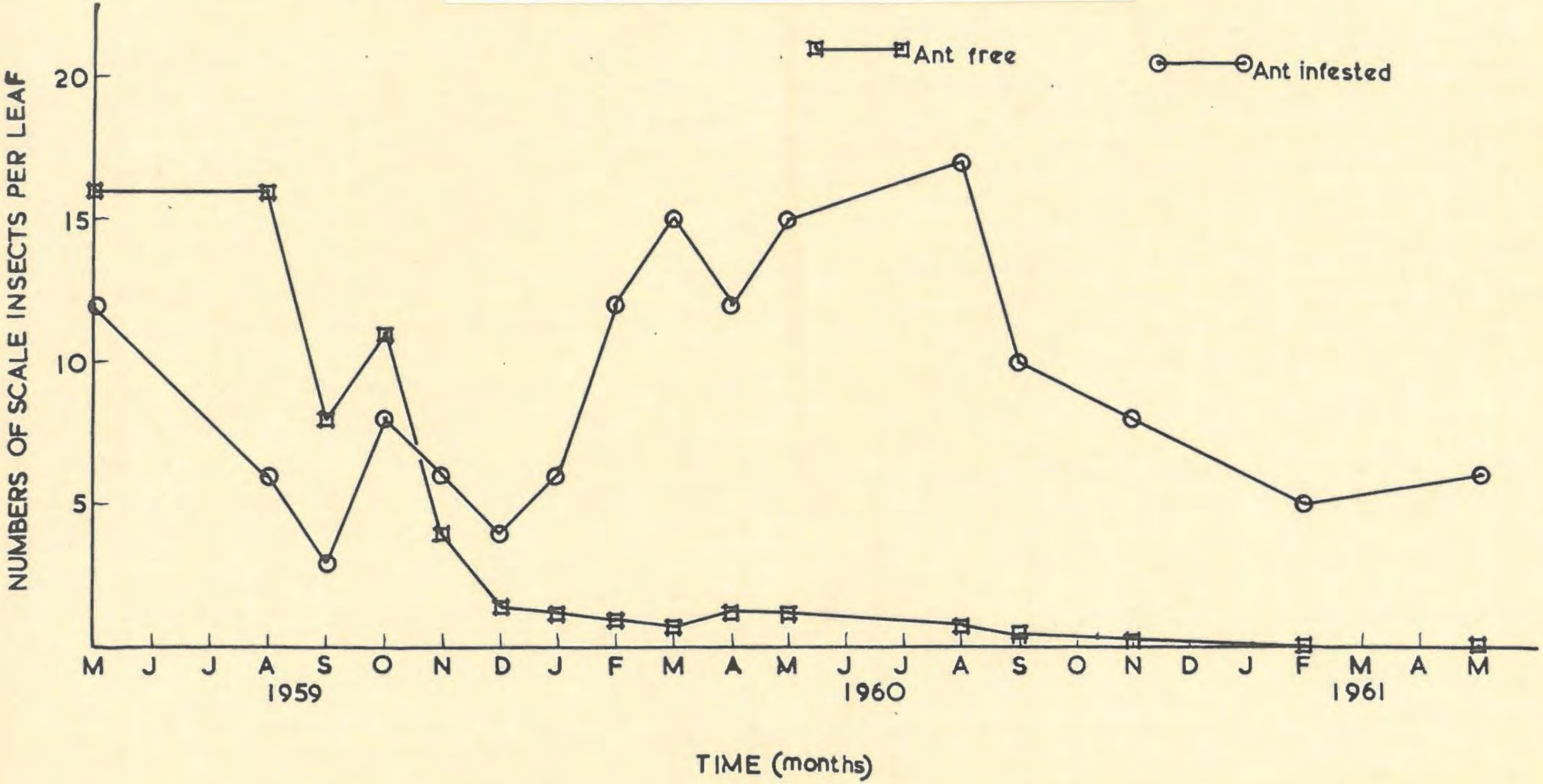
These ..../21

These new categories are largely self-explanatory but two of them require some comment. The penultimate group of *A. aurantii* comprise female scale insect which have apparently died from natural causes. The eighth group of *A. aurantii* (coccid sucked dry) comprises those scale insects which have died either as a result of feeding by a coccinellid, usually a larva, or possibly as a result of host-feeding by the adult parasite, *Aphytis* sp. The scale insects in this category show no signs of external injury, at least under the magnification used for the scale counts (x10). Since the coccids in this group often account for more than 40% of the total sample it is obviously impracticable to examine each one under a compound microscope. Many larval coccinellids, especially the early instars, feed on *A. aurantii* by making a minute hole in the dorsal armour and ingesting the prey's haemolymph by a sucking process. As I will describe in a later section, a new species of coccinellid feeds in this way in the adult stage as well. It is alleged that the parasites *Aphytis chrysomphali* (Mercet) and *A. lingnanensis* Compere destroy more coccids by host-feeding than by true parasitism (Flanders 1951). In host-feeding the adult parasite uses its ovipositor to puncture the tergum of the scale insect and then turns round and feeds on the exuding haemolymph. However, Mr. D.P. Annecke (personal communication) is of the opinion that the importance of host-feeding by the above two species is not proven since it has apparently been seldom observed under laboratory conditions. The position is further complicated by the fact that the parasite of *A. aurantii* found in the Fish River Valley may be a new species of *Aphytis* (Dr. P. DeBach, personal communication). I have watched both this species and *A. chrysomphali* ovipositing in *A. aurantii* in the laboratory but I have never observed host-feeding by either of them. Nevertheless, there are a number of well-attested instances of host-feeding by other species of adult hymenopterous parasites. Edwards (1954) showed that females of *Mormoniella vitripennis* (Walker) can only attain maximum egg production and oviposition if they are allowed to feed on the hosts' haemolymph. Clausen (1940) states that many species of Aphelinus feed on the body fluid that exudes from ovipositor punctures.

The changes taking place in the coccid population on the ant-free trees are, to some extent, unexpected. For the purpose of assessing these population changes the records from all the ant-free trees have been grouped together and similarly both control trees have been treated as one. It was decided to treat the results in this way to avoid repetition since the coccid population changes on one tree are very similar to those on another.

The results of all the monthly coccid counts have been recorded graphically and Figure 6 shows the decline in numbers of live A. aurantii as a result of two years of ant control. One would expect the population on the ant-free trees to start declining almost at once, but as can be seed from the graph this does not occur until six months have passed. The reason for this is as follows. In the absence of ants there is no mechanism for removing the honeydew secreted by C. hesperidum and this results in a greatly increased growth of the sooty mould fungus Capnodium salicinum Montagne. This fungus, which often covers the entire surface of the leaf, appears to afford almost complete protection from the predators and parasites of A. aurantii. Eventually, however, the leaves covered with C. salicinum fall off the trees and, since by this time C. hesperidum has practically disappeared from the trees, there is no further growth of the fungus. It seems possible that the leaf fall may be hastened as a result of the sooty mould fungus interfering with the photosynthetic processes. After about five months of ant control there are very few fungus-infested leaves left on the trees and from this time onwards there is a steady decline in the numbers of live A. aurantii per leaf. Fifteen months after ant control measures had been applied there was an average of less than one live A. aurantii per leaf and six months later this coccid had

6 Mean numbers of live *Aonidiella aurantii* per leaf on ant-free and ant-infested trees.



virtually disappeared from the trees. Reference to Figure 6 shows that while the numbers of live coccids per leaf on the ant-free trees were declining, those on the ant-infested trees were oscillating about a mean of nine per leaf. Although the survey continued for a period of two years the population oscillations on the control trees do not show any regular pattern with time and it may well require a much longer period to establish such a pattern. Ideally one would expect the controls to be unaffected by the changes taking place in the experimental trees. But it seems to be inevitable that when the population on the ant-free trees reaches a very low level the parasites and predators will tend to desert these trees and attempt to attack the coccids on the controls even though ants are patrolling these trees. I suspect that this is why the scale insect population on the ant-infested trees declined during the last nine months of the survey. However, the important result that arises from Figure 6 is that ant control does effectively reduce the population of _A. aurantii_.

The next thing to be considered is what are the agents bringing about this reduction in numbers of _A. aurantii_ on ant-free trees. There is a general prejudice that parasites are more important in controlling scale insects than are predators. This, according to Ebeling (1950), is because parasites are able to fly in the host-seeking stage, whereas a large part of a predator's life is spent as a non-winged larva which has relatively poor powers of locomotion and therefore a low searching ability. Furthermore, it is considered that parasites are more effective when the host population is at a low level because they can complete their larval development in one host insect, while predators in the larval stage require to feed on many coccids before becoming adults.

If, in fact, parasites constitute the main factor in the reduction of numbers of _A. aurantii_ on ant-free trees, then one would expect the rate of parasitism on these trees to be

significantly ..../24

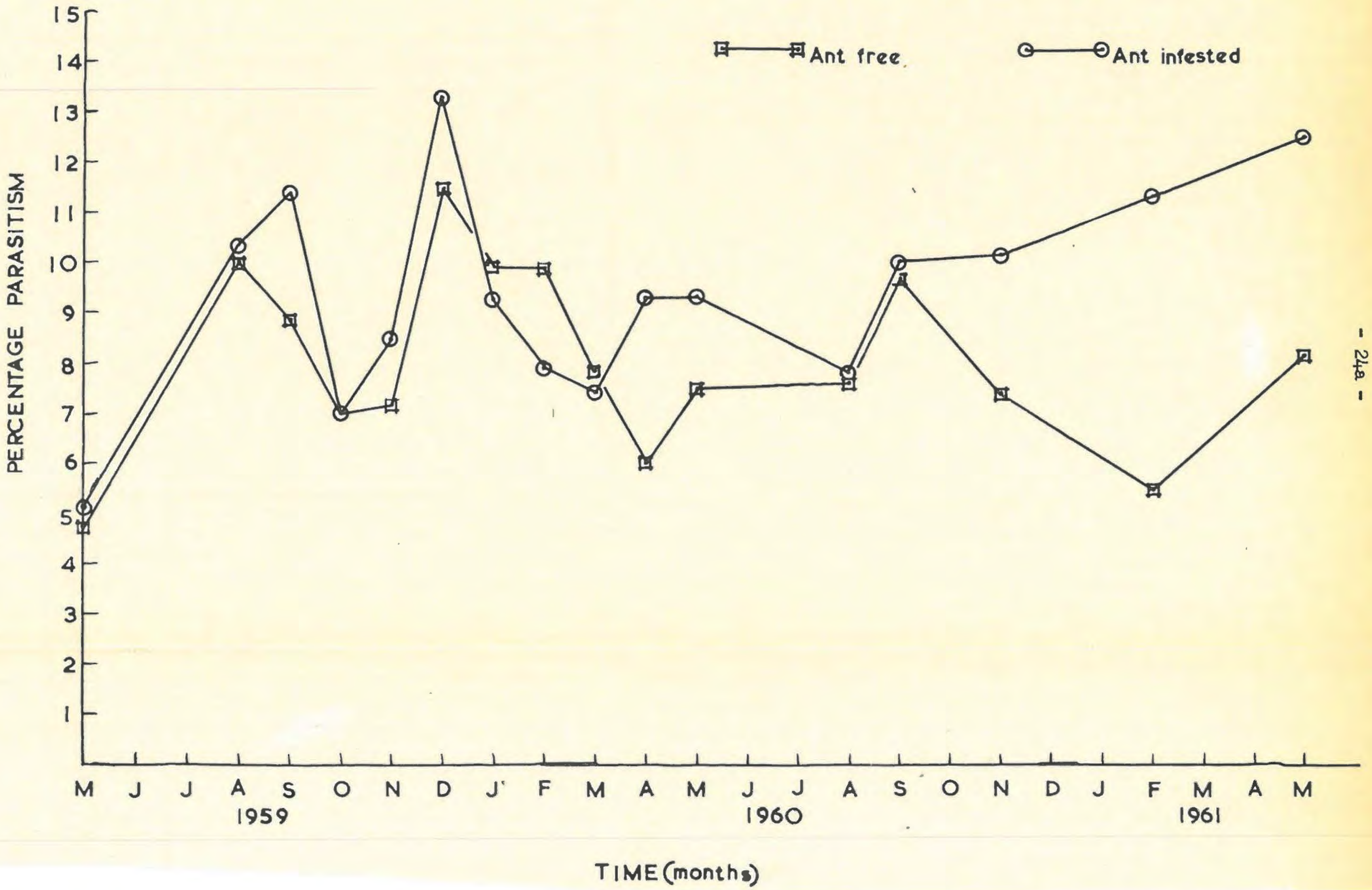
significantly higher than on the ant-infested trees. But when the percentage parasitism of A. aurantii on ant-free and on ant-infested trees is plotted against the time in months it is seen that there is almost no difference between the two. (Figure 7). The rate of parasitism represented in Figure 7 was calculated as the percentage of the total and did not take into account the fact that some of the living coccids were in those instars which would not be parasitised by Aphytis sp. in any case. However, I think the only effect of this would be to reduce the apparent rate of parasitism and would not act differentially between the ant-free and the ant-infested trees. The results presented in Figure 7 would therefore seem to indicate that Aphytis sp. has little effect in reducing the population of A. aurantii on ant-free trees.

However, there still remains the vexed problem of host-feeding by the adult parasites. As mentioned earlier, this habit is considered by some workers to be of more importance than parasitism. No critical work appears to have been done on the relative importance of the two processes, and I have been quite unable to distinguish between those coccids which have died as a result of host-feeding by adult parasites and those which have been attacked by larval coccinellids.

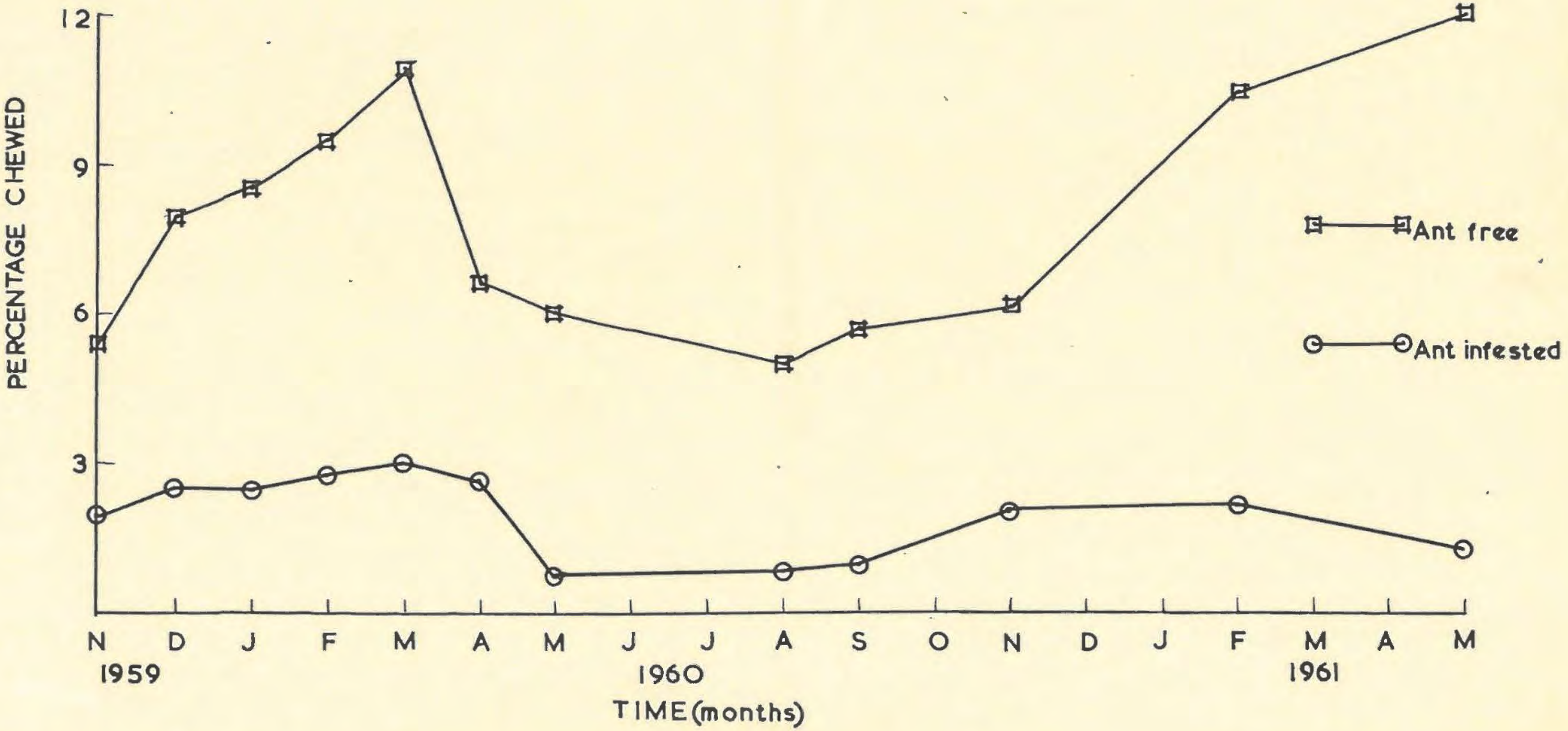
In order to assess the importance of the coccinellids which prey on A. aurantii, I have taken the category 'coccids with dorsal armour partly chewed' as the basis of this and expressed it as a percentage of the total. It is my experience after watching coccinellid larvae and adults feeding on A. aurantii in the laboratory that they first bite a hole in the dorsal armour and then eat the prey. They rarely eat the entire dorsal armour. Unfortunately the coccids falling into the above category were only recorded separately as from November 1959 and therefore the resulting graph is incomplete. The graph shown in Figure 8 clearly indicates that, in the absence of ants, predators have a better chance of attacking

the ..../25

7 Percentage parasitism of *A. aurantii* on ant-free and ant-infested trees.



8 Percentage of *A. aurantii* attacked by adult predators on ant-free and ant-infested trees.



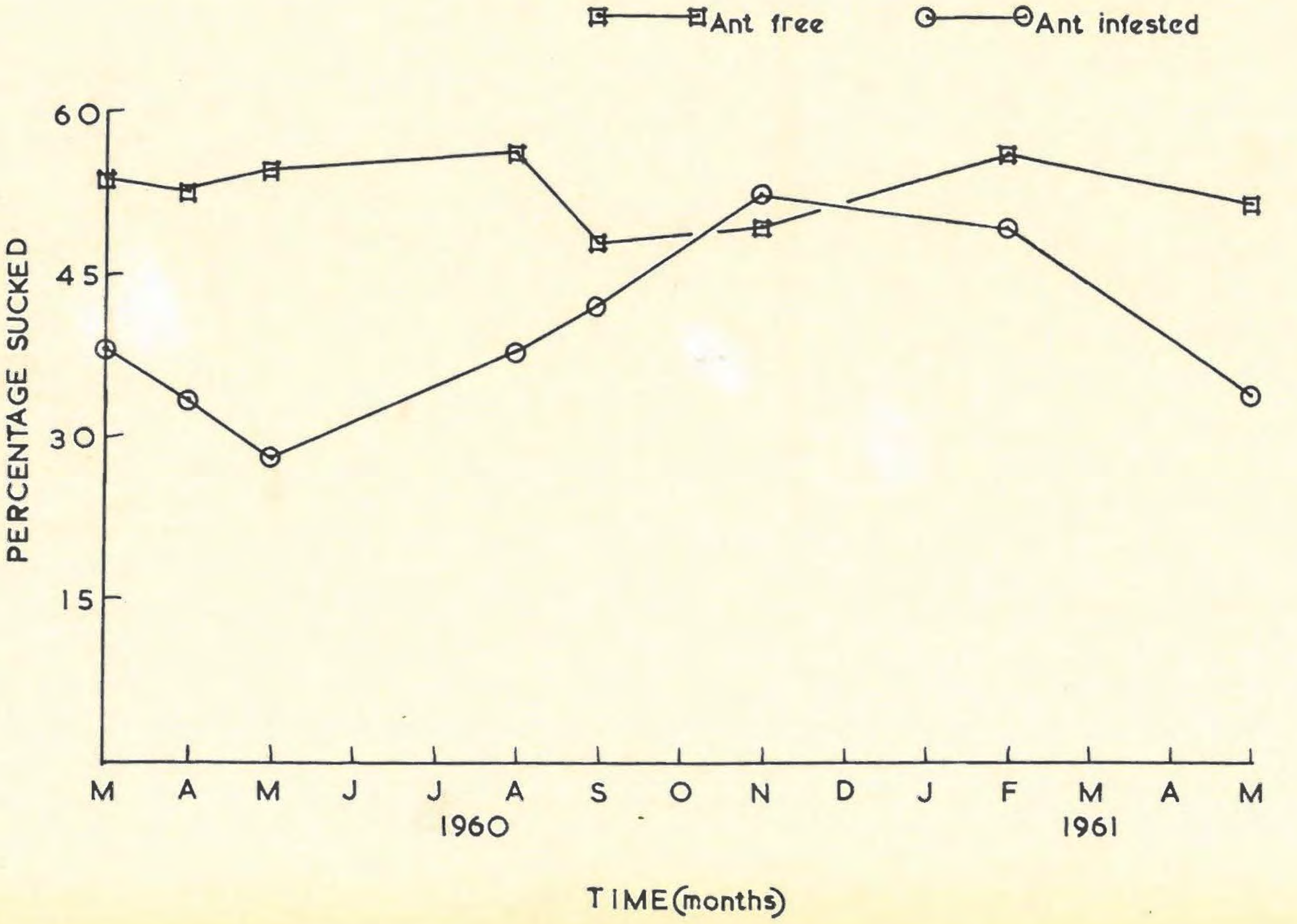
the coccids than when ants are present. It also shows, as one would expect, that there is an increase of predator activity in summer and a decrease in winter. Even when the coccid population density reaches a very low level the predators are still apparently able to exert an appreciable controlling effect on their prey.

There is one further category of dead A. aurantii to be considered. This comprises those which have been attacked by a piercing and sucking type of predator. Such predators are coccinellid larvae of various species, at least one species of adult coccinellid and, possibly, adults of the parasite Aphytis sp. I have constructed a graph showing the percentage of A. aurantii falling into this category on ant-free and on ant-infested trees (Figure 9). From this it can be seen that while there is not a great deal of difference between the two curves, that of the experimental trees is generally at a higher level than the control. Since the percentage of A. aurantii in this category on ant-free trees is, at times, as high as 56%, it seems somewhat improbable that such scale insects have died entirely from attacks by coccinellids. This is especially so since the previous graph shows that on ant-free trees the highest rate of attack is by 'biting and chewing' predators is only 12%. I think therefore that one must accept the fact that at least some of them have probably been killed as a result of host-feeding by Aphytis sp.

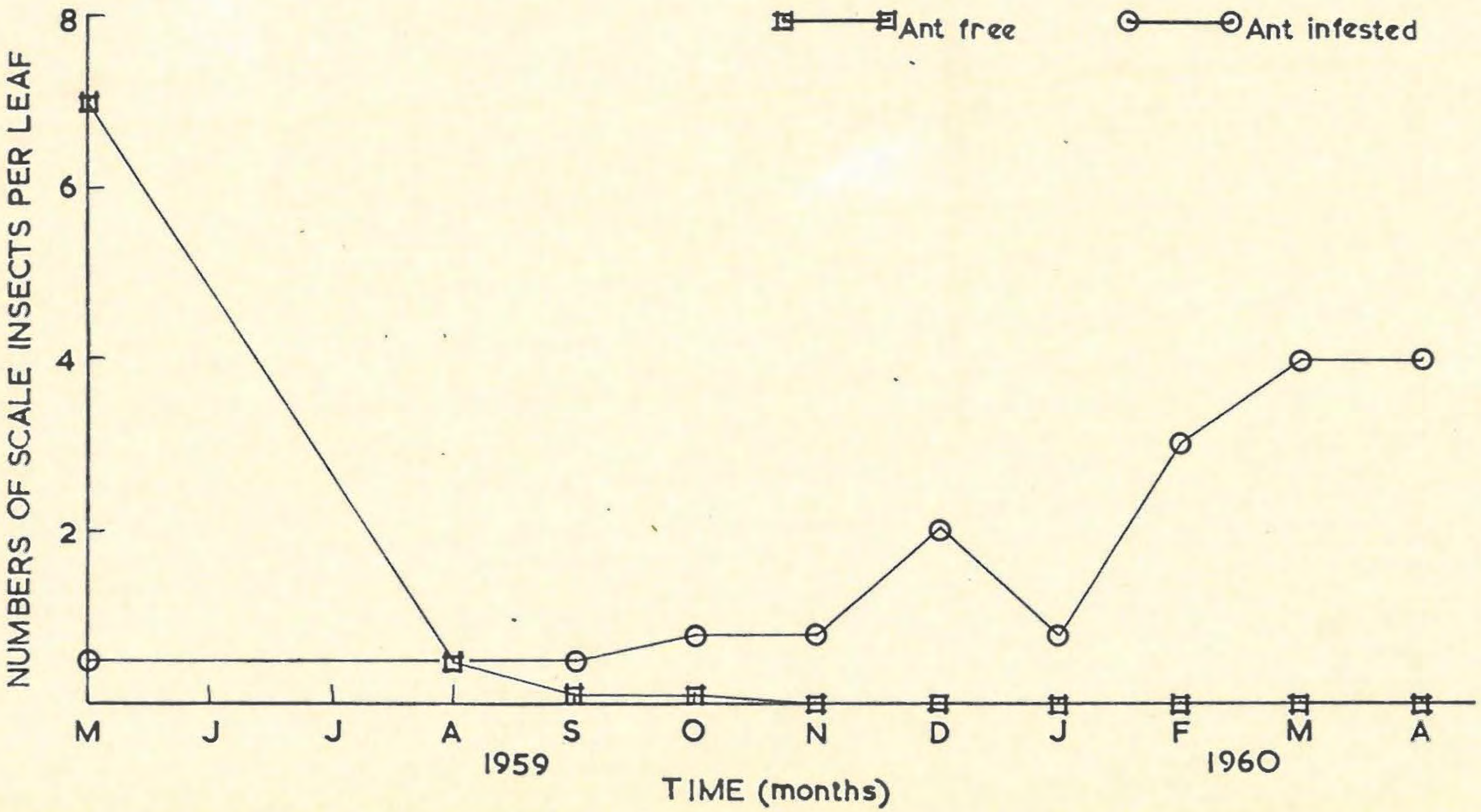
In Figure 10 I have plotted the decline in numbers of live C. hesperidum per leaf over a period of eleven months. After six months of ant control there were virtually no live scale insects left on the leaves and this state of affairs continued for the remaining 18 months of the survey. For this reason there seemed to be no point in continuing the time scale of the graph for more than eleven months from the start. Initially there were rather few coccids on the ant-infested trees, but the population increased during the summer of 1959-60 and thereafter remained at a fairly

constant ..../26

9 Percentage of *A. aurantii* attacked by larval predators and by adult parasites on ant-free and ant-infested trees.



10 Mean numbers of live Coccus hesperidum per leaf on ant-free and ant-infested trees.



constant level.

Some of the most noticeable things on ant-free trees are the clusters of pupae or empty pupal cases of the coccinellid Exochomus flavipes on the undersides of lower branches or low down on the trunks of the trees. In the laboratory both larvae and adults of this species eat C. hesperidum in preference to A. aurantii. The larvae of E. flavipes eat their prey by a sucking process and, when finished, it is left in a characteristic flattened condition. The adults, on the other hand, consume their prey entirely which makes the assessment of their importance much more difficult. A few individuals of the encyrtid parasite Cheiloneurus cyanonotus Waterston were reared from E. flavipes pupae and such parasitism may tend to limit the population increase of this predator. Although no detailed work was done on this I got the impression that the incidence of parasitism was rather low.

It is known that of the many primary parasites which attack C. hesperidum, at least two also indulge in host-feeding in the adult stage. The evidence for this behaviour appears to be much better supported than is the case for Aphytis spp. host feeding on A. aurantii. Flanders (1942) was the first to work on the host-feeding behaviour of Metaphycus helvolus Compere. In 1937 this parasite was introduced into California from South Africa for control of the "soft" scale Saissetia oleae (Bernard); although it is also known to parasitise and host-feed on C. hesperidum. Flanders concluded that host-feeding by M. helvolus is necessary for supplying proteins needed for oogenesis. A year later DeBach (1943) investigated the same problem. In this paper he says "Mortality caused by the feeding of adult females of Metaphycus helvolus (Comp.) upon the black scale accounts for the flattened and dried condition of the host"; and "Since control tests showed that M. helvolus was the responsible factor for the black scale mortality, the additional mortality was ascribed to host feeding". It is interesting to

note ..../27

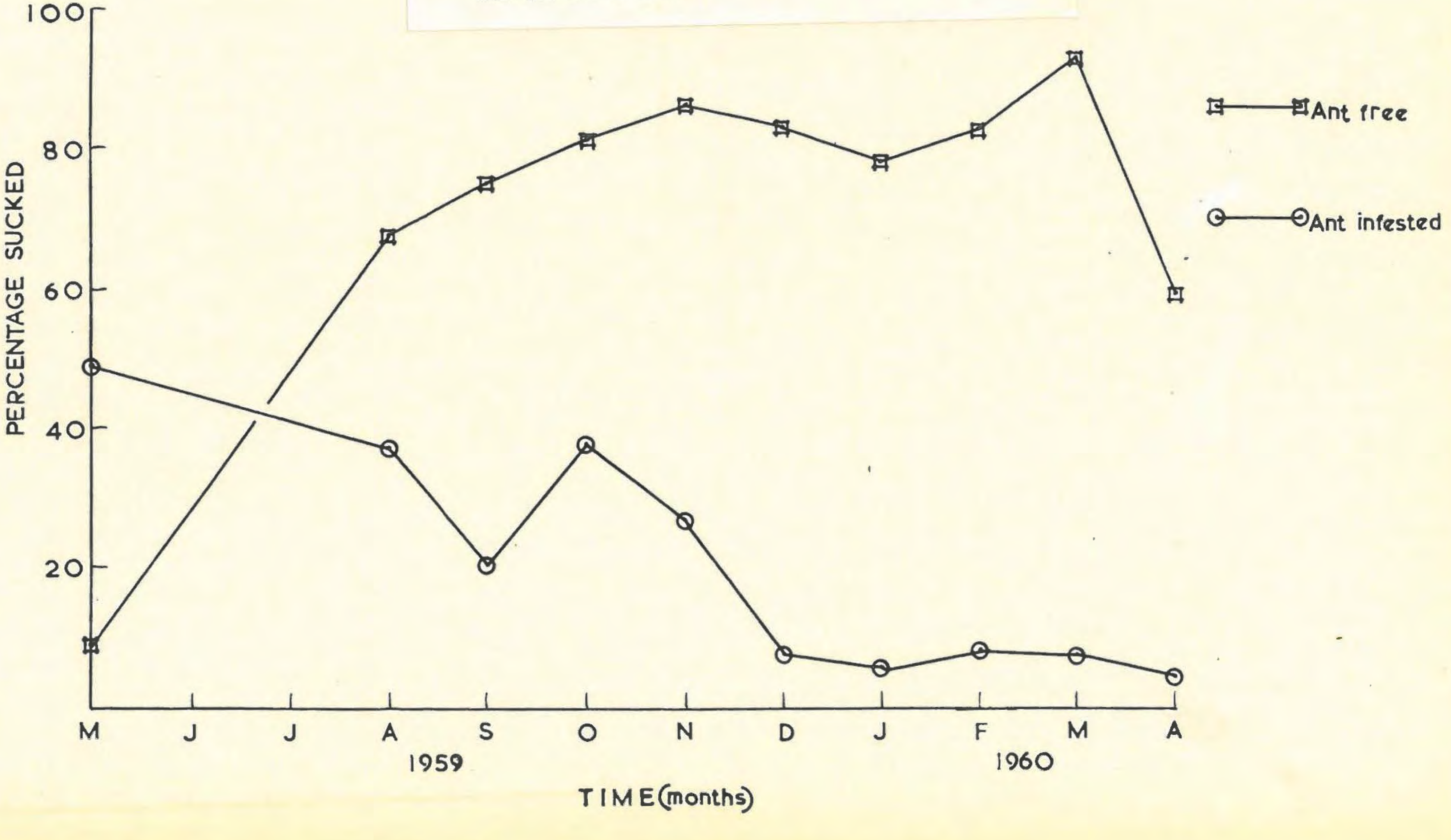
note that in this paper by DeBach no mention is made of the possibility that some of this additional mortality is a result of feeding by coccinellid larvae. According to Ebeling (1950) at least three species of coccinellid prey on black scale in California, and one must therefore conclude that the possible importance of the larvae of these beetles was overlooked by DeBach. One could perhaps argue that the poor powers of locomotion of coccinellid larvae would prevent them from being effective control agents of *C. hesperidum*. While it is true that they are unable to get from one tree to another, I have noticed in the laboratory that once the larvae of *E. flavipes* get onto a leaf infested with *C. hesperidum* they rapidly consume the latter.

Figure 11 shows the proportion of flattened individuals of *C. hesperidum* on ant-free and on ant-infested trees. While the percentage of these coccids on ant-free trees shows an upward trend with time, it is complicated by the fact that that of the control trees falls off almost as rapidly. This may be caused by interactions between the experimental and the control trees in which the agents causing flattening of the soft scale desert the ant-infested trees in favour of those trees without ants.

The remaining factor producing a decline in the numbers of live *C. hesperidum* on ant-free trees is that of parasitism by various species of Chalcidoidea. I have reared nine species of primary parasites from soft brown scale, of which the following three were by far the most common : *Coccophagus scutellaris* (Dalman), *C. anthracinus* Compere and *Euxanthellus subochraceus* Howard. The remaining six were represented by three species of *Coccophagus*, one species of *Euxanthellus* and two of *Metaphycus*, including *M. helvolus*. In addition, two species of hyperparasites were reared : *Tetrastichus* sp. (may be *injuriosus* Compere) which was very common and *Marietta connecta* Compere. Except for a few observations on ovipostion behaviour I have not had the time to study the biology of any of

these ..../28

11 Percentage of C. hesperidum attacked by larval predators and by adult parasites on ant-free and ant-infested trees.



these species under controlled conditions. As I will describe later, work of this nature has been confined to predators of the two species of coccids.

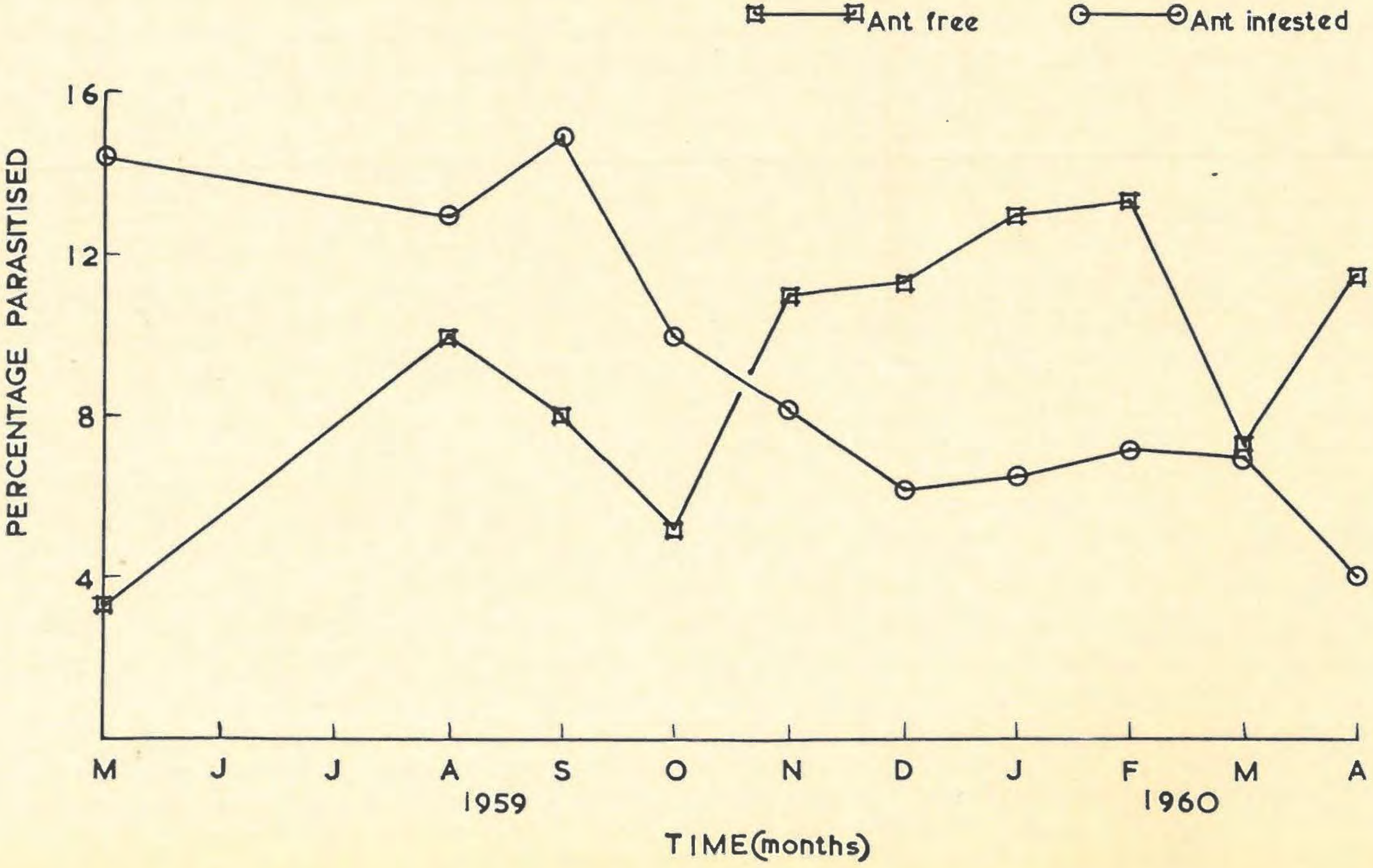
Both Cendana (1937) and Flanders (1937) have studied certain aspects of the biology of the genus Coccophagus. Cendana noted that in C. scutellaris from one to four parasites may develop in a single host and that the life cycle lasts 28 days at 28°C. Flanders studied the reproductive biology of the same species and found that, while the female always develops as a primary parasite, the male is a hyperparasite in females of its own species. Virgin females produce males by parthenongenesis and therefore behave as secondary parasites, but after mating only females are produced and the behaviour of the parent female changes to that of a primary parasite. From the point of view of the biological control of C. hesperidum it is obvious that this dual oviposition behaviour somewhat limits its usefulness. On the other hand it is known that C. scutellaris is able to oviposit very rapidly and is therefore not hindered by ant activity in this respect. This would account for the large numbers of this parasite that are often reared from C. hesperidum on ant-infested trees.

It is claimed that in the absence of ants a species such as M. helvolus will bring about a rapid decline in a population of C. hesperidum, both as a result of its host-feeding activities and its parasitic behaviour (Flanders 1943). The reason why it is unable to exert an appreciable effect on ant-attended soft brown scale is because it takes as long as five minutes to oviposit and even longer to host-feed.

In figure 12 I have plotted the rate of parasitism of C. hesperidum on ant-free and on ant-infested trees against time. A puzzling feature of this graph is the way in which the percentage parasitism on the control trees steadily falls off. Once again

this ..../29

12 Percentage parasitism of C. hesperidum on ant-free and ant-infested trees.



this may be due to migration of the parasites to the more favourable habitat on the ant-free trees. On the latter trees there is an overall increase in the rate of parasitism which was especially marked during the first three months of the experiment.

In conclusion, one can say that by preventing ants from gaining access to the trees the population density of both C. hesperidum and A. aurantii is satisfactorily reduced due to attacks by their natural enemies.

(iv) Current theories of population dynamics and their application to the coccid-parasite-predator complex :

In the previous section I have dealt with the changes occurring in coccid populations as a result of ant control. In this part I intend, firstly, to give a review of some of the more important trends of thought in population dynamics and, secondly, to see how far these ideas can be applied to the above changes.

The terms 'population dynamics' and 'natural control' are used synonymously in the literature to describe the fluctuations occurring in natural populations of animals and also the factors which cause these changes. 'Biological control' has a narrower connotation and covers the population changes brought about by deliberate manipulations of the environment by man. While these terms may appear to be self-explanatory it is as well to have them defined at the outset; it is apparent that much of the present day confusion in population dynamics is due to various words and phrases being misinterpreted by different authors.

It is well known that animal populations fluctuate about a mean density. Their numbers never rise until they are infinitely great, neither do they dwindle to extinction. The central theme in population dynamics involves a study of the factors controlling the amplitude of the fluctuations. What are these factors and

how ..../30

how do they operate?

The first serious attention given to the subject was that by Howard and Fiske (1912) who introduced the term 'facultative agencies' as applied to mortality factors. These were later renamed 'density-dependent factors' by Smith (1935), who also introduced the concept of 'density-independence'. A density-dependent factor is one whose severity of action is proportional to the population density and is usually indentified with a biotic factor. On the other hand a density-independent effect acts without regard to the population numbers and physical factors are put into this category. These useful terms have since been used by many other authors, although Solomon (1949) has pointed out that density-independent effects often operate in combination with density-dependent processes.

The next important work on the theory of population dynamics was done independently on a mathematical basis by Lotka (1925) and Volterra (1926), but their theories were later expanded and treated in much more detail by Nicholson and Bailey (1935). The latter authors consider that the effects of parasites and predators (density-dependent effects) are the most important factors causing fluctuations in the density of the host or prey populations. Physical effects, such as the weather, are thought to have some importance but are secondary to the biotic factors.

Nicholson and Bailey also make the assumption that populations of both parasites and predators search for their hosts or prey in a purely random manner. The emphasis here lies on the word 'populations' since the authors stress that even if the individuals comprising the population carry out a directed search, the searching by the populations as a whole is always random. There is indeed a certain amount of experimental evidence that parasites search for their hosts in a non-random manner. In this

connection ..../31

connection, however, Laing (1938) showed that while the preliminary search for eggs of Sitotroga cerealella (Olivier) by the chalcid, Trichogramma evanescens Westwood may be random, once it has found a host its searching behaviour becomes highly systematic. Again Ullyett (1953) reported that, if a cocoon of the moth, Euproctis terminalia Walker, is broken open in a pine forest, a swarm of the ichneumonid pupal parasites, Pimpla bicolor Bouché, appear within a few minutes, even though none could be observed previously. Clearly this occurrence cannot be described as due to a random searching pattern by the parasites. Much less experimental work appears to have been done on the way in which predators find their prey. However, Banks (1957) has studied the behaviour of three species of coccinellid larvae which feed on aphids. The newly hatched and therefore unfed larvae search for aphid colonies in a random manner. But once one aphid has been found and eaten the search for further prey becomes directed. I have observed second instar larvae of E. flavipes feeding on C. hesperidum and they behave in much the same way as those species studied by Banks. (See appendix).

It therefore seems clear that many species of parasites and predators do search for their hosts or prey in a systematic manner. The question now arises as to whether Nicholson and Bailey are justified in their assumption that populations behave randomly. For a population of insects to seek its food or oviposition sites in a non-random manner requires continual co-operation between the individuals comprising the population. Even in the case of social insects, such as bees, the initial search for food is random although later it becomes systematic. It is worthwhile mentioning that many of the critics of Nicholson and Bailey appear to have overlooked the distinction between the behaviour of individuals and that of populations.

A number of theories of parasite-host and predator-prey interactions, based on the premise of random searching by

populations ....../32

populations, are presented by Nicholson and Bailey and these are supported by detailed mathematical analyses and proofs. While one cannot doubt the validity of the latter, it seems to me that a very real problem arises when one attempts to correlate these theories with actual laboratory or field experiments. The difficulty arises because the original premises are deliberately simplified in order to make the mathematics more manageable. Thus in the simplest example presented, namely the interaction of one host and one parasite species, it is assumed that the interacting species are uninfluenced by the activities of other animals and that the general environmental conditions remain constant. Perhaps the most serious limitation is that the life cycles of the parasite and its host are assumed to be synchronous. It is obvious that all these stipulations would make the experimental verification of the mathematical theory difficult to accomplish under laboratory conditions and virtually impossible in the field. These mathematical theories can, therefore, at best only give an indication of the sort of population fluctuations that might be expected under natural conditions. However, the work of Nicholson and Bailey, in spite of its limitations, has served the important purpose of stimulating further thought and experimental studies on the problem as a whole.

Within the last fifteen or twenty years there has been a considerable amount of both field and laboratory work on various aspects of population dynamics. I propose now to deal with some of the more significant results that have been published.

In 1934 Gause produced, and experimentally verified, a theory that when a predator and its prey interacted with each other the end result would invariably be the anihilation of the prey followed by that of the predator. This theory was demonstrated by using two species of Protozoa as experimental animals, Didinium nasutum (Müller) being the predator and Paramecium caudatum Ehrenberg the prey. As predicted, D. nasutum rapidly consumed the

entire ..../33

entire population of P. caudatum and then itself died out. While these laboratory results seem irrefutable, I would consider that under natural conditions part of the population of P. caudatum might be able to find temporary protective niches and so reproduce without interference from D. nausutum. Gause also recognised this possibility and investigated it by culturing the same two species in a medium containing some sediment. In this way a refuge was provided for the prey but the predators were unable to penetrate the sediment and consequently died from starvation. Nevertheless in field conditions I do not think one would expect to find niches that exclude the prey entirely.

Alternatively, Nicholson and Bailey predicted that when a parasite and its host (or a predator and its prey) interact with each other the population numbers of both willoscillate about a mean density, the amplitude of the oscillations increasing with time. Thus there will be an initial increase of hosts followed later by a similar increase of parasites and this in turn will result in a decrease of hosts and then a decrease of parasites.

The first attempt at an experimental confirmation of this theory cam from Gause (1935) although in actual fact he was testing a similar theory proposed by Volterra (1926). In this instance Gause used Paramecium aurelia Ehrenberg as the predator and the yeast Saccharomyces exiguus Reess-Hansen as the prey. Although he was able to plot a series of sine-like curves for both predator and prey populations his experimental technique was extremely unsatisfactory. In the first place, the use of non-motile yeast cells for the prey is questionable. But more serious than this was the fact that in order to arrive at a correct result he admitted that he was forced to decrease the population density of P. aurelia each day by diluting the culture medium. If this were not done the end result would presumably be the total extinction of the yeast population followed by that of P. aurelia.

In ..../34

In 1941 DeBach and Smith published the results of experiments on the interaction of the parasite, *Mormoniella vitripennis* (Walker), and its hosts, puparia of *Musca domestica* Linnaeus. In this work the conditions laid down by Nicholson and Bailey were closely adhered to. The experiments were devised so that the generations of the host and parasite were exactly synchronised, the host's reproductive rate was fixed artificially at two, a single female parasite arose from each parasitised host and mortality of other kinds in intermediate stages was eliminated. The experiments were continued for seven simulated generations and the resulting fluctuations in both parasite and host population densities closely followed the theoretical predictions of Nicholson and Bailey. However, after this work had been published, Edwards (1954) studied the behaviour and reproductive physiology of the same parasite species. His findings show that DeBach and Smith's choice of four-day old parasites fed on honey was unfortunate, since such parasites will only attack one or two hosts in 24 hours, whereas those which have previously been allowed to feed on the host's haemolymph may parasitise up to 12 hosts in the same period. *M. vitripennis* must apparently feed on its host's haemolymph before it can attain maximum egg production. It is obvious that a completely different set of results might have been obtained if DeBach and Smith had used this type of parasite. As Varley and Edwards (1957) have pointed out, it is important to realise that a satisfactory experimental design often depends on adequate knowledge of parasite behaviour.

Varley (1947) was apparently the first to attempt to verify some of Nicholson and Bailey's theories in the field. He studied the population changes over a period of two years of the knapweed gall-fly, *Urophora jaceana* (Hering), and its two principal chalcid parasites, *Eurytoma curta* Walker and *Habrocytus trypetae* (Thomson). Compared with laboratory experiments, where

environmental ..../35

environmental and biological factors can be controlled more or less at will, field work is greatly complicated by the difficulty in collecting adequate samples and the even more formidable task of correctly interpreting the results. Nevertheless, Varley was able to show that the populations of the gall-fly and its most important parasites were behaving in the manner predicted by Nicholson and Bailey. Varley concluded from his study that oscillations about a steady density are inherent in a host-parasite relationship, but in a fluctuating environment these oscillations cannot be regular.

It is apparent from a survey of the literature of experimental population dynamics that most of the work has been concerned with the parasite-host relationship. However, there is at least one significant study on predator-prey interactions; this is the work of Huffaker (1958). This author used the phytophagous mite, Eotetranychus sexmaculatus (Riley), as the prey and the mite, Typhlodromus occidentalis Nesbitt, as the predator. The experiments were carried out in the laboratory under constant conditions of temperature and humidity and in darkness. Two sorts of experiments were done: in the first, the populations of both prey and predator were confined to a small number of oranges. In this instance, because there was little chance of dispersion by the prey, the latter were soon all eaten and shortly afterwards the predators died of starvation. In the second type of experiment a much larger "universe" containing many more oranges was used. In this situation some of the prey were able to disperse to oranges not occupied by predators and so build up their depleted numbers, until they in turn were found by migrating predators. One such experiment was continued for eight months and when the population numbers of both prey and predator were plotted against time it was found that the numbers of each showed three distinct oscillations. This result is in accordance with the theoretical predictions of Nicholson and Bailey. However, these authors also postulated that the oscillations should

successively ..../36

successively increase in amplitude. In Huffaker's experiment this did not happen and the damping of the oscillations was thought to have been caused by limitations of food available for the prey.

There have thus been at least three fairly satisfactory experimental verifications of Nicholson and Bailey's theories. What one would like to see now is a field experiment dealing with predator-prey interactions; and furthermore it would be interesting to know what happens when one or more species of parasite together with several species of predator act on the same host/prey species.

It is apparent that most of the successful experiments designed to show that density-dependent biotic factors are mainly responsible for periodic oscillations in population numbers have been carried out in the laboratory. In such a situation factors such as wind, rain and snow are entirely eliminated, while others such as temperature and relative humidity can be carefully controlled. A number of ecologists have pointed out that such experimental conditions are entirely artificial and bear no relation to what might happen in the field. This idea, however, is only partly true because there is no evidence to suppose that animal populations in the laboratory will behave in an 'un-natural' manner. Animal populations in natural conditions will presumably react towards each other in the same way as they do in the laboratory. The only difference is that in the field, climatic effects may tend to obscure the basic biological processes.

A number of population ecologists believe that climatic conditions are more important than density-dependent biological processes in controlling numbers of animals. An early exponent of this idea was Uvarov (1931), who reviewed and discussed the problem at great length. He was able to quote a large number of observations comprising many different families of insects in which population numbers appeared to rise and fall in conjunction with

'favourable' ....../37

'favourable' and 'unfavourable' environmental conditions. However, it does not necessarily follow that the climate was directly responsible for the observed changes in population density. There always remains the possibility that it is the activities of the natural enemies that are affected by the climate and that they in turn bring about population changes in their prey. It is noticeable that practically all studies on the supposed effects of weather on population numbers ignore the possible effects of natural enemies. This is shown, for example, by the studies of Andrewartha (1944) and Andrewartha and Birch (1954) when dealing with the population fluctuations of the grasshopper Austroicetes cruciata Saussure in Australia. This insect is particularly suitable for field investigations because its life cycle includes an obligate diapause in the egg stage. There is therefore only one generation each year and virtually only one stage is present at any particular time of the year. It is evident from the observations of Andrewartha that adverse climatic conditions are mainly responsible for bringing about a decrease in the population density of A. cruciata. This was especially marked in a drought year when large numbers of eggs were killed by desiccation and the grass withered prematurely causing many nymphs to die of starvation. Andrewartha and Birch consider that since the weather appears to play such an important rôle in the control of A. cruciata there is no need to study possible density-dependent processes. But nevertheless this species of grasshopper does have natural enemies; there are three insect species which feed on the eggs and one which eats the nymphs and adults. In addition birds of various species prey on the nymphs and adults. Since Andrewartha apparently set out to show that climate is all important in controlling populations of A. cruciata he made no particular effort to study the effects of natural enemies. Obviously it does not follow that natural enemies are of no importance in this instance. More recently Birch (1957) has

discussed ..../38

discussed the role of weather in relation to population changes and in this paper, while admitting that there may be only a few examples of control of natural populations by the weather, he quite rightly argues that all components of the environment must be considered when studying population dynamics.

In conclusion, one can say that whereas most ecologists are agreed that animal populations are regulated in some way, there is still much controversy as to whether environmental or biological processes are the most important. The present evidence seems to indicate that natural enemies acting in a density-dependent manner may have somewhat more significance than environmental conditions, but the effects of the latter obviously cannot be disregarded.

It now remains to consider how far my own experiments conform to the accepted theories of population dynamics. This can only be done in a very general way since the experiments were not designed for this purpose as such, but were done from an economic standpoint. Properly speaking, only the scale insect population changes on the ant-infested trees can be considered in the context of natural control; those on the ant-free trees fall under biological control which is a special aspect of population dynamics. My experiments included only two ant-infested trees and these obviously cannot constitute an adequate sample. This was unavoidable since the sampling of these, and the ant-free, trees had to be done single-handed. In spite of this limitation it might be profitable to examine the population changes on the ant-infested trees, but before doing so I would like to discuss an example of the climate influencing the distribution of a parasite of red scale.

It was initially assumed that Aphytis chrysomphali was responsible for the parasitism of A. aurantii in the Fish River Valley orchards. Later, during the routine sampling of scale insect populations, I noticed that the pupae of the parasites were often of quite different sizes and, moreover, were of different colours. This led me to believe that more than one species of parasite might be attacking the red scale. In order to clear up this point I sent both preserved pupae and live adults to Dr. P. DeBach of the University of California Citrus Experiment Station and he was of the opinion that, although the size and pigmentation differences were not taxonomically significant, the specimens probably represented a new species of *Aphytis*. In a personal communication Dr. DeBach wrote "It is very much like *lingnanensis* but seems to differ in some important but difficult-to-detect aspects." Now this is most interesting for the following reasons. *Aphytis lingnanensis* Compere was introduced into southern California because it was thought it would be more efficient in controlling red scale than *A. chrysomphali*. Several years after its introduction DeBach and Sisojević (1960) reported that *A. lingnanensis* possessed strong biological advantages over *A. chrysomphali* at temperatures of 77° and 87° F., at least in the laboratory. At a constant temperature of 67° F. *A. chrysomphali* had the greater reproductive potential. These laboratory studies indicated that *A. chrysomphali* is better adapted to cool coastal environments while *A. lingnanensis* survives best in the hotter inland areas and this agrees with the known distribution of these two species in the field. I have already shown that the temperature ranges in the Fish River Valley conform very closely to those prevailing in the inland areas of southern California. It is therefore of great interest that the species of *Aphytis* found in the Fish River Valley orchards should be so close, taxonomically, to *A. lingnanensis* of inland southern California. Also, specimens of red scale parasites collected in the climatically milder citrus areas near Grahamstown were identified, by Mr. D.P. Annecke of the Division of Entomology in Pretoria, as *A. chrysomphali*.

Figure 10 shows that the mean numbers of live *C. hesperidum* per leaf on the ant-infested trees remained at a

fairly ..../40

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and above it during the winter (and autumn). Now it is generally accepted that warm weather brings about an increase of insect populations and if this is so, it is clear that the weather is not acting directly on th fairly low level during the winter of 1959 and then gradually increased during the following summer. Taken alone, this might imply that the weather was solely responsible for these population changes. But when the graphs of percentage predation and parasitism (Figures 11 and 12) are examined it can be seen that the severity of these two factors decreases with time. The reason this should happen I have already interpreted as being due to the natural enemies migrating to the more favourable habitats on the nearby ant-free trees. While I consider therefore that the population changes of C. hesperidum on the ant-infested trees have been brought about by the activities of their natural enemies, this is not to deny that climatic effects are not important. Indeed, one would expect the warmth of the summer months to increase the metabolic processes and therefore the production of "crawlers" by the scale insects.

The curve representing the population changes in A. aurantii is shown in Figure 6, and from this it can be seen that the population density undergoes a series of irregular oscillations. Taking a mean density of nine live scale insects per leaf it is apparent the population is below this level during the summer (and spring) months and above it during the winter (and autumn). Now it is generally accepted that warm weather brings about an increase of insect populations and if this is so, it is clear that the weather is not acting directly on the scale insects in this manner. The alternative is that the warm weather of the summer months favours the increase of the natural enemies of the scale insects and the former, in turn, depress the level of the coccid population. Reference to Figures 8 and 9 shows that this indeed appears to be the answer at least in regard to the predators. Both of these graphs indicate that there is a higher proportion of predation during the summer months as compared with the winter. The graph showing the percentage parasitism (Figure 7) is more difficult to interpret since there are some unexpected "peaks" and "troughs" in the curve. Thus in the

summer ..../41

summer of 1959 there is an increase, a decrease and an increase in the rate of parasitism. Similarly a slight increase occurred in the middle months of the winter of 1960. It seems therefore that the weather does not influence the activity of the parasites to such a great extent as it does the predators. What may be causing the oscillations in percentage parasitism is the availability or otherwise of suitable scale insects in which the parasites can lay their eggs. In this connection, Quayle (1911) showed that A. chrysomphali can only parasitise second instar and early third instar individuals of A. aurantii. Once the female scale insect has started to produce "crawlers" it is immune from parasitism.

As far as the decrease in numbers of scale insects per leaf on the ant-free trees is concerned, it is fairly obvious that this has been brought about by predation and parasitism and I have discussed this in an earlier section. One would perhaps have expected the coccid population numbers on these trees to have oscillated about a low mean density following the initial rapid reduction. This would happen when the low population density of scale insects caused the numbers of their natural enemies to decline due to a shortage of food and oviposition sites, which in turn would bring about a resurgence of the coccid population. A similar situation occurred during the control of Opuntia spp. by Cactoblastis cactorum Berg in Australia (Dodd 1936). I feel that if my surveys had continued for another year or so such oscillations might have occurred, but I would not expect the scale insect populations to reach economically damaging proportions.

(v) Discussion :

In the previous sections I have dealt with the problem of ant control and have shown that even by itself it can produce a satisfactory decrease in the population density of both red scale and soft brown scale. In orchards which at the present time require

only ..../42

only occasional treatment with parathion and malathion it would probably be advantageous to initiate a programme of ant control as well. However, since mussel scale suffers from a very low incidence of parasitism and predation one could not expect ant control to produce any significant decrease in the populations of this pest. The great majority of citrus orchards in South Africa are 'blanket' sprayed once or twice a year with highly toxic organophosphorous insecticides with the result that in these orchards the populations of natural enemies are very low. In such situations the additional expenditure directed towards ant control could hardly be justified. If some form of biological control could be brought into operation in these orchards then ant control would assume an integral part of such a system.

Although the beneficial consequences of ant control in citrus orchards have been emphasised for a number of years very few farmers appear to have attempted this on a large scale. In the past, this has undoubtedly been due to lack of effective insecticides and in early efforts at ant control growers had to resort to using tanglefoot barriers around the trunks of the trees.

Early in 1959 I visited a citrus farm in the Sundays River Valley in which ant control was being practised extensively and the results appeared to be most encouraging. The ants, principally <u>A. custodiens</u>, were being controlled by regular applications of parathion, the 25% wettable powder being sprinkled in and around all nest entrances. At the time of visiting the farm the owner informed me that <u>C. hesperidum</u> and <u>A. aurantii</u> had been almost eliminated from the orchards, although occasional small infestations of <u>L. beckii</u> still persisted. The latter species of scale insect was kept under control by 'spot' spraying with organophosphorous insecticides. The cost of ant control for 11,000 trees, including both labour and insecticides, came to only R300 a year.

However ..../43

However, two years later, in spite of continued ant control operations, the situation was not so promising, since A. aurantii had re-infested the orchards to such an extent that spraying with parathion had had to be instituted. The owner is of the opinion that the resurgence of red scale may be due to the accumulated effects of five years of extremely dry conditions, including some severe droughts. Both soft brown scale and mealybugs are absent from the orchards indicating that ant control is still producing beneficial effects in this respect and therefore in the opinion of the farmer it warrants continuation.

The very promising results of ant control on this farm would seem to indicate that the biological control of at least C. hesperidum and A. aurantii needs to be extended to other citrus-growing areas. This is especially so since the costs of controlling scale insects by spraying the trees with insecticides appear to be mounting higher each year. Simmonds (1960) cites an instance of a sum of R40,000 being spent annually on scale insect control on one estate, although the number of trees involved is not given. But however desirable the application of biological control appears, the sudden changeover from chemical to biological control would almost certainly result in a catastrophic increase in the population of one or more species of pests. The most important problem to be overcome is therefore how a change to biological control can best be implemented. Simmonds (1960) has suggested that this could be done by stopping chemical control in certain areas and then releasing very large numbers of natural enemies in order to swamp the expected increase in scale insect numbers. Once reasonable control has been obtained in this region, spraying would gradually be discontinued in adjacent areas. He goes on to point out that such a procedure would necessitate the importation of additional species of natural enemies from overseas and the large-scale breeding and efficient distribution of these. While this seems to be quite a

feasible ..../44

feasible scheme in theory I would consider that the first part of the operation should be aimed at effective and long-lasting ant control. The large-scale release of natural enemies seems pointless if they are going to be inevitably hindered by the activities of ants.

Although the above scheme for initiating biological control is theoretically sound and may eventually work in practice, the inevitable conservatism of the citrus grower must be taken into account. I consider that any owner of large citrus orchards would be well justified in declining to suspend all spraying operations in favour of biological control, due to the risk of a build-up of scale insect populations. Such populations could severely damage the trees and render the fruit unsuitable for export. Furthermore, biological control would result in the large and expensive high pressure boom-spraying equipment being put permanently out of use, although it might be possible to modify such equipment for ant control work.

As an alternative to Simmonds' scheme for implementing biological control of citrus pests, I think the following might be more acceptable to the growers. After obtaining satisfactory ant control, the orchards should be sprayed with one of the commercially available light mineral oils. The rate of application should be such that a massive build-up of scale insect populations is avoided but at the same time not all the coccids are killed. DeBach (1959) and others have shown that oil sprays act as selective insecticides in that they do not kill coccinellids and parasitic Hymenoptera. Applied in the correct dosages an oil spray would ideally leave sufficient live coccids to promote the build-up of natural enemy populations, augmented by laboratory reared specimens, and yet there would be not enough pests to damage the trees. After a few seasons of such treatment the next step would be the more precise integration of chemical and biological control based on the method developed in

California ..../45

California for the control of mussel scale (DeBach 1958, 1959). In this method an oil spray is applied to alternate pairs of rows of trees throughout the orchard each year and in this way half the orchard is untreated at a given time. These untreated rows ensure a resevoir of natural enemies which can move to treated trees as soon as pests start to develop on them. In the following year the spraying operation is arranged so that the formerly unsprayed rows are now sprayed. DeBach (1959) has estimated that this strip treatment could reduce pest control costs by one half as compared with control by organophosphorous materials. The combination of chemical and biological control in this manner is a comparatively recent innovation and, as Stern et al (1959) have pointed out, its practical introduction has been delayed because it was previously considered that the two methods were incompatible.

Once it is judged that satisfactory control of scale insects has been achieved by the alternate strip method the oil sprays could gradually be eliminated, eventually giving rise to complete biological control.

It should be emphasised that before any attempts at biological control are made, natural enemies, particularly parasitic Hymenoptera, should be imported into the country. This applies especially to parasites of L. beckii, since only one species is known to be already established and it never exerts appreciable control of this scale insect. From the work in California, Texas and Florida it should be relatively easy to decide on the most suitable natural enemies to be imported. The initial expenditure for the mass-rearing of parasites and predators may be quite high but one does not expect this to be done by the individual citrus growers. As the natural enemies become established throughout the country it may be possible to reduce the numbers of those liberated.

The comparative costs of biological control as compared

with ..../46

with purely chemical control are difficult to judge. In the initial phases, when a system of integrated chemical and biological control is in operation, it may cost about the same as the present methods of scale control. However, if and when purely biological control is practised, expenditure on ant control will probably be much less than that spent on organophosphates at the present time, as indicated by the following approximate costs.

According to Dr. A.B.M. Whitnall of African Explosives and Chemical Industries (unpublished report and personal communication), during spraying operations against scale insects about ten gallons of spray material are used for each tree. When only A. aurantii and L. beckii are present the most effective, but not necessarily the cheapest, insecticide to use is a combination of three pounds of parathion and half a gallon of Alboleum (a mineral oil) with 100 gallons of water. This mixture has to be applied three times a season and for 1,000 trees the total cost is R338. Where C. hesperidum is a pest as well as either or both of the above scale insects the most effective combination is a mixture of two pounds of parathion together with one of Gusathion in 100 gallons of water. This also has to be applied three times each season and the cost for 1,000 trees is R510. The great difference in the costs of the two treatments is due to the high price of Gusathion which is a comparatively new insecticide. It is probable that as the demand for Gusathion rises its cost to the farmer will fall.

Compared with the costs of the chemical control of scale insects I have calculated those of ant control based on the quantities of insecticide used in my experiments. As was shown earlier, the most promising insecticide for the control of A. steingroeveri is Telodrin in the form of an emulsifiable concentrate applied by mixing it with sand. At a strength of 0.5% active ingredient, 1,000 trees would require 18 gallons of insecticide which at current prices works out at R130. Dieldrin (50% wettable powder) applied

with ..../47

with sand at the same rate as Telodrin is less effective against *A. steingroeveri* but on the other hand it is cheaper; for 1,000 trees it is calculated that the amount of dieldrin required would cost R90. Since Telodrin has only recently become commercially available it is probable that the amount used throughout the country is small compared with, for instance, dieldrin. It is quite possible that, in time, Telodrin may become less expensive and therefore more economical for the purposes of ant control. It should be emphasised that in my experiments the insecticides were only applied to the area covered by the 'skirt' of the tree. More effective and long lasting control could probably be achieved if the whole orchard were treated although, of course, this would increase the expenditure.

In some parts of South Africa the dominant ant species in citrus orchards is *Pheidole megacephala* Fabr. and by all accounts it is more easily controlled than either of the two species of *Anoplolepis*. Whitnall and Whitehead (1953) were able to control *P. megacephala* for four and a half months with chlordane at a strength of 0.2% active ingredient, while I found that the same insecticide at 0.5% was completely unsatisfactory for the control of *A. steingroeveri*. It therefore seems probable that chlordane applied at the rate of 0.5% active ingredient would give good control of *P. megacephala*, while the cost per 1,000 trees would be only R32.

From these figures it appears that the costs for ant control compare very favourably with those for chemical control of scale insects. Even if Telodrin, the most expensive insecticide, had to be applied three times a year it would cost almost the same as the parathion - Alboleum treatment for armoured scale insects.

Even if it turns out that biological control is scarcely cheaper than chemical control and assuming that it is just as effective, an important phase in the development of citrus pest

control ..../48

control will have been reached. This is because with present high rates of application of organophosphorous insecticides there is the very distinct possibility that scale insects will become resistant to these materials. It is therefore most desirable to have a second line of defence against these pests.

I would now like to return to ant control and consider some additional benefits which may accrue from the application of insecticides to the ground beneath the trees. In some citrus-growing areas the false codling moth, Argyroploce leucotreta Meyrick, is a serious pest and no entirely satisfactory chemical measures exist to control it. The most usual method of control is the tedious one of orchard sanitation in which all fallen fruits are collected and destroyed. Although the damage by this moth is caused by the larvae living in the fruit, pupation takes place in the ground. It therefore seems likely that repeated applications of insecticides aimed at ant control could have the important additional effect of reducing the incidence of false codling moth attack. Similarly other citrus pests which pupate in the ground, for example the Mediterranean fruit fly Ceratitis capitata (Wiedemann), might be controlled in this way.

In conclusion it is worth mentioning that Sanger (1960) has shown that applications of aldrin and dieldrin at normal dosage rates do not have any adverse effects on soil micro-organisms. The normal dosage rates for these two insecticides are given, respectively, as two to six pounds and one to three pounds of active ingredient per acre. Only when these insecticides are applied at 100 to 200 pounds per acre is it considered that they are harmful to soil bacteria.

II. BIOLOGICAL ....../49

II. BIOLOGICAL STUDIES ON SCALE INSECT PREDATORS.

(i) The life history and biology of a new predator of red scale :

The coccinellid predator of A. aurantii described in this section represents a new genus and species. However, at the time of writing, the taxonomic description and naming of the beetle had only just been completed and the paper was still in the press. The description of the beetle has been undertaken by Mr. R.D. Pope of the British Museum (Natural History) and the following are some pertinent extracts from three of his letters to me. "It seems to be related to Serangium Blackburn on the one hand and Lotis Mulsant on the other". "As far as I can see it belongs to an undescribed genus which, with a certain amount of difficulty, might be assigned to the Pharini. The trouble is that this group is in need of a thorough revision and its relationship with the rest of the subfamily require to be worked out". "The work has involved a partial revision of a tribe".

From Pope's comments it can be deduced that this beetle has some unusual taxonomic characters, and as I will describe later, it also possesses some peculiar morphoplogical and biological features.

The first specimen of this coccinellid was collected from an orange tree in a private garden in Grahamstown. Subsequently a few more were found on a lemon tree in a commercial orchard in the Belmont Valley near Grahamstown. I have, however, collected them in the greatest numbers from orange trees in the orchards in which my ant control trials were carried out. In all instances the trees from which the beetles were collected were infested with A. aurantii. The first specimen was collected in January, and those from the Belmont Valley in April. Beetles were taken from the orchards in the Fish River Valley in May, June and in early August. The fact that they were found to be quite plentiful in August suggests that they may breed throughout the year, at least in the warm Fish River Valley.

The ..../50

The life history and biology of this coccinellid was studied under controlled conditions in a constant temperature room. The temperature in this room was set at 25° C. while the relative humidity was maintained at 65%. During the day the room was illuminated with two 100 watt and three 40 watt electric light bulbs. These bulbs produced a light intensity on the beetles in their rearing dishes of about 145 metre candles. At night the lights were switched off by means of a time switch. The coccinellids were reared in petri dishes, eight centimetres in diameter, which had been half filled with paraffin wax. The cheapest and most satisfactory wax for this purpose consisted of candle wax softened by the addition of vaseline. Food was provided by pinning leaves infested with A. aurantii flat onto the wax. In this way the leaves were prevented from curling up while drying and therefore the beetles could always be seen. Clear glass lids on the petri dishes prevented the insects from escaping while allowing them to be easily observed. This method of rearing the larvae and adults was found to be entirely satisfactory and no trouble was ever experienced of the lids of the dishes misting over.

The Egg :

The eggs are laid, on their sides, either singly or in groups of up to seven, underneath the dorsal armour of dead scale insects. The eggs are most peculiar in that they have a slender stalk attached to one end and this usually projects from under the coccid's dorsal armour. Measurements on 17 eggs showed that they varied in length between 0.42 and 0.53 millimetres with a mean of 0.48 millimetres (excluding the stalk); the mean length of the stalk was found to be 0.50 millimetres with a minimum of 0.35 and a maximum of 0.60 millimetres. A diagram of one of these eggs is shown in Figure 13. Although the literature has been searched only one reference could be found of any other species of coccinellid which has stalked eggs. This is Scymnus quadrivittatus Mulsant ..../51

Mulsant and according to Whitehead (1957) the eggs of this species sometimes have a transparent filament attached to one end. From a microscopic examination of the stalk of the present species cut transversely it appears that this is solid and is therefore a simple continuation of the chorion. Observation of the oviposition process showed that the stalk is the last part of the egg to issue from the oviduct.

The purpose of the stalk is unclear: it does not have any adhesive function and embryos develop normally in eggs which have had the stalks cut off. It was thought that a possible function of the stalk might be one of absorption of water in the form of dew and to this end the following experiments were done. Eggs were put into desiccators and held at a relative humidity of 30% and a temperature of 23° C. for one, four and ten hours. After each egg had been removed from the desiccator it was placed on the stage of a compound microscope and a small drop of a strong solution of methylene blue was applied to the tip of the stalk by means of an 'Agla' micrometer syringe. The stalk was observed, by reflected light, under both medium and high power objectives but in no instance could any uptake of the dye be seen. In the next series of experiments newly laid eggs were collected and the stalks were cut off some while others were left intact. Each group of eggs were put into separate uncorked glass tubes and these in turn were placed in a desiccator under the same conditions as in the first experiment. After being left for three days the tubes were removed, a small piece of damp cotton wool was put into each and they were corked. Water vapour evaporating from the cotton wool condensed in the form of dew on the walls of the tubes. Under these conditions both lots of eggs hatched normally and at the same time. It therefore seems that the stalks are not concerned with the uptake of water.

When laid, the eggs are pale yellow but during development they gradually turn orange. Just before hatching the first instar

larva ..../52

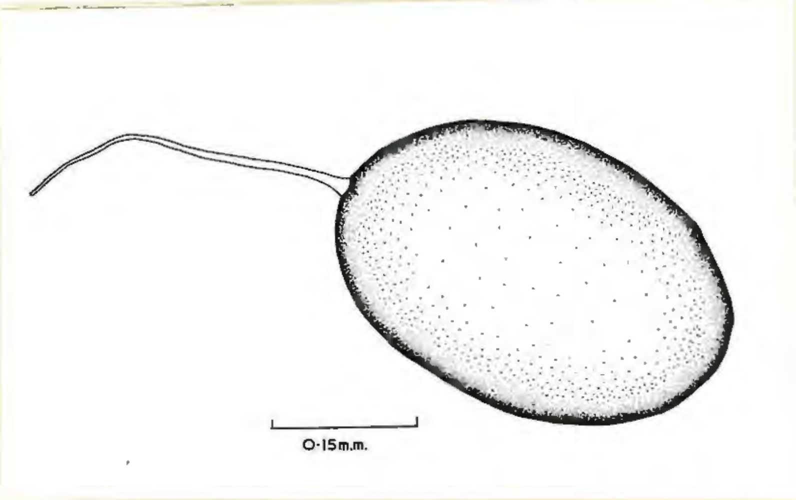

Figure 13.

Egg of new species of coccinellid.

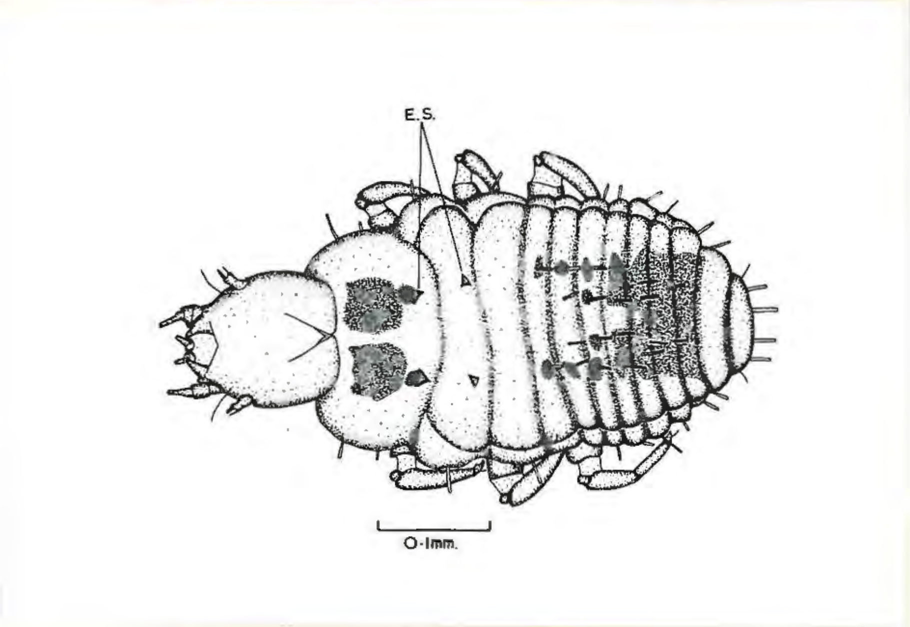

Figure 14.

First instar larva of new species of coccinellid;

E.S. = Egg bursting spines.

larva can be clearly seen through the chorion, the anterior part of the larva being directed towards the stalked end of the egg. On hatching, the chorion ruptures irregularly and the prothorax of the larva is the first to appear; this is followed by the head and then the rest of the body. The complete process of hatching takes between three and five minutes. Examination of the first instar larva reveals what are probably egg-bursting spines situated on the pro- and mesonotum (Figure 14). However, due to the small size of the newly hatched first instar larva, these spines could not be seen in action.

The average duration of the egg stage was 12 days with a range of 11 to 13 days. From a table given by Balduf (1935) it was calculated that the mean duration of the egg stage, in 23 different species, was seven days although the temperature was not stated.

The larvae :

The newly hatched larva, which is on the average 0.53 millimetres in length, remains motionless near its chorion until it has become fully sclerotised; then it wanders off in search of food (Figure 14). It will readily eat unhatched eggs if given the chance. One of the most remarkable things about the first instar larvae is their ability to pierce the dorsal armour of mature females *A. aurantii* and feed on their body fluids. The diameter of such a scale insect is four times the length of a first instar larva. Other first instar coccinellid larvae, *Lotis nigritula* Crotch and *Lindorus lophantae* Blaisdell, which I have observed only manage to feed on the first instar nymphs of *A. aurantii*. It was noticed that larvae of all instars make no attempt to attack scale insect crawlers (mobile first instar nymphs), so long as the latter are moving; recently settled first instar nymphs are readily eaten.

The method of feeding of the larvae is as follows. A minute slit-like cut is first made in the dorsal armour of the prey

and ..../53

and, when this has been accomplished the liquid body contents are sucked out and then regurgitated into the prey, presumably together with digestive enzymes. The process of suction and regurgitation is repeated many times; how long it will continue depends on the size of the prey relative to that of the predator. This method of feeding is apparently common to all species of coccinellid larvae and was first described by Smit (1917). Because the first instar larvae are so small compared with their prey, feeding extends over a long period: it took a four-day old first instar larva an hour and a half to eat a late second instar A. aurantii. The colour of all instars of larvae varied between bright yellow and almost black, according to whether they were fully fed or starving.

Although the method of feeding of this species of coccinellid is the same as that of other species, the structure of the mandibles differ. These differences can best be appreciated by referring to Figures 15 and 16. The larval mandibles of Exochomus flavipes (Thunberg) shown in Figure 15 is very similar to that of Lotis nigritula. The former species preys on C. hesperidum (a "soft" scale) while the food of the latter is A. aurantii and L. beckii (both "armoured" scales). Gage (1920) has illustrated larval mandibles of eleven different species of predatory coccinellids and none of these resemble the mandible of the present species. It is possible that the multi-dentate mandible of this species is a functional adaptation enabling the minute larva to pierce the tough dorsal covering of mature armoured scale insects.

Another unusual feature of the larvae is that they have relatively few setae on their bodies and that these setae are quite short. The setae are of two types: a simple spine which is rather broad at the base but narrows rapidly towards the tip; the other type is in the form of an elongated hollow cylinder with a coronet like distal end. (Figures 17 and 18). These latter setae appear to be the external ducts of glands for they always have a drop of

colourless ..../54

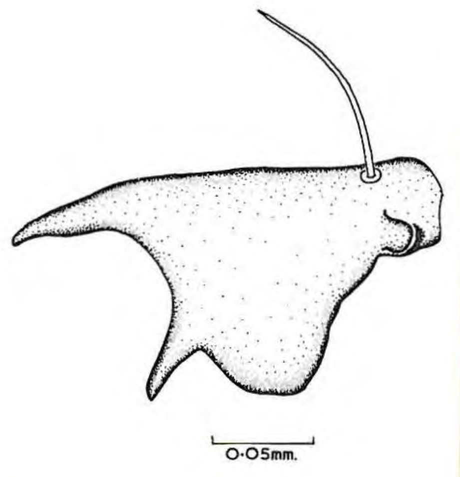

Figure 15.

Larval mandible of *Exochomus flavipes*.

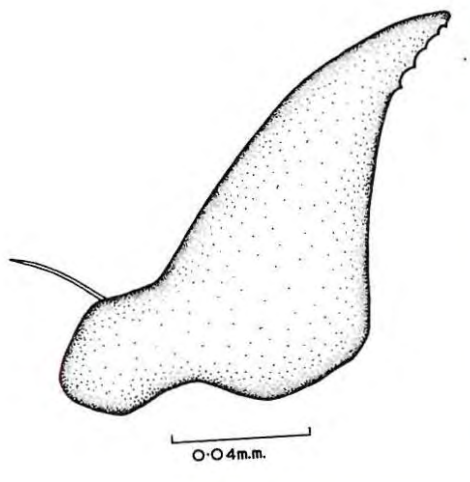

Figure 16.

Larval mandible of new species of coccinellid.

colourless fluid at their tips. It was further noticed that when a bright microscope lamp was shone onto a larva the drops of fluid appeared to undergo a **change of** physical property, which caused the drops to run down the outside of the setae and spread out over the tergum. It took an hour or more before another drop of fluid appeared at the tip of the tube. Several tests were done to find out out how long the lamp had to shine on the larva before the drops ran down the tubes. The lamp was then shone onto the bulb of a mercury thermometer for the same length of time and this caused the temperature to rise to 32° C. It therefore seemed probable that the fluid was either a liquid wax or an oil and that at a **temperature** of about 32° C. it underwent a change of state. It is of interest to note that Ramsay (1935) observed a change of state of the waxy film on the cuticle of Periplaneta americana (Linnaeus) at a temperature of 33° C. In this instance it was shown that at temperatures above this transition point the cuticle of P. americana became very much more permeable to water. Similar results have been obtained with the larvae of other insects (Beament 1945; Wigglesworth 1945).

The functional significance, if any, of this phase change must remain problematical in the absence of more critical observations and experiments. Drops of liquid at the tips of glandular "hairs" have been observed in the larvae and especially the pupae of many species of coccinellid. Flanders (1930a) was able to show, by extraction in alchohol and subsequent evaporation, that such drops of liquid on the pupae of Lindorus lophantae consist of a waxy material. Early observers thought that these drops of fluid protected the otherwise defenceless pupa from natural enemies. However, there is no experimental evidence for this and, until the chemical composition of the fluid has been analysed, it must remain a matter for conjecture. My own feeling is that the drops of waxy material are primarily secreted in order to help with the elimination of excess wax derived from the prey.

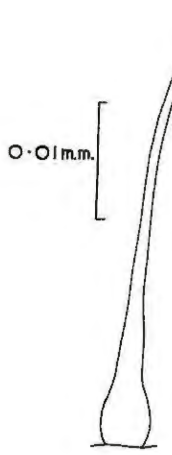

Figure 17.
Larval seta of new species of coccinellid.

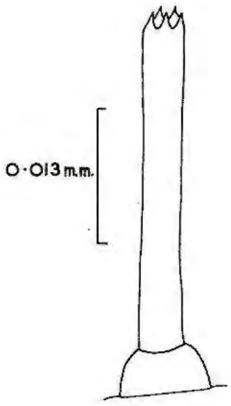

Figure 18.
Larval wax duct of new species of coccinellid.

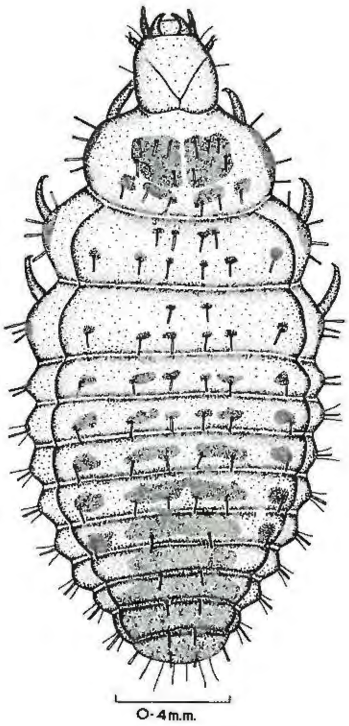

Figure 19.
Fourth instar larva of new species of coccinellid.

The second, third and fourth instars are similar in anatomy to the first instar larvae. They naturally increased in size over each preceding instar and were therefore able to feed more rapidly. Third instar larvae took between nine and a half and thirteen minutes to eat an early second instar nymph of A. aurantii, while the corresponding time for fourth instar larvae was about three and a half minutes.

The life of the fourth instar larva is divided into two distinct phases. There is an initial active period of feeding followed by a non-feeding prepupal stage. In the latter period the larva becomes fixed to the leaf at its posterior end while the head is flexed under the thorax. A fourth instar larva, in the feeding period, is shown in Figure 19.

The pupa :

The exuviae of the fourth instar larva split in the midline from behind the head to the end of the metathoracic region to allow the partial emergence of the pupa. The pupa is pale yellow in colour and is covered, quite thickly, with glandular "hairs". Each of these has a drop of fluid at its tip and also two or three further drops dispersed proximally along the length of the "hair", giving the latter a beaded appearance. A diagram of a pupa, without the last larval exuviae, is shown in Figure 20, while a drawing of a pupal "hair" is depicted in Figure 21.

The average duration of the immature stages has been computed and this is summarised in Table 11.

From this table it can be seen that the average time taken from deposition of the egg to emergence of the adult was 42 days. This is about a week longer than the similar period for most other species of coccinellid (Balduf 1935), although in these instances the temperature during development is not given.

Table 11 ..../56

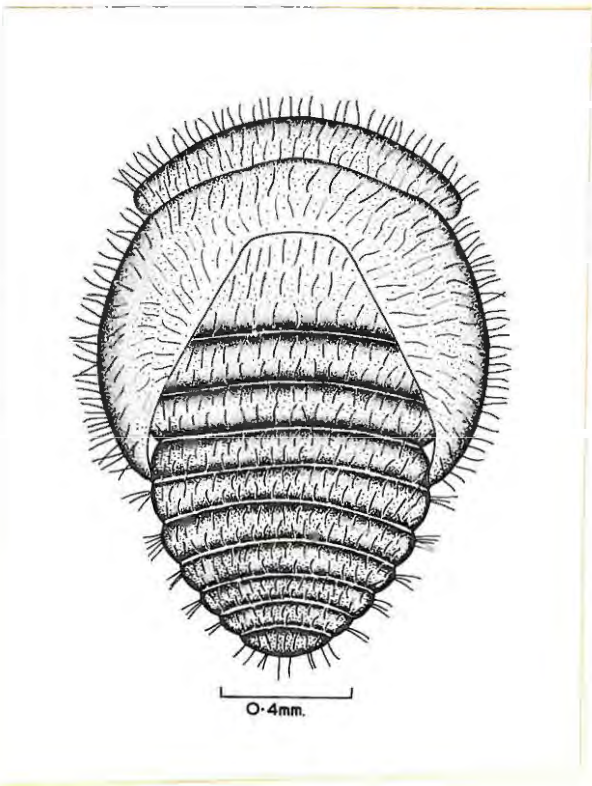

Figure 20.

Pupa of new species of coccinellid.

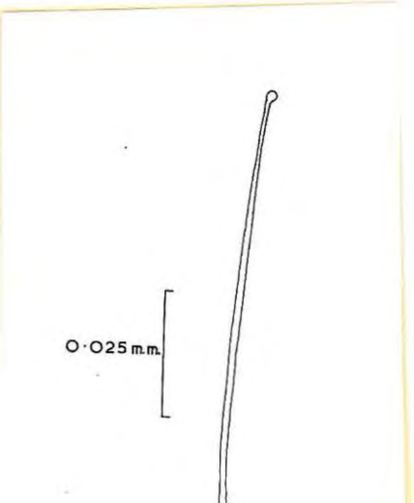

Figure 21.

Pupal wax duct of new species of coccinellid.

TABLE 11.

Duration of the immature stages.

Stage.	Number of observations	Mean duration (days)	Range (days)
Egg	26	12	11 - 13
1st instar larva	14	6	5 - 7
2nd instar larva	11	5	4 - 6
3rd instar larva	11	4	3 - 7
4th instar larva :			
(i) Feeding period	8	5	3 - 7
(ii) Prepupal period	8	2	2 - 3
Pupa	8	8	---

A final observation on mortality among the immature stages is of some interest. For this purpose 36 eggs were divided into four equal groups and a close watch was kept on their subsequent development. From the original number of eggs eleven adult beetles finally emerged. The causes of death of the remainder were as follows : infertile eggs, two; eggs eaten by first instar larvae, seven; starvation in first instar, nine; starvation in second instar, two; starvation in third instar, two; pupae eaten by fourth instar larvae, three. It could be argued that such comparatively high mortalities were partly due to the larvae being confined to single leaves in small dishes and that in the field the mortality might not be quite so great. However, it should be realised that under natural conditions such factors as natural enemies and extremes of temperature and relative humidity may play an important role in causing mortality of the immature stages.

The adult :

The adult beetles are small and shiny black with a very sparse pubescence. (Figure 22). The mean dimensions were found to be: length 1.28 millimetres, width 0.88 millimetres. It was impossible to distinguish between the sexes without recourse to

dissection ..../57

Figure 22.
Adult of new species
of coccinellid.

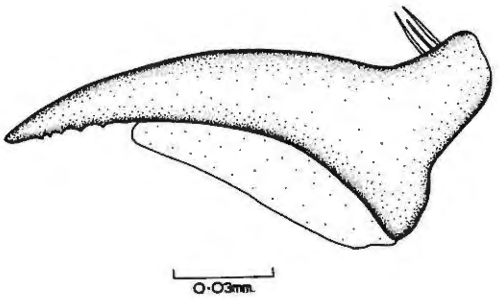

Figure 23.
Adult mandible of
new species of
coccinellid.

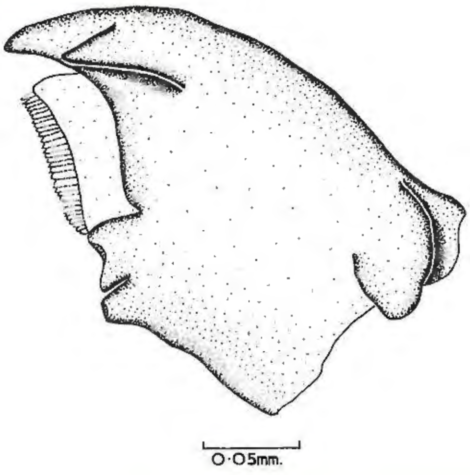

Figure 24.
Adult mandible of
Lotis nigritula.

dissection of the genitalia. During copulation it was observed that the males are slightly smaller than the females, but this size difference is not great enough to enable one to separate the sexes readily.

One of the most unusual characteristics of the adult beetle is its method of feeding. It was the observation of this phenomenon which suggested that the biology of this species should be investigated. In brief, the adults feed in exactly the same manner as the larvae. This method of feeding (involving the alternate suction and regurgitation of the prey's body fluids) has, I believe, never been reported for any other species of adult coccinellid. Certainly it does not occur in any of the other common coccinellids found in either the Belmont or Fish River Valley orchards. In Balduf's (1935) extensive review of the biology of the Coccinellidae there is no mention of such a method of feeding by an adult. It was of interest to discover that the mandibles of the adult are of the same shape and structure as those of the larvae. A drawing of an adult mandible is shown in Figure 23 and, for comparison, that of an adult of Lotis nigritula is given in Figure 24. The latter species is a common predator of both A. aurantii and L. beckii and feeds by first chewing a large hole in the prey's dorsal armour, whereupon the entire scale insect is eaten.

Since the diameter of a mature female A. aurantii is often greater than the length of an adult beetle it is not surprising that rather few scale insects are eaten each day. It was evident that egg-laying females ate more than either virgin females or males. Over a two month period the former ate an average of three A. aurantii a day, with a maximum of eight a day. On the other hand, virgin females and males consumed an average of only one scale a day, with a maximum of four. By way of comparison, two other coccinellid predators of A. aurantii : Lotis neglecta Mulsant and Pharoscymnus sexguttatus (Gyllenhal) were found to eat about ten scale insects

a ..../58

a day. Adults of the new species also ate L. beckii; but, like their larvae, they did not prey on C. hesperidum. On one occasion nine adults were observed, under red light, at hourly intervals during the night. This was done in order to determine whether feeding continued at night. It was found that from 9.30 p.m. to 6.30 a.m. no feeding occurred. Throughout this period the beetles remained motionless on the leaf, and only after the lights were switched on at 6.35 a.m. did some of them start to walk about and feed. The beetles were fairly resistant to starvation and lived for an average of twelve days without food.

Copulation was observed on a number of occasions and it is interesting to note that in every instance the male was mounted well over to the left side of the female's back. This stance suggested that the genitalia of either sex might be asymmetrical. However, the male and female genitalia have been examined both in situ in cleared specimens and after removal from the animal. In neither instance is there any evidence of asymmetry of the genitalia and it therefore seems likely that a temporary twisting may occur during copulation.

Prior to oviposition the female investigated the suitability of a dead scale insect by thrusting her head under the dorsal armour. She then stood on top of the coccid, exserted the ovipositor forwards beneath herself, pushing it under the dorsal armour, and the eggs are deposited. Similar egg-laying behaviour utilising dead scale insects as oviposition sites is well known in many other scale-feeding coccinellids. I was able to make some incomplete records of fecundity using seven individuals. Of these, four were collected in the field and were therefore of unknown age; the remaining three were reared in the constant temperature room. The egg production of these seven beetles is summarised in Table 12.

TABLE 12 ..../59

TABLE 12.

Egg production by female beetles.

Number of individual	Eggs laid	Days kept	Mean No. eggs/day	Remarks.
1	133	62	2.1	Escaped from dish
2	141	106	1.3	Accidentally killed
3	150	114	1.3	Natural death
4	245	123	2.0	" "
5	86	70	1.2	" "
6	73	75	0.9	" "
7	132	93	1.4	" "

N.B. Numbers 1 - 4 were collected in the field; numbers 5 - 6 were reared in the constant temperature room.

The highest number of eggs laid per day was six and this was achieved by No: 4. Beetles Nos: 1, 2 and 7, laid on occasion up to four eggs a day. Although Table 12 is by no means an accurate reflection of the fecundity of this species, it does appear that in comparison with most other species of coccinellid (Balduf 1935) its egg-laying capacity is rather low.

Finally, I was able to make a few observations on the longevity of the adult beetles. Altogether nine beetles were kept under observation from emergence until their death. However, three of these escaped and one was accidentally killed. The remaining five were successfully kept until they died naturally. These five lived for an average of five and a half months, with a minimum of three and a half and a maximum of eight and a half months.

The importance of this species from the point of view of the biological control of A. aurantii is difficult to assess. From the observations on its feeding behaviour it would appear to play a rather minor role in controlling red scale. On the other hand, there is the problem of the quite high percentage of dead A. aurantii, found in the population analyses, which appear to have been sucked dry.

As ..../60

As has been mentioned in the section dealing with the population dynamics of A. aurantii, the commonly accepted view is that all such scale insects have been killed as a result of the predatory behaviour of Aphytis sp. But in view of the method of feeding of the larvae and adults of the present coccinellid it is evident that part of the mortality of A. aurantii must be ascribed to this beetle.

(ii) The feeding habits of some predators :

In this section I shall deal with the feeding behaviour of some of the more common adult predators of A. aurantii and C. hesperidum. I shall also mention whether or not they are able to feed on L. beckii, because, although this species does not occur in the Fish River Valley, it can become quite a serious pest of citrus in the more humid regions of South Africa. While most of the predators belong to the Coccinellidae, I shall also deal briefly with a malachiid predator of A. aurantii.

The three most common coccinellid predators of scale insects in the orchards are Lotis nigritula Crotch, Exochomus flavipes (Thunberg) and Lindorus lophantae Blaisdell. Another, less common, species is Pharoscymnus sexguttatus (Gyllenhal). On occasion, quite large numbers of Cheilomenes lunata (Fabricius) and C. propinqua (Mulsant) were seen but were not collected since they are known to feed only on aphids. (Whitehead 1948). The coccinellids were kept in the constant temperature room and two sets of observations were made on their feeding behaviour. Initially, the food preferences of each species was determined. This was achieved by putting the coccinellid into a dish together with two citrus leaves, each infested with a different species of scale insect. The beetle was left in the dish for 30 hours and at the end of this time it was calculated how many individuals of each species of coccid had been eaten. Each experiment was repeated at least twice. The second

observation ..../61

observation consisted of determining the numbers of the preferred prey that were eaten each day. These observations were carried out over as long a period as possible, usually until the death of the beetle. No attempt was made to distinguish between the feeding habits of males and females, since in three out of four species studied it was impossible to separate the sexes except by dissection. Balduf (1935) states that it is generally true to say that egg-laying females eat more than either virgin females or males.

L. nigritula can be found in small numbers in ant-infested trees but after about four months of ant control they become very much more abundant. The feeding choice experiments show that this species will eat A. aurantii much more readily than C. hesperidum; similarly it prefers A. aurantii to L. beckii, although in this instance the preference is not so marked. In the constant temperature room L. nigritula ate, on the average, 20 A. aurantii a day. This rate of feeding was maintained until shortly before death when it fell to about six a day.

According to Geyer (1947) E. flavipes feeds mainly on such soft-bodied insects as aphids and mealybugs and my observations on its feeding preferences confirms this. It is quite unable to feed on L. beckii and, while it is able to eat A. aurantii, it never manages to live for more than a few days when given this coccid alone. Its rate of feeding on the soft-bodied C. hesperidum averaged about 35 a day.

L. lophantae appears to be a much more generalised predator than the other species. In the preference experiments it ate almost equal proportions of all three species of coccid. Because there was no clear-cut preference this coccinellid was given all three species of coccid (separately) in the second set of observations. These experiments showed that it ate, on the average, 24 A. aurantii a day; while the numbers for L. beckii and C. hesperidum were 22 and 11 respectively.

Whitehead (1948) studied the morphology and some aspects of the biology of P. sexguttatus. According to him the preferred prey of this species is A. aurantii and he goes on to say that "... the amount of red scale the adults consume is phenomenal". Since he does not mention under what conditions of temperature and relative humidity his observations were made, it is difficult to compare his results with mine. However, I did make some observations on the feeding rate of this species, in the constant temperature room, in order to compare it with that of L. nigritula and L. lophantae. Over a period of three weeks P. sexguttatus ate an average of 25 A. aurantii a day. Therefore, under the same conditions, this species does not eat significantly more A. aurantii than either L. nigritula or L. lophantae.

I have already shown above that the new species of coccinellid is only active during the day. Some casual observations on P. sexguttatus indicated that it too is largely inactive during the night. In order to investigate this point further, I recorded its rate of feeding over the periods 6.00 a.m. - 6.00 p.m. and 6.00 p.m. - 6.00 a.m. Five sets of observations were made in the light and five in the dark. During these experiments the lights in the constant temperature room were switched on at 5.30 a.m. and switched off at 7.30 p.m. These experiments showed that P. sexguttatus ate 17 A. aurantii during the first twelve hours and only eight during the same period at night.

The only predator that was studied under controlled conditions was the malachiid Colotes oneili Pic. This small beetle was originally described from material collected from citrus trees in the Sundays River Valley but, as far as I know, no account has been published of its biology. Although it is predominantly green in colour and only two millimetres in length, it often occurs in such large numbers on citrus trees that it is more readily noticed than the larger coccinellids. Specimens were kept in the constant

temperature ..../63

temperature room together with leaves infested with A. aurantii but neither copulation nor oviposition were observed. The movements of the beetle are very rapid and they are therefore difficult to observe under a microscope. However, on a number of occasions they were seen feeding on the crawlers and white-cap stages of A. aurantii. The beetles were never observed eating the more mature stages of A. aurantii, except where the dorsal armour had been accidentally removed. It is possible that they also feed on the many species of mites that are found on citrus trees.

From the point of view of the biological control of A. aurantii and C. hesperidum, the coccinellids L. nigritula and E. flavipes appear to be the most important species of predator. Certainly they were the most abundant after ant control measures had been applied. These two species have fairly restricted feeding habits and neither can be expected to compete for the other's food supply. Although P. sexguttatus is also restricted to one species of prey it never occurred in any great numbers. This may be due to the egg and larval stages being adversely affected by the harsh climatic conditions of the Fish River Valley. The remaining coccinellid, L. lophantae, is a more generalised predator and is probably only of importance in the early stages of biological control when both species of coccid are still plentiful. Thereafter it has to compete with L. nigritula and E. flavipes for its food. Flanders (1930b) found that females of L. lophantae will only oviposit after they have fed on the eggs of Saissetia oleae (Bernard). The latter is a "soft" scale and therefore similar to C. hesperidum. Flanders also found that the first and second instar larvae of L. lophantae were unable to survive on a diet of S. oleae alone, A. aurantii being necessary for their development. If it is assumed that L. lophantae behaves in the same way towards the crawlers of C. hesperidum as it does towards the eggs of S. oleae, then this may explain why the coccinellid becomes uncommon a short time after ant control has been

applied ..../64

applied; after about five months of ant control C. hesperidum becomes extremely scarce. Although the malachiid C. oneili is often very common on trees infested with A. aurantii it probably plays a minor role in the biological control of this coccid since the beetle feeds only on the first instar nymphs.

(iii) Notes on miscellaneous mites associated with citrus trees :

While examining leaves during the coccid population analysis six species of mites were commonly seen, although not necessarily altogether on the same leaf. Three species are scavengers, two are predacious and one feeds on fungus.

Tyrophagus brauni Türk feeds on the dead remains of C. hesperidum and in the constant temperature room it breeds very rapidly on this diet. Another scavenger, Eupalopsis sp. is invariably found, together with its eggs, underneath the dorsal armour of dead individuals of A. aurantii which form its food. Likewise, Tydeus munsteri Meyer & Ryke scavenges on dead red scales. Clusters of empty choria of this species of mite are often found on the underside of leaves near the petioles.

The two predacious forms are Typhlodromus sp. and Kleemania sp. Since neither of these species is very common it was not possible to make any detailed observations on their feeding habits. However, both have been seen eating recently settled first instar nymphs of A. aurantii and, in addition, the former species once ate a pupa of Aphytis sp., while Kleemania sp. fed on a species of thrips. It seems unlikely that either of these species can exert any appreciable control of A. aurantii.

The remaining species of mite, Micreremus sp. is found only on leaves infested with the black fungus Capnodium salicinum Montagne, commonly called sooty mould. As was explained earlier, this fungus grows on the honeydew produced by C. hesperidum.

Micreremus sp. ..../65

Micreremus sp. eats this fungus but, since this mite is so small, it is improbable that it can significantly reduce the growth of the sooty mould.

According to Dr. M.K. Meyer (personal communication) Eupalopsis sp. and Micreremus sp. probably represent new species, but at the time of writing neither has been described. It is not known whether any of these six species of mites occur in other habitats but it is probable that at least the two predacious forms may do so. In any case, they can all be said to be of academic interest rather than economic importance.

III. WIND DISPERSAL OF SCALE INSECT CRAWLERS.

(i) Introduction :

Surprisingly little attention has been paid to the ways in which the first instar nymphs of scale insects are spread from one tree to another. The size of these individuals varies from one species to another but they are generally less than one millimetre in length. Such small insects naturally have poor powers of locomotion, and in this connection Hulley (1960) has shown that crawlers of the mussel scale, L. beckii, walk for about an hour on a dusty leaf when the air temperature is 28°C. before finally settling and producing wax threads; on clean leaves he found that they walk for about half an hour longer. Similar precise observations do not appear to have been made for either C. hesperidum or A. aurantii but they are probably of the same order. It is inconceivable that the crawlers could pass from one tree to another relying solely on their own limited powers of locomotion, except possibly on closely growing indigenous trees and shrubs. In citrus orchards, where the trees may be up to 20 feet apart, other dispersal mechanisms must be at work. Ebeling (1950) considers that crawlers of A. aurantii can be distributed as a result of them crawling on to birds' feet. In support of this he states that red scale is often abundant on susceptible host plants growing around bird baths. While this method of dispersal may be of some importance it is generally thought that dissemination by the wind occurs more frequently.

The first work to be done on wind dispersal of crawlers was that of Quayle (1916) using the unarmoured scale insect S. oleae, and in one experiment, A. aurantii. In an experiment with S. oleae, Quayle suspended a branch of an orange tree heavily infested with this coccid from a pole in the middle of an area of barren ground. At varying distances from the pole he set up sheets of fly-paper, both on the windward and the leeward side. Subsequent examination

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showed that no crawlers could be found on the sheets on the windward side while on the leeward side crawlers were caught at distances of up to 70 yards away, although the greatest numbers were trapped at a distance of 26 yards. In an experiment involving A. aurantii, Quayle found that crawlers of this species were trapped at distances of between two and 50 yards on the leeward side.

More recently Hely (1960), using a similar technique to that employed by Quayle, has shown that crawlers of Ceroplastes destructor Newstead are carried over distances of up to 100 feet by the wind.

The wind dispersal of four species of mealybug on cacao trees has been studied by Cornwell (1960) in Ghana. He found that in the open the mean daily wind speed was 1.1 miles per hour with a maximum of seven miles per hour; but in closely planted cacao the average daily wind speed eight feet above the ground was only 0.09 miles per hour. Traps set up within the plantations suggested that the mealybugs were being dispersed by the wind and yet laboratory experiments showed that all instars withstood removal at air speeds of up to ten miles per hour. A further observation showed that the insects could easily be dislodged by gently tapping the wood on which they were walking. Cornwell suggests that the agitation of the leaves and twigs by the wind causes the mealybugs to be dislodged and they are then dispersed by the air movements. However, it is difficult to see how a daily average wind speed as low as that recorded within the plantations could rustle the leaves sufficiently to dislodge the mealybugs.

Finally, some laboratory studies on the effects of wind on the crawlers of mealybugs and unarmoured scale insects have been done by Yasumatsu and Nakao (1957). In these experiments the crawlers were put onto the outside of glass tubes in various positions around the circumference. An air current created by a fan was directed at right angles to the long axis of the tube so that some of the crawlers were on the windward and some on the leeward side of the tube. None of the crawlers were blown off at speeds of up to five miles per hour. At a speed of ten miles per hour about half the crawlers were removed from the windward side but all remained on the leeward side. Depending on the species, between 50 and 95% of the crawlers were dislodged on the windward side at a speed of 15 miles per hour and at the same speed between 10 and 65% were removed from the leeward side. The latter were presumably dislodged as a result of wind turbulence.

These few experiments show that moderately strong winds are needed to remove crawlers of various species of scale insect and mealybug from smooth surfaces. Since citrus leaves are often covered with a fine layer of dust, I have done some laboratory experiments to determine at what wind speeds crawlers of _A. aurantii_, _C. hesperidum_ and _L. beckii_ are blown off clean and dusty leaves. These experiments are described in the following section.

(ii) Laboratory studies :

The apparatus for all the experiments was set up in the following way. A newly picked citrus leaf was pinned out as flat as possible onto a piece of cork held horizontally by a clamp. The air stream was produced by sealing one end of a piece of polythene tubing and connecting the other end to a compressed air supply. A Along the length of the tube were a number of small holes about five millimetres apart. The air stream from this apparatus was directed at an angle of 45° to the leaf surface, the polythene tube being clamped at a distance of six centimetres from the centre of the leaf. A stereoscopic microscope was set up directly over the leaf so that behaviour of the crawlers could be observed. The experiments were done in the day time and therefore the light was more or less non-directional; the room temperature was 25° C. The pressure of the air entering the polythene tube could be regulated by opening and closing a tap and this was supplied with arbitrary graduations on a circular scale. The wind speed, in metres per minute, for each of the tap openings was determined by means of a Biram's air meter placed at a distance of six centimetres from the polythene tube. Recently emerged crawlers were used and each experiment was started by placing one of these on the centre of the leaf and then gradually opening the air tap. The behaviour of the crawler was observed and the air tap slowly opened until the insect was blown away, each experiment being repeated at least 20 times.

Apart from clean and dusty leaves being used, the crawlers were subjected to air streams of two different kinds. At first, a gradually increasing velocity was used, as described above. In later experiments the insects were subjected to sudden wind blasts of various speeds.

When crawlers of A. aurantii were put onto a clean leaf they immediately started to walk; but as the velocity of the wind increased the rate of progress was diminished until at about half the speed at which they were finally blown away, they started to perform "circus movements". These movements consisted of the crawlers turning round and round on the same spot and continued until they were dislodged by the wind. This behaviour was not evident when the crawlers were on dusty leaves nor was it shown when they were subjected to sudden wind blasts on clean leaves. Furthermore, neither of the other two species of scale insect performed these movements. The significance of this interesting behaviour is somewhat obscure although it may in some way prepare the crawler for its impending dispersal to other trees. On the other hand, it may merely be an artifact since under natural conditions the wind occurs in sudden gusts and not in a regularly increasing velocity. The mean wind speed required to remove crawlers of A. aurantii from clean leaves when the former is increasing gradually is 314 metres per minute, with a minimum of 187 and a maximum of 381 metres per minute.

When crawlers of L. beckii are subjected to a gradually increasing wind velocity on clean leaves they are blown off at a mean speed of 260 metres per minute (minimum = 111, maximum = 328 metres per minute). These crawlers walk more and more slowly as the wind speed increases until at about one third of the final speed they stop and flatten down on the substrate. Although this behaviour does not occur in a similar situation on dusty leaves it seems likely that the flattening is an attempt to prevent the crawler from being blown away.

The crawlers of C. hesperidum show neither "circus movements" nor flattening and they continue walking until dislodged at a mean wind velocity of 232 metres per minute (minimum = 140, maximum = 358 metres per minute).

In the remaining experiments, i.e. gradually increasing wind velocity on dusty leaves and sudden wind blasts on clean leaves no unusual forms of behaviour are apparent and so these results, together with the above, are presented in Tables 13 (a) and (b).

TABLE 13 (a)

Wind speed, in metres per minute, required to dislodge scale insect crawlers from clean and dusty leaves under conditions of increasing velocity.

Species	Mean speed	Minimum speed	Maximum speed
A. aurantii			
Clean leaf	314	187	381
Dusty leaf	300	223	358
L. beckii			
Clean leaf	260	111	328
Dusty leaf	286	116	351
C. hesperidum			
Clean leaf	232	140	358

TABLE 13 (b) ..../71

TABLE 13 (b)

Wind speed, in metres per minute, required to dislodge scale insect crawlers from clean leaves under conditions of sudden blasts.

Species	Mean speed	Maximum speed	Minimum speed
L. beckii	263	88	358
C. hesperidum	246	140	313
A. aurantii	206	88	343

A number of statistical tests of the significance of the difference between the mean speeds were done, using the correction given by Chambers (1955) for samples of less than 50. One such test showed that there is a highly significant difference between the mean speed required to remove A. aurantii from a clean leaf using a gradually increasing wind velocity and that needed to dislodge the same species from the same situation when subjected to a sudden blast of air (P = 0.001). There is also a significant difference between the speed required to dislodge crawlers of A. aurantii and those of L. beckii from clean leaves when both were subjected to an increasing velocity (P = 0.02). Similarly, it can be shown that there is a significant difference between the velocity needed to blow crawlers of these two species off clean leaves under conditions of a sudden wind blast (P = 0.02). All other tests of the difference between the means are not significant.

The mean wind velocities needed to blow crawlers of these three species of scale insects off leaves are of the same order as those found by Cornwell (1960) using mealybugs on twigs of wood and by Yasumatsu and Nakao (1957) using unarmoured scale insects on glass.

In the light of Cornwell's observation that mealybug crawlers are easily dislodged by gently tapping the twig on which they were walking, I attempted to discover whether this is true also of scale insect crawlers. From a few simple experiments I found that it is by no means easy to dislodge crawlers in this way. No

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further observations were made since it is difficult to see how a sufficiently precise apparatus could be set up to test this even from a qualitative standpoint.

(iii) Field studies :

The few attempts that I made to study the dispersal of scale insects by the wind were largely unsuccessful, but before discussing these it is necessary to consider the structure of wind in natural conditions. This has been done in some detail by Giblett (1932) and the following is a summary of his more important and relevant findings. The motion of air in a wind is not a steady flow but consists of gusts and lulls accompanied by small changes in direction. Superimposed on the velocity changes comprising the gust-lull sequence are many smaller irregular oscillations both in wind speed and direction. Convection currents, caused by vertical temperature differences, give rise to gusts and lulls, while changes in wind direction are the result of vortices set up in the main air stream by friction with the ground and by obstructions such as trees and buildings. When a gust front passes an observer there will be a sudden rise in wind velocity, a change in wind direction, a fall in temperature and in humidity and a decrease in small scale turbulence.

Three types of traps are commonly used to sample small airborne insects: suction traps, sticky traps and tow nets. Comparing these three traps Johnson (1950) found that in calm conditions a suction trap was the most efficient, but when the wind speed was between two and ten miles an hour there was no difference between this and a sticky trap. Tow nets were most efficient at quite high wind speeds. Suction traps could not be used in my experiments since they require an electrical supply; various forms of sticky traps were therefore erected in the centre of an orchard.

Initially I used a trap consisting of a wooden frame 30 centimetres square which had vertical strips of transparent adhesive tape fastened to it. The tapes were 13 millimetres wide and a space equal to this was left between successive tapes. By providing these slots for the wind to pass through I hoped to lessen turbulence at the trapping surface. The trap was fixed immovably to a post and was about 1.5 metres above the ground. However, no insects of any kind were caught with this trap and this was ascribed to the fact that the adhesive surfaces seldom faced directly into the wind.

The remaining two types of trap to be used were both fitted with a vane so that the trapping surface always faced into the wind. The first of these traps consisted of a sheet of thin polythene fixed to a rotating thermohygrograph drum, the latter making one revolution every 24 hours. The drum was enclosed on three sides and the top by a cardboard case, the open side always facing the wind. The polythene sheet was coated with an adhesive consisting of a mixture of nine parts by weight of castor oil to ten of rosin. This adhesive is based on that used by May (1945) for sampling coarse aerosols, but while he recommended three parts of castor oil to two or rosin this was found to be much too fluid for my purposes. The main advantages of a castor oil-rosin mixture are that it does not dry out on exposure to the sun, neither is it affected by the rain and, in addition, it readily dissolves in benzene. The trap was about one and a half metres above the ground and nearby a Biram's air meter, to which a vane was attached, was set up on a pole at the same height. Half hourly records of the flow of wind, in metres, past the trap were made so that some idea of the average wind speed could be obtained. Wet and dry bulb readings were taken every half hour using a whirling hygrometer. The purpose of using a trap on a revolving drum was to attempt to record possible diurnal variations in the wind dispersal of crawlers. However, even though the trap was placed as close as possible to a heavily red scale-infested tree, no insects of any description were caught, and this was probably due, in part, to the relatively small trapping

area ..../74

area exposed at any one time.

A final set of experiments were carried out using a frame similar to that described for the first experiment, except that in this instance it had a vane attached to it and the trapping surface was a sheet of polythene coated with the castor oil-rosin mixture. As before, half hourly records of the flow of wind and wet and dry bulb readings were made. Although, for each experiment, the trap remained in position for 24 hours, no readings of wind speed, humidity and temperature were made during the night. These experiments were somewhat more hopeful since, although no or few crawlers were caught, various other species of arthropods were found on the traps. At the end of one such experiment the following animals had been trapped on the screen; one red scale crawler, one male (i.e. winged) mussel scale, two Aphytis sp., eight other Hymenoptera, four Thysanoptera, three Diptera, three mites, two Coleoptera and one Psocoptera. The mean of 21 half-hourly records of wind speed was 70.3 metres per minute, with a maximum (over half an hour) of 131.4 metres per minute. The average temperature reading was 20° C. while that of the relative humidity was 66%.

If indeed the force of the wind alone disperses scale insect crawlers then it is not surprising that only one was trapped in the above experiment since the average wind speed was so low. On the other hand, the method of recording the flow of wind every half hour is not very satisfactory since it does not directly record the velocities attained during individual gusts. What is really needed for this purpose is a continuously recording anemometer.

The more or less complete failure of my field experiments has led me to believe that scale insect crawlers are dispersed in the following manner. The force of the wind, combined possibly with the shaking of the leaves and twigs, dislodges the crawlers and, because they are so small and light, they are carried up into the air.

During ..../75

During periods of little wind movement they gradually drift downwards where they may or may not land on suitable host plants. Many different workers have trapped both winged and apterous insects at various heights. Freeman (1945) fixed tow nets to a wireless mast at heights of ten, 177 and 277 feet above the ground and caught large numbers of arthropods. A number of these were wingless; in particular, Collembola, psocid and jassid nymphs and spiders and mites, these being taken at all three heights. In order to test my hypothesis one would need to set up a series of tow nets or sticky traps at various heights ranging from about five metres to about 20 metres above the ground. Sticky screens, with the adhesive surfaces facing upwards, would have to be erected at tree height. A sensitive continuously recording anemometer and a thermohygrograph with a 24-hour drum should be set up in the vicinity of the traps. If such an experiment were carried out I believe that quite large numbers of scale insect crawlers, together with other small insects, might be trapped.

GENERAL CONCLUSIONS ..../76

GENERAL CONCLUSIONS.

The results of experiments dealing with ant control demonstrate quite convincingly the beneficial consequences of this practice. By the relatively simple and inexpensive method of killing the ants on the ground the populations of *Coccus hesperidum* were, in the short space of three months, reduced to a very low level and this was maintained for a further period of eight months. Although observations on soft scale populations were discontinued after this period there is no reason to suppose that, providing the ants continued to be denied access to the trees, the numbers of this species of scale insect would ever increase to economically damaging levels.

As far as *Aonidiella aurantii* is concerned, ant control produced similar effects although the time taken to reduce the numbers of this species to an economically acceptable level was seven months. The slower rate of decline in numbers of *A. aurantii*, as compared with *C. hesperidum*, can probably be attributed to two factors. In the first instance, the initial population density of the former species was more than twice that of the latter. Secondly, whereas *A. aurantii* is attacked by only one species of Hymenopterous parasite, at least nine different species of parasite attack *C. hesperidum*. Although probably fewer species of predator feed on soft brown scale than on red scale, the soft exoskeleton of the former species provides little defence against either larval or adult coccinellids. Laboratory studies showed that the waxy armour of *A. aurantii* conferred adequate protection against the larvae of most species of predator.

There can be little doubt that the decline in numbers of both *A. aurantii* and *C. hesperidum* was due entirely to the activities of their natural enemies which were unhindered by ant patrols. Concurrent observations on nearby ant-infested trees demonstrated that the coccid populations on these trees showed no tendency to decline to low levels.

Since ..../77

Since I have been able to demonstrate that ant control is relatively inexpensive when compared with chemical methods of controlling scale insects, it is recommended that attempts should be made to encourage growers to adopt this procedure as standard practice. Bartlett (1961) has reported that ant control has been of great practical value in the citrus growing areas of California. It has extended the period of effectiveness of chemical control treatments and in some instances it has elminated the need for these treatments. There is no reason to suppose that the same beneficial consequences of ant control cannot be realised in South Africa.

However, before ant control could become an effective second line of defence against the major coccid pests of citrus, a number of different species of parasites and predators would have to be introduced into this country. This applies especially to A. aurantii since it is a serious pest in all citrus growing areas of South Africa. There are at least 15 species of predators, mainly coccinellids, which attack red scale and my laboratory and field studies on five of these seem to indicate that, taken together with the others, they are sufficiently effective predators. That is to say, they are effective enough not to warrant the introduction of any further species of predator. On the other hand, there are only three parasites of A. aurantii and not all are found together in the same climatic area. One of these, Habrolepis rouxi Compere, is very rare in its occurrence and probably contributes little towards the biological control of red scale. The rarity of this parasite is probably due to the fact that it is apparently an indigenous species and it has therefore not had enough time to become properly adapted to A. aurantii, the latter species having been introduced into South Africa about 100 years ago. The remaining two species of red scale parasite belong to the genus Aphytis. Before the present investigation was undertaken it was thought that only one species of Aphytis parasitised red scale, this being A. chrysomphali. Moreover,

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it was assumed that this species was of general occurrence throughout the citrus growing regions (Simmonds 1960). It now appears more likely that A. chrysomphali occurs predominantly in the more humid coastal areas. I have collected this species from citrus orchards near Grahamstown which are about 25 miles from the coast. On the other hand, A. chrysomphali appears to be absent from the hot inland Fish River Valley region. Its place in this area is taken by a previously unrecorded form, Aphytis sp. (near lingnanensis). This type of distribution of the two species of Aphytis corresponds with that found in Southern California (DeBach and Sisojević 1960).

Although both species of Aphytis appear to be fairly common in their respective climatic areas, I consider it unlikely that either of them would be able to cope effectively with A. aurantii in the event of a change from chemical to biological control. Citrus entomologists in California are constantly seeking new and more effective parasites of red scale, releasing them and evaluating their potential as scale insect control agents. It should therefore be relatively simple to arrange for the introduction into this country from California those species of parasite which show promise of effecting a high degree of control of A. aurantii.

C. hesperidum is generally of lesser economic importance than A. aurantii and in most areas it is effectively kept in check by its numerous species of parasites and predators. This is especially so when ants are controlled; even in the presence of vigorous ant patrols this coccid seldom reaches damaging proportions except where organophosphorous insecticides have been used extensively. Neither of the two farms on which my field studies were done, one in the Fish River Valley and the other near Grahamstown, had ever been sprayed with parathion, malathion or Gusathion. Both farms supported only localised groups of trees infested with soft brown scale and the latter were never in any great numbers. However, both in California (Bartlett and Ewart 1951) and in South Africa

(Annecke 1959) ..../79

(Annecke 1959) serious outbreaks of C. hesperidum have been associated with the regular applications of organophosphorous insecticides. The most likely cause of these outbreaks of the scale insect is the almost complete elimination of its natural enemies by the insecticides. In the event of a changeover from chemical to biological control, it would probably be only necessary to breed and release large numbers of parasites and predators which already occur in this country.

Mussel scale, Lepidosaphes beckii, is, according to Simmonds (1960), a serious pest in most areas. This species was not studied in relation to ant control since it did not occur at all in the Fish River Valley orchards. In the orchards near Grahamstown, where field work on wind dispersal was attempted, L. beckii was quite common. Ants were very seldom seen on mussel scale infested trees and, as mentioned earlier, these trees had never been treated with organophosphorous insecticides. Such conditions would therefore seem ideal for biological control of this coccid to occur and yet no such event had taken place. The answer to this must lie in the comparative scarcity and ineffectiveness of the natural enemies of L. beckii. Carnegie (1955) studied the biology of mussel scale in Eastern Cape orchards and found only one species of parasite. This species exhibited such a low incidence of attack that its importance in biological control must be negligible. Although Carnegie found nine species of predators which feed on mussel scale, none appeared to be of any great importance. He suggests that most of these predators prefer to feed on A. aurantii rather than L. beckii. In the course of feeding observations on three common coccinellid predators of A. aurantii I noticed that they all showed a slight, but not statistically significant, preference for red scale over mussel scale. It therefore appears that if the biological control of L. beckii is to meet with any degree of success it is imperative that effective natural enemies be introduced into South Africa.

Even though biological control of the three main scale insect pests of citrus may eventually be accomplished, consideration should be given to the problem of wind dispersal of the first instar nymphs of these species. The field work of Quayle (1916), Cornwell (1960) and Hely (1960) indicates that wind is the chief dispersing agent of various species of coccid and pseudococcid. None of these three authors used red, mussel or soft brown scale as experimental insects, although Quayle did include some very preliminary work on red scale. My successful experiments on the wind dispersal of first instar nymphs of A. aurantii, L. beckii and C. hesperidum were confined to laboratory studies. It was found that the mean wind velocity required to dislodge first instar nymphs of the various species from different surfaces varied between approximately 200 and 300 metres per minute. When I attempted to correlate these results with field trapping the outcome was largely unsuccessful; the probable reasons for this failure are discussed in the relevant section. Although I was unable to trap significant numbers of scale insects this does not preclude the possibility that they are dispersed by the wind.

The importance of the prevention of the wind dispersal of scale insects in relation to either chemical or biological control lies in the fact that each species has many alternative host plants. Munro and Fouché (1936) have listed all the known host plants of scale insects in South Africa and according to them A. aurantii can be found on 200 different species of plants; the respective figures for C. hesperidum and L. beckii are 77 and five. Carnegie (1955) states that there are at least 27 known host plants of L. beckii, although he does not give any authority for this view. It is therefore obvious that when citrus orchards border on tracts of indigenous bush the chance of re-infestation by one or all species of scale insect is ever present.

The erection of wind-breaks around orchards therefore assumes some importance. Since individual orchards usually extend

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over many acres it is obvious that fully effective wind-breaks are impossible to grow or construct. Many orchards in the Eastern Cape are surrounded, at least on the windward sides, by pine trees. There is usually only a single row of trees and they are planted so far apart that it seems unlikely that they can constitute anything like an effective wind-break. On at least one farm in the Sundays River Valley I saw wind-breaks constructed in the form of a bamboo fence in which the stems were placed close together. The fences were about three metres high and were erected on both sides of untarred roads where these passed between orchards. Although the purpose of these fences was to prevent dust thrown up by vehicles from settling on the trees, they appeared to form quite effective wind-breaks as well. Although the effect of dust does not directly concern us it is worth pointing out that heavy infestations of both _A. aurantii_ and _L. beckii_ are often associated with the presence of dusty leaves on the trees. Hulley (1960) was able to show that first instar nymphs of _L. beckii_ settle more readily on dusty than on clean leaves.

A final problem remains and that is the one of acquanting citrus growers with the results of scientific investigations such as the present work. It is obvious that the average grower will have neither the time nor the inclination to read and digest information contained in scientific journals. Probably the best approach would be to publish articles in an easily understood form in the more popular and widely read farmer's magazines. Further information could be disseminated by means of lectures given to growers by government and citrus co-operative entomologists. As a result of all this one can hope that in the not too distant future some form of biological control will become a standard practice in checking the populations of scale insects.

SUMMARY ..../82

SUMMARY.

1. The present investigation is concerned mainly with a study of the population changes of the scale insects Aonidiella aurantii (Mask.) and Coccus hesperidum L., in citrus orchards, occurring as a direct result of ant control. A study has also been made of the biology of a new genus of coccinellid, while the feeding preferences of various other coccinellid predators of scale insects are described. The investigation concludes with some preliminary work on the wind dispersal of first instar nymphs of A. aurantii, C. hesperidum and Lepidosaphes beckii (Newm.)

2. The orchards in which the ant control work was done are situated in the Fish River Valley region of the Eastern Cape Province. The dominant ant species in these orchards is Anoplolepis steingroeveri Forel and six different insecticides were used in ant control trials. Of these, chlordane, Thiodan and Sevin have little effect on the ants. Aldrin is slightly inferior to dieldrin which in turn is less effective than Telodrin. It is recommended that either dieldrin or Telodrin applied at a rate of 0.5% active ingredient should be used to control A. steingroeveri.

3. As a result of monthly surveys, based on random leaf samples, it was found that the population density of C. hesperidum declined rapidly; after six months of ant control there was an average of less than one live scale insect per leaf. A similar decline in the numbers of live A. aurantii is recorded although in this instance a period of 15 months elapsed before comparable control of this coccid was achieved.

4. It is clearly apparent that the decline in numbers of the scale insects is due to the fact that their natural enemies are unhindered by ant patrols. A study of the incidence of attack by parasites and predators indicates that the latter may be of slightly more importance than the former, at least with regard to C. hesperidum.

5. A scheme ..../83

5. A scheme is suggested in which there is a gradual change from the present widely used chemical methods of control of scale insects to one of biological control. At one stage this involves the use of an integrated system of chemical and biological control.

6. During the course of the work a new genus and species of coccinellid was discovered but at the time of writing its taxonomic description has not been published. A study of the biology, life history and anatomy of the new species is presented. Further laboratory work concerns the feeding preferences of the three most common species of coccinellid found in Eastern Cape citrus orchards. Of these, *Lotis nigritula* Crotch prefers *A. aurantii* to *C. hesperidum*, while for *Exochomus flavipes* (Thunb.) the preference is reversed. *Lindorus lophantae* Blaisd. shows no marked preference for one or other of these two species of scale insect.

7. Successful studies of the wind dispersal of first instar nymphs of *A. aurantii*, *C. hesperidum* and *L. beckii* are confined to work done in the laboratory. Wind velocities of between 200 and 300 metres per minute are required to dislodge the nymphs from leaves. Attempts to trap nymphs on sticky surfaces in the field were largely unsuccessful and suggestions are put forward to account for this.

8. Finally, it is recommended that citrus growers should be encouraged to apply methods of biological control of scale insects in order to forestall the development of resistance to insecticides by these pests.

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APPENDIX ..../94

APPENDIX.

The behaviour of individual coccinellid larvae on citrus leaves :

Some observations were made on the behaviour of individual second instar larvae of the coccinellid Exochomus flavipes Thunb. on leaves infested with C. hesperidum. The experiments were done to see if any searching pattern towards the prey was evident.

The observations were made in a constant temperature room, the temperature being 27° C. while the relative humidity was kept at 70%. A newly picked leaf was selected and all but mature scale insects were removed, the reason for this being that immature soft brown scales often walk around the leaf after it has been brought into the laboratory. A cork was cut in half and the petiolar end of the leaf was placed between the two halves which were then clamped firmly. The leaf was thus held in a horizontal plane some distance above the bench. A mirror was clamped between the lower surface of the leaf and the bench so that both surfaces of the leaf could be easily seen. The upper surface was illuminated by a 40 watt 'pearl' bulb held 46 centimetres above the centre of the leaf while the mirror reflected some of this light onto the lower surface.

A single larva was put onto the leaf and its behaviour observed while at the same time a track of its movements was drawn. The path taken by a larva in one of these experiments is shown in Figure 25. In this diagram the leaf is somewhat stylised while the midrib and veins have been omitted in order to avoid a confusion of lines. Positions of scale insects are shown by oval dots; the numbers 1 to 14 alongside the track are reference points so that the course of the larva can be easily followed. The diagram shows that the larva apparently wandered aimlessly for a considerable distance until it encountered a scale insect just before point 7. After eating this coccid the larva found and fed on seven more in quite rapid succession. It is noticeable that at point 2 the larva

passed ..../95

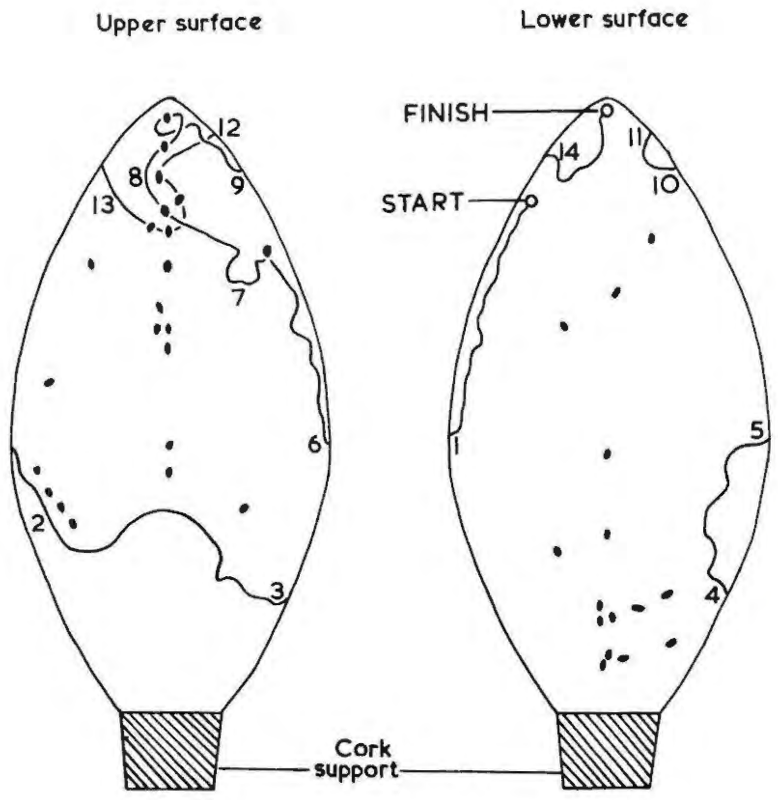

Figure 25.

Path taken by second instar larva of Exochomus flavipes searching for its prey.

passed close and parallel to four scale insects without sensing their presence.

From this and the other experiments in the series the following points emerge. The larva is apparently unable to detect its prey from a distance; any encounter with the prey comes about because it is in the direct path of the larva. Banks (1957) recorded a similar occurrence when observing the behaviour of larvae of the coccinellid Propylea quatuordecempunctata (Linnaeus) feeding on Aphis fabae Scopoli. This predator is unable to detect the presence of an aphid even at a distance of only three millimetres. In addition, Fleschner (1950) showed that larvae of the coccinellid Stethorus picipes Casey and of the Neuroptera Chrysopa californica Coquillett and Conwentzia hageni Banks were unable to sense the presence of their prey, Paratetranychus citri (McGregor), until actual physical contact had been made.

The second point of interest concerns the behaviour of the larva once it has encountered and fed on a scale insect. Reference to Figure 23 shows that after feeding on the first coccid the rate of change of direction of the larva increased although it was still unable to detect its prey at a distance. Between points 7 and 8 in the diagram it passed straight between two scale insects and found another directly in its path. At point 8 the larva again passed close to a coccid without detecting it, only to encounter another shortly afterwards. Both Banks and Fleschner record a similar type of behaviour in the respective species studied by them.

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